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Soil microbial community structure and activity along a montane elevational gradient on the Tibetan Plateau

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ABSTRACT

Knowledge about the distribution pattern and function of soil microbial communities is essential for understanding their vital role in ecosystem functioning. However, little is known about the elevational patterns of microbial communities at high altitudes on the Tibetan Plateau, a region that is very sensitive to global change. We investigated the microbial community composition and functional patterns along an elevational gradient (3100–4600 m above sea level) on Mount Segrila using phospholipid fatty acids (PLFAs) and community level physiological profiles (CLPP). Soil microbes were abundant even at higher altitudes and ranged from 1.52 to 3.53 μmol per g organic carbon (OC) by total PLFAs. Soil microbial biomass (expressed as Total PLFAs) declined at higher elevations, and the highest abundance was observed at the low-elevation site. Fungal to bacterial ratio decreased with increasing elevation. While no consistent elevational pattern was observed for PLFA profiles, richness and diversity of carbon source utilization by the microbial community decreased significantly at higher altitudes. Soil microbes at higher altitudes had the potential to metabolize relatively more recalcitrant carbon components while microbes at lower altitudes tended to utilize labile carbon sources. The results were in line with the chemical composition of soil organic matter. Increasing O-alkyl C and decreasing alkyl C content indicate slow decomposition at higher elevations. Variations in structure and activity of microbial community were mainly attributable to MAT, pH, and litter C:N. Our results indicate that pH is a major factor affecting microbial communities, and the impact of soil pH is closely correlated with temperature and vegetation changes along the elevational gradient. As future climate warming may lead to temperature increases and an upward migration of vegetation, our results provide fundamental knowledge of soil microbial communities in the Tibetan alpine region and may help to predict responses of the below-ground community to global climate change.

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1. Introduction

Understanding of microbial community structure and its function is essential as soil microorganisms play vital roles in regulating ecosystem function and influence a variety of important ecosystem processes related to soil organic matter turnover and biogeochemical cycling [34]. In recent years the spatial pattern of microbial communities in montane regions has attracted great interest with the advent of molecular techniques. The dramatic environmental gradients over short distances in montane regions provide a unique opportunity to assess the effect of high turnover of aboveground vegetation, local soil conditions and climate regimes on spatial patterning of microbial communities along elevational gradients [21]. In addition, as the microbial community is more sensitive than plants and animals to impacts of environmental change [4] changes in microbial community composition and activity with altitude may in turn affect the stability of the ecosystem under climate change.

So far research on elevational patterns of microbial community or activity in mountain areas has been conducted below 3500 m above sea level (a.s.l.). Results have shown contrasting elevational patterns of plant and bacterial taxon richness and phylogenetic diversity in the Colorado Rocky Mountains [5] and bacteria in

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eastern Peru (200–3450 m a.s.l.) [10]. Other studies have indicated that as altitude increases microbial population [20], bacterial population [15] and fungal diversity [27] decrease. In contrast [21], reported increases in fungal population and relative numbers of Gram-negative bacteria with increasing elevation in the Austrian Central Alps (1500–2530 m a.s.l.). However [29], did not find any elevational gradient in soil bacterial richness/diversity on Changbai Mts., China, while a mid-elevation richness/diversity "peak" was detected for both bacteria [31] and archaea [32] on Mt. Fuji. The contradictory results are attributed to many factors, including both biotic factors such as vegetation and interactions with other microorganisms, and abiotic factors such as elevation, mean annual temperature (MAT) and precipitation (MAP), soil pH, temperature, and nutrient availability. The contribution of different variables to the microbial community varies with the target microbial groups investigated and is sometimes site-specific [5,8,10,29,39,42]. In contrast to diversity/composition changes, studies on microbial activities along the elevational gradient are very limited. Decreases in microbial activities such as dehydrogenase activity [21] and other enzyme activities and CO_2 evolution [28] with increasing altitude have been reported. The changes of microbial activities were mostly correlated with variations of climatic factors and differences in microbial community composition.

The Tibetan Plateau is the largest and highest plateau in the world with an average altitude of 4000 m a.s.l. The harsh geographic and climatic conditions contribute to one of the most challenging environments for plants and microorganisms, and the fragile ecosystem is very sensitive and vulnerable to climate change and anthropogenic perturbation [37]. Understanding the vertical distribution patterns of microbial communities can provide fundamental knowledge about microbes at high elevational areas, which might be of great significance for predicting microbial community response to environmental change. Recent Geochip based studies showed the importance of soil microbial communities in N and C cycles in alpine meadow [41] and Tibetan grasslands [38]. However, little is known about the shift in microbial community structure and activities along an alpine climosequence. The present study aimed to investigate the composition and activity of the microbial community along an elevational gradient and to explore the driving forces affecting microbial community structure and activity. We selected Mount Segrila to investigate the spatial patterns of microbial community structure and function at high altitudes above 3500 m a.s.l. Mount Segrila situated on the southeastern part of the Tibetan Plateau, and is representative of the typical montane frigid-temperate forest of southeast Tibet. Compared to previous studies in Tibetan Plateau, mean annual precipitation in the study site is high and distinct vegetation types are observed along the elevational gradients. We hypothesized that vegetation and soil organic carbon might be the main variables affecting elevational patterns of soil microbial community structure and activity.

