Li *et al. Annals of Microbiology* (2023) 73:20
https://doi.org/10.1186/s13213-023-01717-8

Annals of Microbiology

UNIVERSITÀ DEGLI STUDI DI MILANO

ORIGINAL ARTICLE

Open Access

Spatial distribution pattern across multiple microbial groups along an environmental stress gradient in tobacco soil

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Abstract

Background It has become commonplace to explore the spatial distribution patterns of microbial communities in natural ecosystems. However, few have looked at the responses of community diversity, structure, and assembly processes from different microbial groups to changes in environmental stress caused by altitude.

Purpose We investigated the spatial and biogeographical patterns of different microbial groups, including bacteria, fungi, and protists, from tobacco soil along an altitudinal gradient to evaluate the influence of geographic distance and environmental stress on microbial distribution pattern.

Methods DDR (distance decay relationship) model was calculated to evaluate the spatial distribution pattern. Then, NCM (neutral community model) and two null-modelling-based approaches, NST (normalized stochasticity ratio) and iCAMP (the infer community assembly mechanism by phylogenetic-bin-based null model analysis), were used to reveal the importance of stochastic and deterministic processes to microbial community assembly by utilizing high-throughput sequencing data.

Result Bacterial community *α*-diversity decreased significantly ($P < 0.05$) with increasing environmental stress. Moreover, all communities exhibited a significant DDR pattern ($P < 0.001$), with the slope of bacteria (0.146) being significantly higher ($P < 0.05$) than that of fungi (0.059) and protists (0.060). The results of NCM and the two null-modelling-based approaches revealed the importance of stochastic processes to bacterial (83.4%) and protist (69.9%) communities, which were primarily shaped by drift and dispersal limitation, respectively; meanwhile, deterministic processes were important to the fungal community (53.7%). Additionally, we found a significant correlation between the assembly process and geographic distance ($P < 0.05$).

Conclusion Our study provides a complementary perspective to the study of multiple hierarchical groups across different spatial scales (i.e., horizontal and vertical scales).

Keywords Geographic distance, Community assembly, Multiple microbial communities, Tobacco soil, Environmental stress gradients

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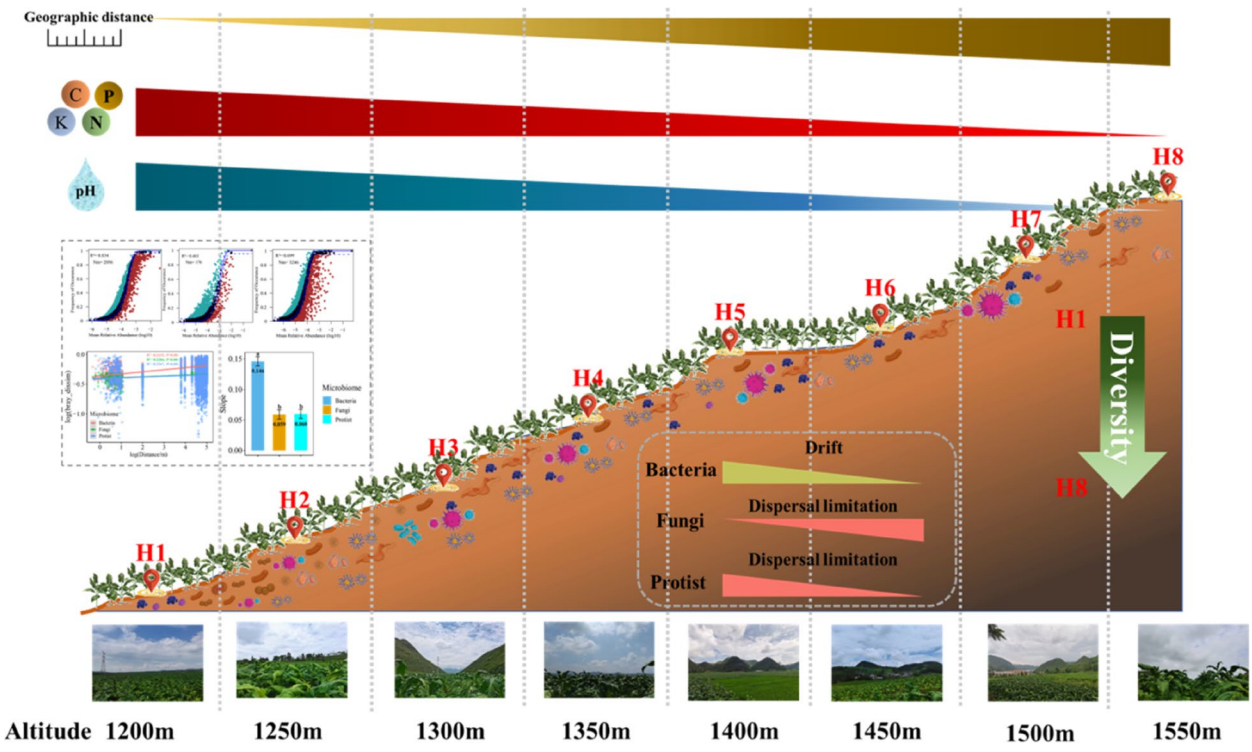
Graphical Abstract



Introduction

Soil microorganisms, as a vital component in terrestrial ecosystems (Fierer et al. 2003), play critical roles in numerous key ecological processes, including decomposition and geochemical cycling (Allison et al. 2013; Comerford et al. 2013), and in the health of many macroorganisms important to agricultural production (Naylor et al. 2020; Toju et al. 2018). However, environmental stress is increasing worldwide (e.g., increasing temperature and changing precipitation patterns) (Ramsey et al. 2005; Yuan et al. 2021), which strongly affects soil microbial communities (Edwards et al. 2015; Guo et al. 2018b). Numerous studies have provided evidence that environmental stress could alter microbial community composition and create shifts in ecosystem function (Hall et al. 2018; Trivedi et al. 2013), by driving the adaptation and acclimation strategies of the soil microbiome, creating physiological costs at the organismal level (Zhong et al. 2022). Understanding the mechanisms underlying microbiome assembly is urgently needed to mitigate the effects of potential changes in ecosystem services (Chen et al. 2019). However, how the assembly processes of the dominant microbial groups (i.e., bacteria, fungi, and protists) respond to increasing environmental stress remains poorly understood (Hernandez et al. 2021; Zhong et al. 2022).

How to understand and characterize fundamental distribution patterns within the biosphere is a critical challenge in ecology (Shade et al. 2018). Some evidences have shown that microorganisms possess biogeographic patterns similar to those of macroorganisms, despite the differences in their size and diversity (Chalmandrier et al. 2019; Kivlin and Hawkes 2020). Thus, microecology faces the same challenge as macroecology. Furthermore, an additional important issue for microecology is to investigate the factors controlling microbial community assembly (Stegen et al. 2013), which could shape the structure, functions, and biogeography of microbial communities (Hanson et al. 2012; Logares et al. 2018; Zhou and Ning 2017). In general, microbial community assembly is primarily influenced by deterministic and stochastic processes (Zhou and Ning 2017). Some studies have indicated that deterministic processes relate to selection, which would trigger the relationships between environmental factors and biological species (Lozupone and Knight 2007). Meanwhile, niche-based research has indicated that the deterministic processes of microbial communities are due to microbe fitness and different habitat

preferences (Lima-Mendez et al. 2015; Liu et al. 2015), whereas the stochastic processes of community assembly are mainly related to dispersal, ecological drift and random events of birth–death (Chase and Myers 2011). A previous study provided a spatial scale model of biodiversity could adequately document the biological changes at a given scale (Green and Bohannan 2006).

