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Differential responses of soil microbial biomass, diversity, and compositions to altitudinal gradients depend on plant and soil characteristics

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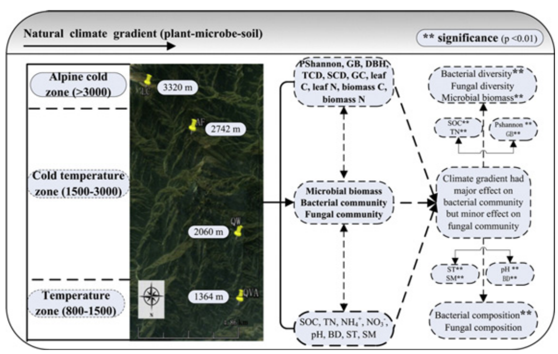
HIGHLIGHTS

- Microbial biomass reflects the C/N in plant-soil systems along altitudinal gradients.
- Bacterial diversity varied more than fungal diversity along altitudinal gradients.
- Altitudinal gradient largely affected bacterial composition not fungal composition.
- Microbial alpha diversity was mainly coupled with plant diversity, SOC and TN.
- Microbial beta diversity and composition mainly differed with ST and SM.

GRAPHICAL ABSTRACT



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ABSTRACT

Alt'itudinal gradients strongly affect plant biodiversity, but the effects on microbial patterns remain unclear, especially in the large scale. We therefore designed an altitudinal gradient experiment that covered three climate zones to monitor soil microbial community dynamics and to compare those with plant and soil characteristics. Illumina sequencing of the 16S rRNA gene and ITS gene was used to analyze soil microbial (bacterial and fungal) diversity and composition, and fumigation–extraction was used to determine microbial biomass; the plant community metrics (i.e., percent cover, Shannon-Wiener, grass biomass, and carbon/nitrogen in leaf and biomass) and soil properties (i.e., soil moisture, soil temperature, bulk density, organic carbon, total nitrogen, and available nitrogen) were determined. The results showed that carbon/nitrogen in microbial biomass was higher at medium altitude and was positively related to carbon and nitrogen in both soil and grass biomass along the altitudinal gradients. Soil bacterial alpha diversity was significantly higher at medium altitude but fungal alpha diversity did not affected by altitudinal gradients; the effect of altitudinal gradients on bacterial beta diversity was larger than that on fungal beta diversity, although both groups were significantly affected by altitudinal gradients. Moreover, *Alpha-proteobacteria*, *Beta-proteobacteria*, and *Gemmatimonadetes* were significantly more abundant in higher altitude than in lower altitude, both *Acidobacteria* and *Actinobacteria* significantly declined with increasing altitude; other bacterial taxa such as *Chloroflexi*, *Nitrospirae*, *Gamma-proteobacteria*, and *Delta-proteobacteria* were significantly higher at medium altitudes. For fungal taxa, *Basidiomycota* and *Ascomycota* were the dominant phyla and responded insignificantly to the altitudinal gradients. The responses of microbial alpha diversity were mostly associated with plant Shannon index, organic carbon, and total nitrogen, whereas microbial beta diversity and composition mainly depended on soil moisture and temperature. Overall, these results suggest that soil bacteria rather than fungi can reflect changes in plant and soil characteristics along altitudinal gradients.

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Abbreviations

QVA	*Q aliena* var. acutiserrata community
QW	*Quercus wutaishanica* community
AF	*Abies fargesii* community
LC	*Larix chinensis* community

Plant characteristics

pshannon	Shannon–Wiener diversity index
GB	grass biomass
DBH	diameter at breast height
TCD	tree crown density
SCD	shrub crown density
GC	grass coverage

Soil characteristics

SOC	soil organic carbon
TN	total nitrogen
NH_4^+	ammonium
NO_3^-	nitrate
BD	Soil bulk density
ST	soil temperature
SM	soil moisture
MBC	microbial biomass carbon
MBN	microbial biomass nitrogen
NMDS	Nonmetric multidimensional scaling analysis
	ANOSIM analysis of similarities

1. Introduction

Altitudinal gradients are characterized by drastic changes in biotic and abiotic characteristics over geographical distances, and thus have been recognized as a natural experiments to assess ecological and evolutionary responses of the microbial community to changing environments (Körner, 2007; Siles and Margesin, 2017). It is presently fueled by our emerging understanding of the complex interactions between soil conditions and plant community in relation to changing altitude, which can improve the predication for microbial process (Siles and Margesin, 2016; Sundqvist et al., 2013). Moreover, climatic factors, indicated by air temperature, precipitation and UV radiation, can also vary with altitudes, thus creating complex environmental changes along the altitudinal gradients (Körner, 2007). Under such circumstances, microbial species, especially for aerobic microbes, are mostly affected because of the changing oxygen concentration (Bahram et al., 2012). Thus, the altitudinal gradients can provide a framework for understanding the biodiversity patterns in earth's major environmental gradients and further predict the diversity loss patterns resulting from climate change (Mayor et al., 2017)