2. Materials and methods

2.1. Site description

The study was carried out at Mount Segrila (29°21′–29°50′ N, 94°28′–94°51′ E) on the southeastern part of the Tibetan Plateau. The mountain is located on the convergence of the east Nyainqentanglha range and the east Himalaya range and is representative of the typical montane frigid-temperate forest of southeast Tibet. The altitude of the peak is 5200 m a.s.l. The climate is humid and frigid with a mean annual temperature (MAT) of −0.73 °C, mean annual precipitation (MAP) of 1134 mm, and annual evaporation of 544 mm. Mount Segrila has four distinct vegetation types, namely temperate coniferous and broad-leaved mixed forests (3000–3500 m), frigid dark coniferous forests (3500–4200 m), alpine subfrigid shrub meadow (4200–4500 m), and alpine frigid meadow (above 4500 m) [18]. The forest stands between 2700 and 4300 m and is characterized by *Pinus armandi*, *Pinus densata*, *Picea likiangensis* var. *linzhensis*, and *Abies georgei* var. *smithii*. Shrubs were abundant at higher altitudes of 4300–4500 m a.s.l., e.g., *Sabina saltuaila*, *Rhododendron hiale* and *Rhododendron nyingchiense*. Alpine meadow is dominated by *Rhododendron bulu*, *Carex* sp., *Saussurea* spp., *Potentilla* sp., *Polygonum* spp. and *Poa annua*. Vegetation above 4500 m a.s.l. has patchy distribution of *Cassiope selaginodes, Rheum nobile* and some *Rhodiola* spp.

2.2. Soil sampling and soil chemical characterization

We selected five sampling sites in the natural open grasslands along the west slope of Mount Segrila at altitudes of 3100–4600 m a.s.l. (Fig. 1). The changes in the dominant plant species along the altitude gradient are shown in Table 1. Samples of the topsoil (0–15 cm) were collected in July 2011 from the five study sites along the elevational gradient, and at each site five sampling quadrats (area approximately 5 × 5 m) were selected. At each quadrat three soil monoliths (20 × 20 cm) were randomly collected and composited as one replicate and thus pooled to yield five composite samples per altitude. Litters were collected at each sampling quadrat and composited into one replicate. The soil was placed in polyethylene bags, stored on ice and transported to the laboratory for further treatment. The soil samples were sieved (<2 mm) to remove visible stones, animals, root fragments and plant material before freeze-drying in a lyophilizer, and were stored at −20 °C prior to lipid extraction. Sub-soil samples for analysis of community level physiological profiles were kept at 4 °C. For bulk soil analysis the soil samples were air-dried and sieved (<2 mm). Soil pH was measured in 1 M KCl (soil: water ratio of 1:2.5). Soil available phosphorus (AP) was extracted with 0.5 M $NaHCO_3$ (Olsen–P). Soil organic carbon (SOC) was measured by wet oxidation followed by titration with ferrous ammonium sulfate. The litters were oven-dried at 65 °C, ground and sieved (60 μm). Total carbon (TC) and total nitrogen (TN) of soil and litters were measured with an elemental analyzer (EA1108, Fisons Instruments SpA, Milan, Italy).

2.3. PLFA analysis

The culture-independent method of phospholipid fatty acids (PLFA) was explored to characterize the microbial community structure [11]. Lipid extraction and PLFAs were performed according to [11]. Briefly, 5 g of freeze-dried soil was extracted with 19 ml of a single-phase mix of chloroform: methanol: citrate buffer solution (1:2:0.8, v/v/v, pH = 4.0) for lipid extraction. After extraction, the collected non-polar phase was fractioned into neutral lipids, glycolipids and phospholipids by sequential elution with chloroform (6 ml), acetone (6 ml) and methanol (3 ml), respectively, using pre-packed silica solid phase extraction columns (500 mg/3 ml, Cleanert™ Silica-SPE, Bonna-Agela Technologies Inc., Wilmington, DE). The phospholipid fraction was then methylated with a methanol–toluol (1:1) solution (1 ml) and 0.2 M methanolic KOH (1 ml) to produce fatty acids methyl esters (FAMEs). After addition of fatty acid 19:0 as internal standard, samples were analyzed on an Agilent 6850 Series II gas chromatograph (Agilent Technologies Inc., Santa Clara, CA) and identified with a microbial identification system, MIDI Sherlock 6.1 (MIDI Inc., Newark, DE).

We used the fatty acid nomenclature described by Ref. [11]. The total sum of extracted PLFAs (total PLFAs, μmol $(g\ OC)^{-1}$) was used to quantify microbial biomass. Gram-positive bacteria were estimated by the iso- and anteiso-branched saturated fatty acids (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0). The straight chain fatty acids (14:0,

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