Understanding the variation of microbial structure in spatial scaling could help in providing insights for setting conservation priorities (Du et al. 2021). Additionally, many previous studies have provided evidence that robust spatial distribution patterns are present in numerous ecosystems (e.g., grassland, river, and tidal wetland) (Grundmann 2004; Meyer et al. 2018; Shade et al. 2018). The DDR, based on mathematical models of real-world observations of the spatial distribution pattern of microorganisms (Nekola and White 1999), has been proven to be a fundamental law in ecological systems (Horner-Devine et al. 2004). The slopes of DDR could reflect the spatial turnover rates of a community (Du et al. 2021), which describe the similarity of a community with change in geographic distance (Nekola and McGill 2014; Nekola and White 1999). Spatial distribution patterns have been observed not only in bacterial communities but also in fungal communities from different ecosystems (Li et al. 2020; Liu et al. 2019). However, to date, no experiments have been performed to simultaneously investigate the spatial turnover of more than two microbial organismal groups (Wang et al. 2021).

In order to better understand the assembly patterns of soil microorganisms and their potential contributions to ecosystem function, it is important for us to evaluate the deterministic/stochastic processes of microbial communities (Bahram et al. 2018; Cline and Zak 2014). The most promising ways for understanding how stress and geographic distance affect microbial community assembly are NCM (Sloan et al. 2006) and the two null-modelling-based approaches of NST (Stegen et al. 2013) and iCAMP (Ning et al. 2019). Previous studies have demonstrated the practicality of NCM by evaluating the importance of stochastic processes acting on community assembly in a variety of ecological systems (Burns et al. 2016; Zhou and Ning 2017). In detail, this model supports researchers by quantifying the importance of the processes of dispersal and ecological drift in microbial community assembly (Tong et al. 2019). The other null model approaches classify organisms into specific niches, based on their niche preferences, to predict the deterministic processes of a community (Bell 2010; Webb et al. 2002). Furthermore, the processes of neutral-based stochasticity and niche-based determinism greatly influence microbial community assembly (Ferrenberg et al. 2013; Tian et al. 2017) and could explain the observed patterns of diversity, composition distribution, and species interaction within communities (Wang et al. 2021). Therefore, it could provide important new insights for the health assessment and management of tobacco soil by revealing the variation patterns and assembly mechanisms of soil microbial communities.

In this study, eight tobacco experimental plots were chosen along an altitudinal gradient with a total of 76 collected soil samples. We not only evaluated the specific relationship of composition and spatial distance between multiple microbial communities but also revealed the potential of environmental conditions to mediate community assembly along an environmental stress gradient. We hypothesized that (i) microbial community diversity, composition, and structure will change along an environmental stress gradient in a regular pattern, but that the response of each community (bacteria, fungi, and protists) will be different; (ii) as geographic distance increases, the similarity of the microbial community will decrease, with the bacterial community displaying the highest turnover rates; (iii) the different microbial communities would possess different community assembly processes, and that there would be a significant influence of geographic distance on the assembly process.

Materials and methods

Study site and soil sampling

The study sites were situated at the Wenshan Zhuang and Miao Autonomous Prefecture of Yunnan-Kweichow Plateau in Yunnan province, China, and experience a subtropical climate. Annually, average temperature is 19 °C, frost-free period 356 days, sunshine 2228.9 h, and rainfall about 779 mm. The dominate soil types are classified as calcareous soil by FAO (Food and Agriculture Organization of the United Nations) (Liu et al. 2009).

The study was conducted in late July, 2021, within eight distinct areas, each with a different altitude: H1 (23°17′N, 104°37′E, 1200 m high), H2 (23°22′N, 104°36′E, 1250 m high), H3 (23°43′N, 104°47′E, 1300 m high), H4 (23°56′N, 104°17′E, 1350 m high), H5 (23°34′N, 104°21′E, 1400 m high), H6 (23°56′N, 104°17′E, 1450 m high), H7 (23°32′N, 104°18′E, 1500 m high), and H8 (23°6′N, 104°35′E, 1550 m high). Tobacco had been cultivated in the experimental plots (one experimental plot per altitude) under a rotation regime with potato since 2003, with each plot size being larger than 300 m^2. All experimental plots received similar agronomic management.

Soil samples from each experimental plot were collected using a random sampling strategy as follows: a soil auger, of 5-cm inner diameter and able to collect to a 20 cm depth, was used at each point to collect soil. By referring to the previous method of random sampling

(5-point sampling method) (Du et al. 2021), five soil samples were collected within 1 m^2 and then mixed to form a composite sample. In total, 76 composite soil samples (H1, 8 samples; H2, 10 samples; H3, 10 samples; H4, 9 samples; H5, 10 samples; H6, 9 samples; H7, 10 samples; and H8, 10 samples) were collected in July 2021. Each composite sample was divided into two parts: one part was used to quantify the soil physicochemical properties, while the other part was use for DNA extraction.

Soil physicochemical analysis

The soil physicochemical properties were measured using previously described methods (Du et al. 2021), including pH, soil organic matter (TOM), total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), nitrate nitrogen (NO_3^--N), ammonia nitrogen (NH_4^+-N), available phosphorus (AP), and available potassium (AK). Properties were quantified at the Institute of Soil Science, Chinese Academy of Sciences (Nanjing, China).

DNA extraction, PCR amplification, and sequencing

Microbial DNA was extracted from 0.5 g of thoroughly mixed soil using the Mobio DNeasy® PowerSoil® Kit, following the manufacturer's instruction. Universal primers of 16S rRNA genes for bacteria (515F: 5′-GTGCCAGCMGCCGCGGTAA-3′, 806R: 5′-GGACTACHVGGGTWTCTAAT-3′), ITS genes for fungi (5.8F: 5′-AACTTTYRRCAAYGGATCWCT-3′, 4R: 5′-AGCCTCCGCTTATTGATATGCTTAART-3′), and 18S genes for protists (first-step primer: 615F of 5′-AGTGTCGATTCGGTTAAAARGCTCGTAGTYG-3′, 963R of 5′-:AAGATCGTACTGAAGARGAYATCCTTGGTG-3′; second-step primer: 615F of 5′-AGTGTCGATTCGGTTAAAARGCTCGTAGTYG-3′, 947R of 5′-AAGARGAYATCCTTGGTG-3′), supplemented with sample-specific barcodes (Caporaso et al. 2012; Yarza et al. 2014), were used to perform PCR. Samples were sequenced on the Illumina Hiseq platform at Magigene Biotechnology Co., Ltd. (Guangzhou, China).

Bioinformatics

First, we assigned both the forward and reverse reads to different samples according to their barcodes. Then, FLASH (Magoč and Salzberg 2011) was applied to merge the forward and reverse reads of individual samples, and the combined reads were filtered using Btrim (Kong 2011) to remove the ambiguous sequences. Next, Trim N was used to delete sequences containing N, and Trim by Sequence Length was used to trim the sequences based on the length. The Greengenes database (DeSantis et al. 2006), ITS RefSeq database (Schoch et al. 2014), and Protist Ribosomal Reference (PR^2) database (Guillou et al. 2012) were used as references to check for chimeras in the bacterial, fungal, and protist communities, respectively. Singletons were retained (Jousset et al. 2017), and sequences were clustered into operational taxonomic units (OTUs) using UPARSE (Edgar 2013) at a 97% threshold. Moreover, for ITS gene sequences, the ITSx tool was used to identify ITS sequences and extract the ITS regions. Random resampling of 60,000, 25,000, and 30,000 sequences per bacterial, fungal, and protistan sample, respectively, was performed to generate a new resampled OTU table. The RDP (Ribosomal Database Project) classifier was used to assign bacterial, fungal, and protistan OTUs with the Greengenes ribosomal database (Wang et al. 2007), UNITE database (Abarenkov et al. 2010), and PR^2 database (Guillou et al. 2012), respectively, with confidence values > 0.8 (Wang et al. 2007).