Being an integral part of forest ecosystems, soil microorganisms can mediate biogeochemical cycles in terrestrial ecosystems (Van der Heijden et al., 2008). Thus, in dynamic environments, small shifts in soil microbe may lead to significant changes of nutrient transformation in plant- soil system (Bragazza et al., 2015; Deng et al., 2016). This leads to a hypothesis that soil microbe might reflect the changes of above- and below-ground properties along the altitudinal gradients. Moreover, several studies also documented the differential responses of soil microbial community to climatic factors and analyzed how these changed with environmental conditions (Bryant et al., 2008; Miki, 2012). For instance, Cregger et al. (2012) predicated that differential responses of the soil microbial community to climate change were dependent on available substrates and the above-ground plant community. Serna-Chavez et al. (2013) reviewed that moisture availability and soil nutrients rather than temperature primarily drove changes in soil microbial biomass. However, other studies indicated that climate-induced changes in soil temperature and moisture had no effects on *Gram-positive bacteria* because they have high tolerance and can spatially explore the soil for areas with increased water and nutrients (Manzoni et al., 2012). While Shen et al. (2016) also revealed that microbial functional genes dramatically increased along an elevation gradient, but the bacterial taxonomic and phylogenetic diversity based on 16S rRNA gene sequencing did not exhibit such a similar trend. Therefore, this leads to the further hypothesis that altitudinal gradients might have differential effects on soil microbial biomass and composition and the microbial process in different ecosystems.

Recently, although several studies revealed the horizontal distribution of microbial communities (Bahram et al., 2012; Meng et al., 2013), few studies have examined microbial diversity patterns along the altitudinal gradients, especially in large altitudinal scales. A previous study found that soil bacterial richness significantly decreased from lowest altitude (2460 m) to highest altitude (3380 m) in the Colorado Rocky Mountains (Bryant et al., 2008), whereas another study found that soil bacteria at medium altitude (820 m) showed the highest diversity in subtropical mountainous forest of China (Meng et al., 2013). Bahram et al. (2012) revealed that fungal diversity decreased monotonically with increasing altitudes in the hyrcanian forests of northern Iran, however, Susan et al. (2015) observed an insignificant response of fungal community diversity along a short (300 m) altitudinal gradient in an area Scots pine (*Pinus sylvestris* L.). These differences lead to the hypothesis that spatial and elevation scales affect temperature fluctuations and climate types, which account for the different patterns of microbial richness and community (Classen et al., 2015). Particularly, large altitude scales are associated with different climate zones and may contain other complex abiotic and biotic factors, which greatly limit our understanding of microbial community dynamics along the altitudinal gradients.

To comprehensively understand changes in microbial biomass, diversity (bacteria and fungi), and community composition along altitudinal gradients, we examined large altitudinal gradients at Taibai Mountain, which is the highest mountain in the Qinling Range of eastern mainland China, and the elevation changes from 470 to 3767 m above sea level (Tang and Fang, 2006). Several studies performed in this range have revealed the contrasting altitudinal above-plant diversity patterns along large climate gradients (Qiao et al., 2015; Tang et al., 2012). However, soil microbial community responses to this type of altitudinal/climatic gradient and associated climate zones were not well-understood. In this study, we used fumigation–extraction and Illumina sequencing to analyze the changes in soil microbial biomass, diversity (bacterial and fungal), and community (bacterial and fungal) composition along four altitudinal gradients (average of 1364, 2060, 2741, and 3320 m above sea level), which covered three climate zones (warm temperate zone, cold temperate zone, and alpine cold zone). Based on previous studies related to soil microbes in terrestrial ecosystems (Bryant et al., 2008; Van der Heijden et al., 2008), we hypothesized that soil microbial biomass can be used to reflect the plant–soil system and that, compared to fungal community, bacterial community may vary more along the altitudinal gradients. Moreover, we also predicted that soil bacterial and fungal community compositions characterizing this large altitudinal scale would respond differently to climate conditions and plant and soil characteristics. Therefore, the objectives of this study were to: (1) understand how microbial biomass responded to altitudinal gradients, (2) compare the responses of microbial (bacterial and fungal) diversity and community composition to altitudinal gradients, and (3) evaluate the relationships between the soil microbial community and plant and soil characteristics along the altitudinal gradients.