Statistical analysis

Detailed statistical analyses were carried out using an in-house pipeline (http://mem.rcees.ac.cn:8080) (Feng et al. 2017). Two measures of alpha-diversity were calculated to assess the biodiversity of microbial communities. Richness index was obtained by counting the observed species numbers in the resampled OTU table. Phylogenetic diversity was calculated after selecting the OTUs both in the tree file and OTU table. The correlation between microbial communities and soil properties was calculated by Mantel test (Goslee and Urban 2007). Furthermore, we used VPA (variation partitioning analysis), with adjusted R^2 coefficients based on CCA (canonical correspondence analysis), to quantify the relative effects of environmental and spatial factors in structuring community variation (Liu et al. 2015). The community's dissimilarity was tested using MRPP, ANOSIM, and PERMANOVA (Anderson 2001). Microbial community diversity was visualized by nonmetric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarity matrix of the bacterial, fungal, and protistan communities. Core OTUs, defined as OTUs present in all eight altitudinal gradients, were visualized by Venn diagram using the R package "RColorBrewer." By ensuring the normal distribution, comparisons of soil variables and microbial diversities among the eight sites were tested using the analysis of variance (ANOVA) implemented through least significant difference (LSD) test and Tukey post hoc tests. The Euclidean distance, based on the coordinates of sampling sites, was used to estimate the geographical distance matrix.

We evaluated the DDR based on the taxonomic dissimilarity matrix and estimated the distance decay rate (β) by

the regression of log-transformed dissimilarity and log-transformed geographical distance. DDR was calculated by the following equation:

$$\log(Dissim) = \beta \times \log(D) + C \quad (1)$$

Dissim is the community dissimilarity, *c* is the intercept parameter, *D* is the geographic distance, log was performed using log 10, and β is the slope of DDR or spatial turnover rate. Permutation tests were performed to determine the significant differences in turnover rates (β) among the communities.

To evaluate the potential importance of stochastic processes in shaping the microbial community, NCM was used to predict the relationship between OTU detection frequency and their relative abundance (Sloan et al. 2006). Next, two null-modelling-based approaches, NST and iCAMP, were applied to infer community assembly mechanisms.

Results

Quantification of the stress gradient by edaphic physicochemical properties

Some of the measured soil physical and chemical properties showed significant differences across the altitudinal gradient (Fig. S1). pH ($R=0.57$, $P<0.001$), TN ($R=0.46$, $P<0.001$), TP ($R=0.35$, $P=0.002$), TK ($R=0.23$, $P=0.046$), AP ($R=0.24$, $P=0.035$), AK ($R=0.28$, $P=0.013$), and NO_3^--N ($R=0.38$, $P<0.001$) decreased significantly with increasing altitude (Fig. S2). Moreover, TP and TN were the most responsive to altitude change as there was a significant difference in each pair of altitude samples (ANOVA, $P<0.05$), followed by AP, NO_3^-N, and pH (Fig. S1). Other properties (i.e., SOM, TOC, NH_4^+-N), although exhibiting significant differences among treatment, did not respond to altitude ($P>0.05$) (Figs. S1, S2). PCA (principal components analysis) results of edaphic physicochemical properties displayed a significant separation with spatial scale (Fig. S3). The above results proved that tobacco soil physical and chemical properties had a strong vertical scale distribution pattern along the altitudinal gradient, specifically in nutrient content (i.e., NPK) and pH value. Thus, hereafter, we identified the environmental stress gradient as following the soil properties of these eight sites.

The response of diversity, composition, and structure from multiple microbial communities in tobacco soil to the environmental stress gradient

Using a 97% similar threshold, 10,596 bacterial OTUs, 7387 fungal OTUs, and 10,689 protistan OTUs were obtained across the 228 samples (76 soil samples × three microbial communities). Bacterial and fungal observed richness both showed significant differences among the eight altitudes (Fig. 1a, ANOVA, $P<0.001$), while the protistan observed richness displayed no difference (ANOVA, $P>0.05$). Comparing the diversity among the three microbial groups, bacteria possessed the highest observed richness of species, followed by protists, while fungi had the lowest diversity (Fig. 1a). In addition, the observed richness of bacteria, fungi, and protists all decreased with increasing altitude, but only bacterial richness exhibited a significant linear correlation to altitude (Fig. S4; $P=0.007$). This indicated there was a significant altitude gradient in the richness of bacteria, but not for fungi and protists. The differences in group structures were visualized using NMDS (nonmetric multidimensional scaling) based on Bray–Curtis dissimilarity. The results showed that altitude significantly changed the structure of the soil bacterial (stress = 0.097), fungal (stress = 0.185), and protistan (stress = 0.139) communities, with the β-diversity among different sites showing significant separation between groups (Fig. 1b). Further analysis of dissimilarity test revealed significant differences among different altitudes (Table S1). Overall, altitude reshaped the bacterial, fungal, and protistan communities in tobacco soil α and β-diversity.

Altitude could also affect the composition of bacterial, fungal, and protistan communities. The core OTUs of the three groups were assessed using a Venn diagram, with 684 bacterial OTUs (6.46% of total OTUs), 259 fungal OTUs (3.51% of total OTUs), and 519 protistan OTUs (4.86% of total OTUs) present at all altitudes (Fig. 1c). The relative abundances of taxa at the phylum level were calculated for all three microbial groups. The dominant bacteria (relative sequence abundance > 1%) of all tobacco soil samples were Proteobacteria (35.1–43.0%), Actinobacteria (8.6–18.2%), *Acidobacteria* (5.8–13.4%), *Chloroflexi* (4.3–13.0%), *Gemmatimonadetes* (3.3–10.4%), Unclassified (4.9–7.5%), *Bacteroidetes* (3.2–11.0%), Candidatus Saccharibacteria (2.1–7.8%), Nitrospirae (0.7–2.3%), *Verrucomicrobia* (0.9–2.1%), and *Firmicutes* (0.5–1.4%). The dominant fungal phyla were Ascomycota (31.9–66.1%), Basidiomycota (7.3–44.9%), Unclassified (15.4–29.3%), Zygomycota (1.6–11.5%), and Chytridiomycota (0.4–3.8%). The dominant protistan phyla were Archaeplastida (52.0–76.2%), *Opisthokonta* (8.9–22.0%), *Rhizaria* (4.6–18.5%), Amoebozoa (1.8–5.4%), Stramenopiles (1.8–8.0%), Alveolata (2.0–3.5%), and Unclassified (0.9–2.5%) (Fig. 1d). The above results showed that the compositions of the three microbial groups possessed great variation among the eight different altitudes.

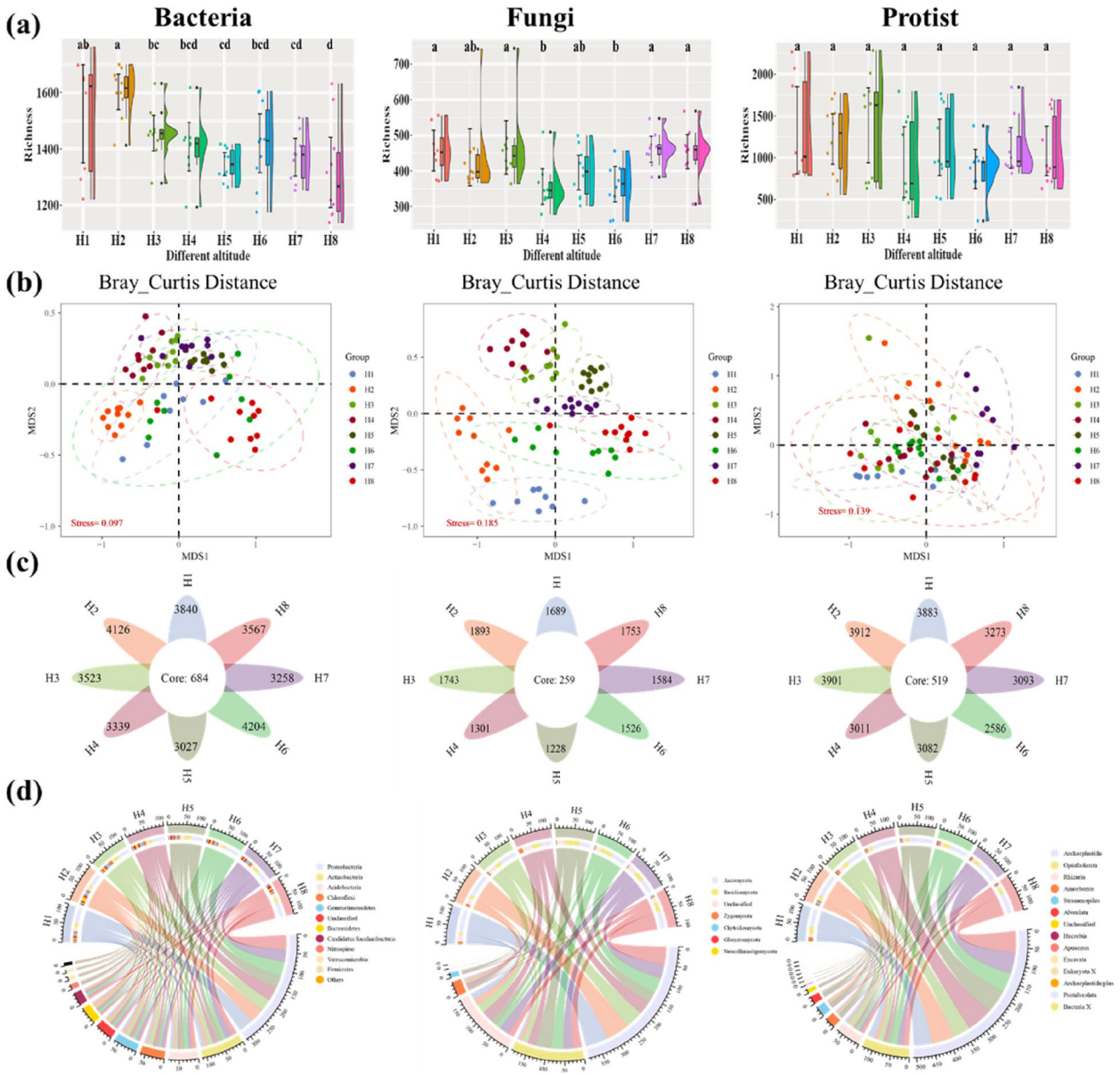


Fig. 1 The diversity, structure, and composition of soil microbial communities in tobacco soil across eight altitudes. **a** The richness of soil bacterial, fungal, and protistan communities and the significance of ANOVA test: different letters indicate significant differences based on the false discovery rate *P*-value ($P < 0.05$). **b** Nonmetric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarity matrix of bacterial, fungal, and protistan communities ($n = 76$ per community). Ellipses represented the 95% confidence intervals. **c** Venn plot of the bacterial, fungal, and protistan communities. **d** Relative abundances of the dominant phyla of the bacterial, fungal, and protistan communities. The upper half circles are sample information, and the off-circles are species taxonomic information (phylum level)

Spatial turnovers of bacterial, fungal, and protistan community structure in tobacco soil

To calculate and compare spatial turnover of the three microbial communities in tobacco soil, their DDRs were estimated. First, we evaluated the DDR of all communities, and the results indicated that the taxonomic composition dissimilarity (Bray–Curtis distance) of the bacterial ($R^2 = 0.2435$, $P < 0.001$), fungal ($R^2 = 0.2284$, $P < 0.001$), and protistan ($R^2 = 0.2367$, $P < 0.001$) communities was significantly correlated with geographic distance (Euclidean distance) (Fig. 2a), whereby the increased community dissimilarity with geographical distance indicated that the taxa of these distinct microbial groups exhibited a generally similar spatial pattern. Second, the DDR slopes (β) indicated significant differences in spatial turnover

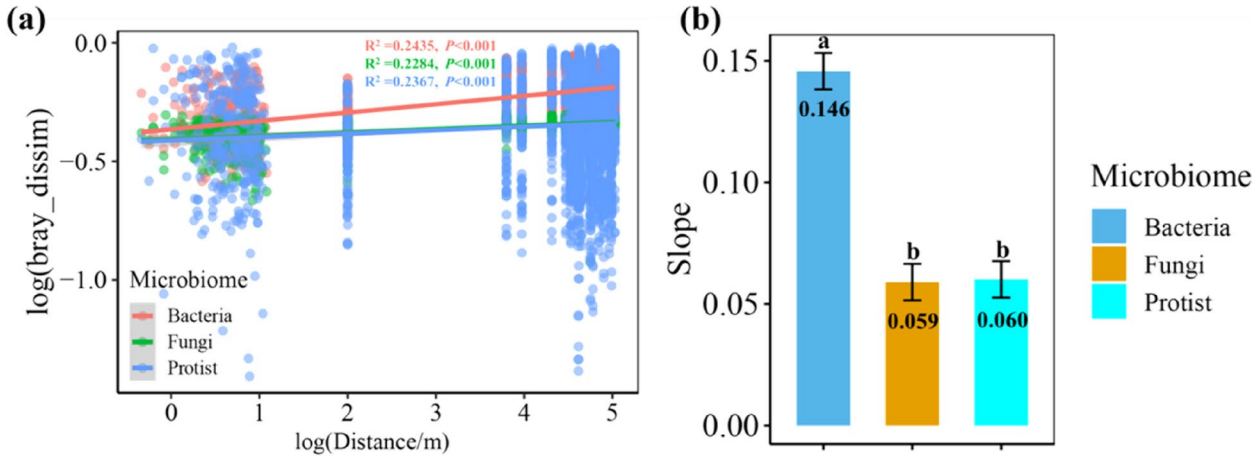


Fig. 2 Distance-decay relationship (DDR) for the three soil microbial communities. **a** DDR based on Sørensen dissimilarity along geographic distances for the bacterial, fungal, and protistan communities. Equation for the linear relationships is given in the plot with the corresponding *P*-values, which were corrected for nonindependence of pairwise comparisons using a permutation test. Solid lines are the mean fits, and shading represents the 95% confidence intervals. **b** DDR slope significance test of soil communities and the significance of ANOVA test. Each bar and error bar are the mean and standard deviation, respectively. Different letters indicate significant differences based on the false discovery rate *P*-value ($P < 0.05$). The values on the bars are the slope β of DDR, representing the spatial turnover rate of species

rate among the microbial groups (Fig. 2b). Slope of the bacterial community ($\beta = 0.146$) was significantly higher (ANOVA, $P < 0.001$) than that of the fungal ($\beta = 0.059$) and protistan ($\beta = 0.060$) communities, while there was no difference between the fungal and protistan communities (ANOVA, $P > 0.05$), indicating that the bacterial community possessed the highest conversion rate in tobacco soil.

Relative influence and contribution of environmental factors and geographical distance on microbial community distribution

To evaluate the impact of environmental factors and geographic distance on the soil microbial community, the Mantel test (i.e., Bray–Curtis dissimilarity) was used (Fig. 3a, b, c). The results showed that the dissimilarity of bacterial, fungal, and protistan communities in tobacco soil was all strongly correlated with geographic distance (i.e., altitude and latitude, $P < 0.001$) and environmental stress (i.e., pH,$P < 0.05$). The bacterial community was significantly correlated with some soil nutrients, i.e., SOM ($r = 0.177$, $P < 0.001$), TOC ($r = 0.180$, $P < 0.001$), TK ($r = 0.167$, $P < 0.01$), AK ($r = 0.093$, $P < 0.05$), and NO_3^--N ($r = 0.124$, $P < 0.01$). The fungal community was significantly correlated with TN ($r = 0.126$, $P < 0.01$), TK ($r = 0.169$, $P < 0.001$), and NO_3^--N ($r = 0.065$, $P < 0.05$), and the protistan community was significantly correlated with SOM ($r = 0.085$, $P < 0.05$), TN ($r = 0.098$, $P < 0.05$), TK ($r = 0.146$, $P < 0.01$), AP ($r = 0.165$, $P < 0.05$), NO_3^--N ($r = 0.228$, $P < 0.001$), and NH4$^+$-N ($r = 0.245$, $P < 0.05$). These results indicated that in addition to geographic distance, environmental stress and soil nutrients had significant influence on tobacco soil microbial communities.

In order to further evaluate the relative contribution of soil nutrients, environmental pressure, and geographical distance to the bacterial, fungal, and protistan communities, VPA (variance partitioning analysis) was performed. The results indicated that environmental and spatial factors could explain only a portion of the bacterial (30.1%), fungal (20.7%), and protistan (21.1%) communities' variation (Fig. 3d, e, f). The VPAs performed on environmental stress (i.e., pH), soil nutrients (i.e., SOM, TOC, TN, TP, TK, AP, AK, NO_3^-N, and NH_4^+-N), and geographic spatial (i.e., altitude, latitude, and longitude) models showed that for the three communities (i.e., bacterial, fungal, and protistan communities) in tobacco soil, the pure environmental stress explained a mean of 2.1%, 1.4%, and 1.1%; the pure geographic spatial explained a mean of 6.0%, 4.4%, and 5.1%; and pure soil nutrients explained a mean of 14.6%, 12.7%, and 12.6% of the communities variations, respectively. Consequently, the majority of variation (69.9%, 79.3%, 78.9% for the bacterial, fungal, and protistan communities, respectively) could not be explained, indicating the potential importance of neutral or stochastic processes for community assembly.

The importance of stochastic and deterministic processes in the assembly of different microbial communities in tobacco soils

The NCM could evaluate the correlations between the OTUs' occurrence frequency and the variations of relative abundance (Fig. 4a, Table 1), with 83.4%, 46.3%, and

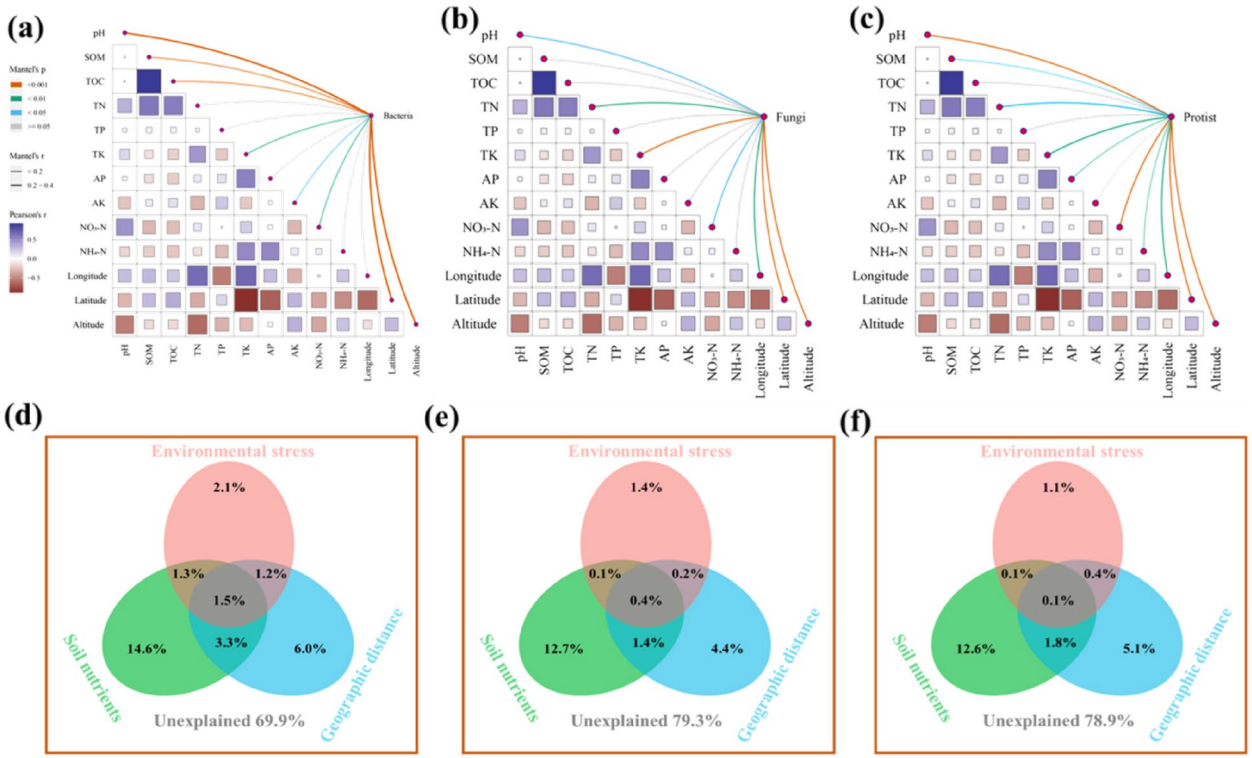


Fig. 3 Mantel test and the variance partitioning analysis (VPA) between microbial community and geographic/edaphic variables factors. Mantel test between the Bray–Curtis dissimilarity of **a** bacterial, **b** fungal, and **c** protistan communities and geographic/edaphic variables factors. The geographic distance was calculated by Euclidean distance. Heatmaps show the Pearson correlation between environmental variables, and different colored lines show the *P*-values Mantel correlation, which were corrected for nonindependence of pairwise comparisons using a permutation test. Variation partitioning analysis based on CCA illustrating the effects of geographic/edaphic variables factors on the bacterial (**d**), fungal (**e**), and protistan (**f**) communities in tobacco soils. The environmental stress group consisted of pH, the soil nutrients group consisted of SOM, TOC, TN, TP, TK, AP, AK, NO_3^--N, and $NH4^+$-N, and the geographic spatial group consisted of altitude, latitude, and longitude

69.9% of explained community variance for bacterial, fungal, and protistan communities, respectively. The results of this study show that stochastic processes played a very dominate role in shaping the bacterial and protistan communities, while deterministic processes played a dominate role in shaping the fungal community.

Furthermore, a null model test, namely null model test on Permdisp, was also used to evaluate the relative importance of stochastic and deterministic processes in shaping the bacterial, fungal, and protistan communities. The null model test results showed that dissimilarities of the bacterial and protistan communities were significantly lower than expected based on null expectations (ANOVA, $P < 0.001$, Table 1), suggesting the importance of stochastic processes in community assembly. Also, based on null expectation, the dissimilarity of fungal communities was significantly higher than expected, which indicated the importance of deterministic processes in fungal community assembly. To further quantify the relative importance of homogenous selection, heterogeneous selection, homogenous dispersal, dispersal limitation, and drift processes in shaping succession of the soil microbial communities, NST and iCAMP were used (Figs. 4b and 5).

NST results showed that while stochasticity was the predominant overall mechanism for the bacterial and protistan communities, determinism was the predominant mechanism at three altitudes (H1: 47.4%, H4: 39.3%, and H6: 46.0%) for the protistan communities. Determinism was observed to be the overall predominant mechanism in the fungal community (Fig. 4b). These results revealed that stochasticity was stronger in the bacterial community than protistan and was weakest in the fungal community. Next, we used a second null model approach, iCAMP, which consisted of phylogenetic matrices, further clarify different assembly processes and quantify their relative importance. We found that drift dominated bacterial community assembly (Figs. 5a and S5), while dispersal limitation dominated assembly of the fungal and protistan communities (Fig. 5b, c, Fig. S6, and Fig. S7). By combining the results of NST and iCAMP, we found that

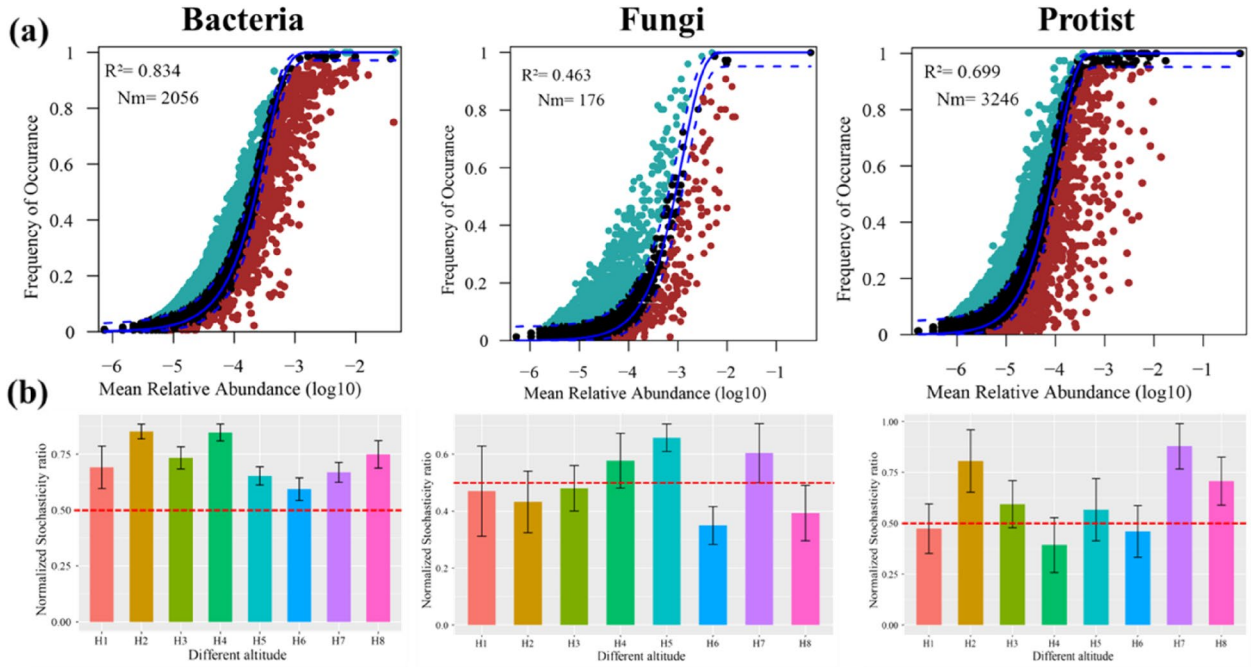


Fig. 4 Fit of the neutral community model (NCM) and null model of community assembly. **a** The predicted occurrence frequencies for bacterial, fungal, and protistan communities, respectively. The solid blue lines indicate the best fit to the NCM, and the dashed blue lines represent 95% confidence intervals around the model prediction. OTUs that occur more (blue color) or less (red color) frequently than predicted by the NCM are shown. Nm indicates the metacommunity size times immigration; R^2 indicates the fit to this model. **b** Normalized stochasticity ratio of bacterial, fungal, and protistan communities in different sample groups. Different colors represent different altitudes (from H1 with red color to H8 with hot pink color). Each bar and error bar are the mean and standard deviation, respectively. Red dashed lines represent the 50% NST value, which is the cut-off value between stochastic and deterministic processes

Table 1 Significance tests of the differences of dissimilarity among the bacterial, fungal, and protistan communities and null model simulations and overall stochastic and deterministic ratios

	Dissimilarity of actual communities	Dissimilarity of the null expectations	*F*	*P*	Stochastic ratio	Deterministic ratio
Bacteria	0.437	0.596	282.37	< 0.001***	83.40%	16.60%
Fungi	0.718	0.681	24,785.52	< 0.001***	46.30%	53.70%
Protist	0.336	0.682	262.6	< 0.001***	69.90%	30.10%

The *P*-values were corrected for nonindependence of pairwise comparisons using a permutation test and significantly differed at the level of 0.001***

only fungal community assembly was more strongly impacted by deterministic processes than stochastic processes in tobacco soil.

Effects of geographical distance and environmental factors on microbial community assembly

Geographic distance, environmental stress, and soil nutrients were detectable factors in influencing assembly of the microbial communities. First, we precisely distinguished each assembly process (i.e., homogeneous selection, heterogeneous selection, homogenizing dispersal, dispersal limitation, and drift) over spatial distance. The results revealed that all assembly processes of the bacterial community were significantly correlated with geographic distance ($P < 0.001$), i.e., the percentage of dispersal limitation and heterogeneous selection rose significantly, while the heterogeneous dispersal, homogeneous selection, and drift decreased as distance increased (Fig. 5a). Except for heterogeneous selection, all other assembly processes of the fungal community were significantly correlated with geographic distance ($P < 0.001$), i.e., the percentage of dispersal limitation rose significantly, while the heterogeneous dispersal, homogeneous selection, and drift decreased as distance increased (Fig. 5b). However, for the protistan community, only dispersal limitation ($P < 0.001$) and heterogeneous selection

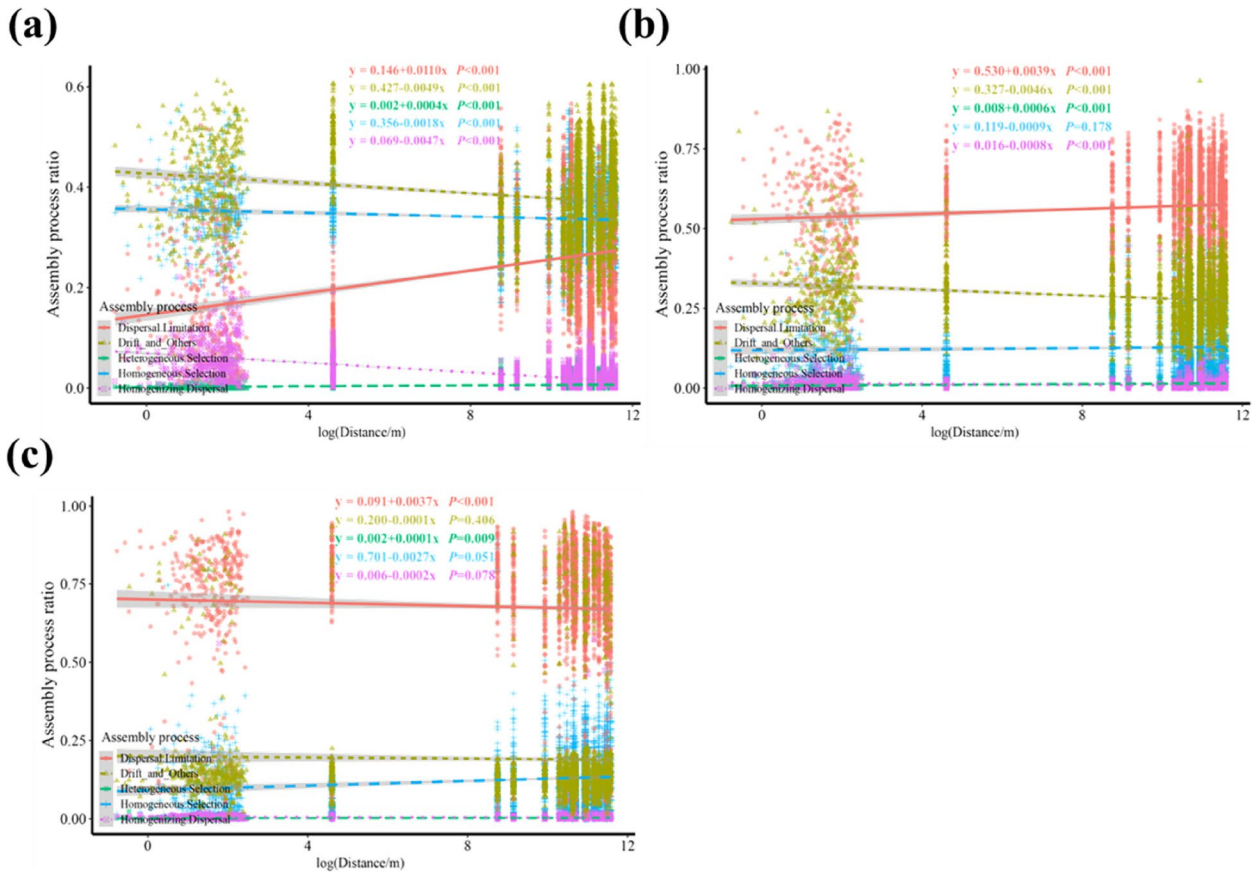


Fig. 5 The relative percentages of different assembly processes of microbial communities in tobacco soil based on infer community assembly mechanisms by phylogenetic-bin (iCAMP) measurement over geographic distances for **a** bacterial, **b** fungal, and **c** protistan communities. Different colors represent different assembly processes. Equation for the linear relationships is presented in the plot with the corresponding *P*-values, which were corrected for nonindependence of pairwise comparisons using a permutation test. Solid lines indicate the mean fits, and the shading represents 95% confidence intervals

($P=0.009$) rose significantly as distance increased (Fig. 5c). Together, these results indicated that the influence of dispersal limitation will strengthen and play an increasingly important role in the formation of community structure for bacteria, fungi, and protists with increasing spatial distance in tobacco soil.

Furthermore, we assessed whether environmental factors could explain the variation or differences of community composition during assembly. Mantel test results of assembly processes and environmental factors for the bacterial community showed that pH significantly influenced heterogeneous selection ($r=0.119$, $P=0.004$) and dispersal limitation ($r=0.213$, $P=0.002$), TN only significantly influenced dispersal limitation ($r=0.196$, $P=0.001$), and NO_3^--N only significantly influenced homogeneous selection ($r=0.134$, $P=0.042$) (Table S2). For the fungal community assembly processes, heterogeneous selection was significantly influenced by TK ($r=0.085$, $P=0.008$), AP ($r=0.169$, $P=0.002$) and NO_3^--N ($r=0.243$, $P=0.002$); homogeneous selection was significantly influenced by TOC ($r=0.075$, $P=0.041$) and AK ($r=0.114$, $P=0.026$); and dispersal limitation was only significantly influenced by TN ($r=0.120$, $P=0.008$) (Table S3). While for the protistan community, only homogeneous selection was significantly influenced by pH ($r=0.179$, $P=0.016$) (Table S4).

Discussion

One of the central issues in microecology is to shed light onto the underlying processes and mechanisms of complex microbial communities and the relative influence of various factors on their assembly (Nemergut et al. 2013; Thompson et al. 2017). To date, a number of studies have been done on the spatial distribution patterns of soil microorganisms, but few of these have considered the

response of the microbiome assembly process to environmental changes caused by altitude (Chen et al. 2019; Hanson et al. 2012; Zhang et al. 2018). Furthermore, many studies have only explored natural ecosystems, such as grasslands (Du et al. 2021; Wang et al. 2021). Previous studies revealed that soil microbial communities in different habitats have different spatial distribution patterns (Martiny et al. 2011; Wang et al. 2017). Therefore, in this study, we evaluated the specific relationship between community structure and spatial distance of multiple microbial groups in a tobacco soil ecosystem. Meanwhile, the potential of environmental conditions to regulate community assembly across environmental pressure gradients at different taxonomic levels was analyzed. Our study helps illuminate the spatial patterns of microorganisms in farmland ecosystems under anthropogenic disturbance and to reveal their underlying processes and mechanisms.

Many previous studies have shown that altitude was an important factor shaping soil properties, and different physiochemical soil property gradients will be formed along an altitudinal gradient (Feng et al. 2021; Li et al. 2022; Shedayi et al. 2016). Our results showed that with increasing altitude, soil pH decreased significantly ($P < 0.05$), from neutral to acidic, and soil nutrient (i.e., N, P, K) content also decreased significantly (Figs. S1, S2). These changes in soil properties along altitude could significantly increase the survival pressure on soil microorganisms (Hernandez et al. 2021); therefore, we regard that, in our study setup, increasing altitude shaped an environmental stress gradient in the tobacco soil, and the higher the altitude, the greater the environmental stress.

It is well-known that gradients of different soil variables will be formed along an altitudinal gradient (Feng et al. 2021; Li et al. 2022; Shedayi et al. 2016). Soil nutrient composition has a significant impact on the diversity, composition, and structure of soil microbial communities (Guo et al. 2018a; Wang et al. 2021). Thus, the most obvious phenomenon of increasing altitude was the change of soil variables, which subsequently decreased community diversity and altered community composition (Hernandez et al. 2021; Rocca et al. 2019; Zhang et al. 2021). In our study, diversities of the bacterial, fungal, and protistan communities all decreased ($\beta = 0.663$, 0.043, and 0.842, respectively) with the increasing environmental stress caused by altitude (Fig. S4). The NMDS and dissimilarity test results indicated that the bacterial, fungal, and protistan community structures were also significantly different along the environmental stress gradient (Fig. 1b, Table S1). There are several potential reasons for why increased environmental stress reduces community diversity and alters community structure. Firstly, this result might be caused by the variation in environmental nutrients (i.e., NPK) and geographic conditions along the altitudinal gradient (Chen et al. 2019). Mantel test showed that the bacterial, fungal, and protistan communities were significantly correlated with soil nutrients (Fig. 3a, $P < 0.05$). Secondly, the niche width that a habitat could provide has been reduced. Previous studies have shown that the niche width of non-native species decreased with increasing altitude (Ahmad et al. 2021). Thirdly, an environmental filter (e.g., pH) was increased along stress gradients from H10 to H8 (Hernandez et al. 2021; Zhang et al. 2021). We found that pH was significantly correlated with the microbial community (Fig. 3a, $P < 0.01$). Therefore, as altitude continues to increase, more diverse microbial communities will be formed along the environmental stress gradients.

Soil variable differences caused by altitude are not the only factor that could affect microbial communities. Geographic distance also plays an important role in shaping communities (Du et al. 2021; Liu et al. 2014; Wang et al. 2021). Previous studies have demonstrated soil microbial communities possess clear spatial scaling patterns in DDR (Deng et al. 2016, 2018), but this has rarely been shown to occur simultaneously in multiple communities (Du et al. 2021; Wang et al. 2021), especially for bacteria, fungi, and protists together. In this study, we observed a significant DDR for the bacterial, fungal, and protistan communities in tobacco soil (Fig. 2a). This biogeographical pattern suggested these communities have comparable spatial sensitivity (Logares et al. 2013). The geographic distance as an indicator of microbial dispersal (Xiong et al. 2012), and our Mantel test results, revealed a strong correlation between soil bacterial, fungal, and protistan communities with geographic distance (Fig. 3a). Furthermore, previous studies have shown that the effects of geographic distance and environmental filtration on microorganisms were covariant (Hanson et al. 2012; Logares et al. 2020). Additionally, the Mantel test revealed a strong correlation between soil bacterial, fungal, and protistan communities and pH (Fig. 3a). Current consensus within the scientific community is that soil pH is a critical driver for microbial community diversity and structure at local (Zhou et al. 2017), regional (Liu et al. 2014), and continental (Bahram et al. 2018) scales. Furthermore, we observed a steeper slope in bacterial community, indicating that soil bacteria possessed greater dissimilarity over geographic distance than the fungal and protistan communities (Fig. 3b). The difference in spatial turnover patterns between the communities might be explained by species characteristics (e.g., body size) (De Bie et al. 2012), niche selection (Ahmad et al. 2021), and microbial dispersal limitation (Du et al. 2021). Firstly, in contrast to fungi and protists, bacteria experience greater difficultly in dispersal and drift due

to their smaller size (De Bie et al. 2012). Secondly, due to the differences in ecological niches at different elevations, the biomass of different communities may increase with the change of soil variables (Bell 2010). Finally, microbial dispersal limitation, which describes when the movement and colonization of species in a new location is restricted, may be another factor leading to more-dissimilar structures among communities (Zhou and Ning 2017).

Although soil variables and geographic distance were identified as playing important roles in reshaping the microbial community, our VPA results demonstrated that environmental and spatial factors accounted for a small proportion (20.7–30.1%) of community variation, meaning they had only a minor effect on the communities (Fig. 3b). Several previous studies that used VPA have also found that a large proportion of microbial community variation among different habitats are unexplained (Chen et al. 2019; Roguet et al. 2015; Zhang et al. 2018). This result could have several possible explanations. First, although we measured several soil variables, there were still a number of variables unaccounted for in this study, some of which may be important factors affecting the large portion of unexplained community variation (Chen et al. 2019; Lindström and Langenheder 2012; Nabout et al. 2009). Second, biotic interactions are also recognized to be an important mechanism that could influence the community distribution based on niche-based theory (Zhou and Ning 2017), and these interactions cannot be quantified by VPA (Lima-Mendez et al. 2015; Wei et al. 2016). Third, VPA tends to undervalue the contribution of environmental variables (Gilbert and Bennett 2010). Therefore, caution should be exercised when using VPA to measure the contribution of environmental and spatial variables to community variation (Chen et al. 2019), and it should be used as an exploratory tool together with other approaches. In our study, we used the neutral community model (Sloan et al. 2006) and null model (i.e., NST and iCAMP) (Ning et al. 2019; Stegen et al. 2013) to estimate the relative importance of stochastic and deterministic processes, which could overcome the shortcomings of VPA by relating community composition to environmental and spatial variables.

The process of microbial community assembly is determined by either deterministic or stochastic processes (Stegen et al. 2013). NCM could be used to quantify some ecological processes that are difficult to observed directly but can greatly affect the microbial community (i.e., dispersal and ecological drift) (Tong et al. 2019). The NST and iCAMP approaches (Ning et al. 2019; Stegen et al. 2013) allowed us to detect the relative influences of stochastic and deterministic processes based on taxonomic dissimilarity. Our results estimated a major part of the variation in the bacterial and protistan communities (Figs. 4 and 5), suggesting a critical role for stochastic balance between the loss and gain of microorganisms (e.g., stochastic births, deaths, and immigration) in the community assembly process (Hanson et al. 2012; Sloan et al. 2006). Another important impact of stochastic processes is that community similarity is predicted to decrease along geographic distance gradients due to dispersal limitation as calculated by neutral theory (Chase and Myers 2011). This was confirmed by the significantly strong DDR patterns of microbial communities in our study (Fig. 2a). In addition, the fungal community was demonstrated to be impacted by deterministic processes (Figs. 4 and 5), including both heterogeneous and homogeneous selections and partially by dispersal limitation (Du et al. 2021; Ning et al. 2019; Zhou and Ning 2017), revealing the importance of determinism in shaping the tobacco soil community.

Mantel test was used to measure the correlation between the assembly processes dissimilarity of the microbial communities and environmental factors. The results indicated the drift of the bacterial community was not influenced by any of the tested soil variables (Table S2). However, the deterministic processes of the fungal community were dominated by several factors including TOC, TN, TP, TK, AP, AK, and NO_3^--N (Table S3), and only pH influenced homogeneous selection of the protistan community (Table S4). These results suggested niche selection might be a major factor in shaping the fungal community (Bebber and Chaloner 2022; Crowther et al. 2014), but not for the bacterial and protistan communities of tobacco soil. Furthermore, not all assembly processes of the three communities displayed significant correlation with altitude ($P > 0.05$) (Figs. S5, S6 and S7). But all assembly processes in bacteria ($P < 0.001$), fungal assembly, except for homogeneous selection ($P < 0.001$), and dispersal limitation process of the protozoan communities ($P < 0.001$) were significantly related to geographic distance (Fig. 5). These results indicated bacterial communities were most sensitive to geographic distance, followed by the fungal and protozoan communities, which may be related to niche selection and organism size as mentioned earlier (Ahmad et al. 2021; De Bie et al. 2012). On the other hand, our results indicated that spatial distance mainly affects fungal and protozoan communities by influencing dispersal limitations (Fig. 5b and c), while bacteria were mainly affected by drift (Fig. 5a), which may account for why bacteria possessed the highest stochastic ratio among the three communities. In conclusion, the above results indicated that at a certain spatial scale, the increase of species turnover in the tobacco soil fungal community was mainly due to niche selection and dispersal limitation.

Conclusion

Our study systematically revealed how multiple communities scaled along an altitudinal profile in tobacco soil and shed light onto the underlying processes and mechanisms. We found highly similar results across the communities analyzed along an environmental stress gradient, with biodiversity scaling differently with increasing altitude and communities displaying higher diversity at lower altitude sites. This was due to the loss of soil nutrients with altitude, niche selection, and the increase of environmental filtering (i.e., pH). In addition, all microbial communities displayed clear spatial scaling patterns, with bacteria possessing the highest spatial turnover rates, which could be driven by drift. Furthermore, fungi showed the importance of determinism in shaping the community, which could be driven simultaneously by both niche selection and dispersal limitation. Our findings provide a complementary perspective to the study of multiple communities across different horizontal and vertical spatial scales. However, our work has left some questions unanswered, with further research still necessary to evaluate which biotic interactions influence community assembly along environmental stress gradients and over geographic distance.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13213-023-01717-8.

Additional file 1: Table S1. The dissimilarity test of microbial community structure among all altitudinal samples based on Bray–Curtis distance. The significant levels were described as 0.001***, 0.01**, and 0.05*. **Table S2.** Mantel test between the assembly process dissimilarity of bacterial community and environmental factors. Environmental factors significantly correlated with the assembly process dissimilarity at the levels of 0.0001***, 0.01**, and 0.05* are in bold. **Table S3.** Mantel test between the assembly process dissimilarity of fungal community and environmental factors. Environmental factors significantly correlated with the assembly process dissimilarity at the levels of 0.0001***, 0.01**, and 0.05* are in bold. **Table S4.** Mantel test between the assembly process dissimilarity of protistan community and environmental factors. Environmental factors significantly correlated with the assembly process dissimilarity at the levels of 0.0001***, 0.01**, and 0.05* are in bold. **Fig. S1.** The soil properties of different altitudes, including pH, soil organic matter (TOM), total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), nitrate nitrogen (NO_3^-—N), and ammonia nitrogen (NH_4^+-N), available phosphorus (AP), available potassium (AK). Different letters (a, b, c, d, e) indicate significant differences (ANOVA, $P < 0.05$). **Fig. S2.** Pearson correlation between soil properties and altitude. Shaded areas indicate 95% confidence interval. **Fig. S3.** Principal Component Analysis (PCA) of tobacco soil properties. Different colors indicate altitude. **Fig. S4.** Pearson correlation between community diversity (*i.e.,* observed richness) and altitude. Shaded areas indicate 95% confidence interval. **Fig. S5.** Pearson correlation between bacterial community assembly processes (*i.e.,* heterogeneous selection, homogeneous selection, dispersal limitation, homogenizing dispersal and drift) and altitude. Shaded areas indicate 95% confidence interval. **Fig. S6.** Pearson correlation between fungal community assembly processes (*i.e.,* heterogeneous selection, homogeneous selection, dispersal limitation, homogenizing dispersal and drift) and altitude. Shaded areas indicate 95% confidence interval. **Fig. S7.** Pearson correlation between protistan community assembly processes (*i.e.,* heterogeneous selection, homogeneous selection, dispersal limitation, homogenizing dispersal and drift) and altitude. Shaded areas indicate 95% confidence interval. **Supplementary data 1.** The relative abundance of bacteria at phylum level. **Supplementary data 2.** The relative abundance of fungi at phylum level. **Supplementary data 3.** The relative abundance of protist at phylum level. **Supplementary data 4**.

Acknowledgements

We thank Dr. James Walter Voordeckers for carefully editing the grammar of the manuscript and for some valuable suggestions for this manuscript.

Authors' contributions

PL, TX, QH, and YZ designed the experiments. YY, ZW, XD, BW, and WL took samples and performed all data measurement. SG and YY contributed to the data analysis. PL and YZ wrote the manuscript. All authors read and approved the manuscript.

Funding

This research was supported by the Wenshan Tobacco Company of Yunnan Province (2021530000241033) of China.

Availability of data and materials

All 16S rRNA gene libraries from Illumina amplicon sequencing were submitted to the ScienceDB (https://www.scidb.cn/s/iq6VZn) under the project https://doi.org/10.57760/sciencedb.06737. All ITS gene libraries from Illumina amplicon sequencing were submitted to the ScienceDB (https://www.scidb.cn/s/YzYnau) under the project https://doi.org/10.57760/sciencedb.06738. All ITS 18S rRNA gene libraries from Illumina amplicon sequencing were submitted to the ScienceDB (https://www.scidb.cn/s/ryuEje) under the project https://doi.org/10.57760/sciencedb.06743.

Declarations

Ethics approval and consent to participate

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication

All of the authors have read and approved the manuscript. This work has not been published previously, nor is it being considered by any other peer-reviewed journal.

Competing interests

The authors declare that they have no competing interests.

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Received: 4 November 2022 Accepted: 29 March 2023
Published online: 14 June 2023

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