



Original research paper

## Relative roles of competition, environmental selection and spatial processes in structuring soil bacterial communities in the Qinghai-Tibetan Plateau



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### ABSTRACT

The structure and dynamics of microbial communities may be influenced by environmental selection, spatial processes and competition. However, the relative strengths of these processes need to be further elucidated. Here, with a large scale sampling along an elevational gradient of 2000 m in the Qinghai-Tibetan Plateau, we examined the interplay among the three processes, as well as their relative importance to the biogeography of bacterial communities. Variation partitioning showed that environmental selection, competition and spatial variables jointly explained 37% of the total variation among the bacterial communities. The non-spatially structured environmental variables explained more variation than spatial distance or competition. Two environmental factors, elevation and soil pH, were shown to be the main cues determining soil bacterial communities. Environmental variables and spatial distance also exerted indirect effects on community variation via competition. The main conclusion of this study is consistent with the idea that “the environment selects”. Competition and spatial processes were less important in shaping bacterial communities of Qinghai-Tibetan Plateau.

### 1. Introduction

Elucidating the mechanisms that structure ecological communities has been a central theme in ecological and biogeographical research (Martiny et al., 2006; Heino et al., 2014). Ecological and bio-geographical patterns of animals and plants have attracted increasing interest in the last decade, but the distributions of microorganisms, which play key roles in all ecosystems, have been of interest only relatively recently. It was previously assumed that, due to large populations, small size, short generation time, and high dispersability, bacterial taxa are dispersed virtually everywhere (Martiny et al., 2006). However, with the advent of molecular techniques, a rapidly growing body of evidence suggests that bacterial distributions may be limited by dispersal and thus exhibit spatial patterns (Martiny et al., 2006).

Indeed, spatial processes generate and maintain microbial diversity

(Nekola and White, 1999; Papke and Ward, 2004; Horner-Devine et al., 2004). Niche-based processes become important when local environmental conditions determine the assembly of microbial communities: “Everything is everywhere, but the environment selects” (Baas-Becking, 1934). Niche-dependent diversity patterns of microbial communities have been widely observed. For example, salinity (Lozupone and Knight, 2007), pH (Fierer and Jackson, 2006; Rousk et al., 2010; Griffiths et al., 2011), C/N ratio (Bates et al., 2011) and the structure of the plant community (Lundberg et al., 2012) may be major determinants of microbial community structure. Studies have attempted to verify the relative importance of environmental variables (niche axes) and dispersal (deterministic versus stochastic processes) (Heino et al., 2014), or specify which factors exert the strongest influences on microbial communities in nature (Horner-Devine et al., 2004; Papke and Ward, 2004). Some studies have shown that environmental

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**Table 1**  
Brief description of the samples across different vegetation types in the Qinghai-Tibetan Plateau.

| Vegetation type                  | Location           | Elevation (m) | Sample No. | Dominant plant species   |
|----------------------------------|--------------------|---------------|------------|--|
| Gobi bare land (BA)              | 36.172°N, 94.768°E | 3089–3105     | 6          | <i>Sympegma regelii</i> Bunge;<br><i>Ephedra przewalskii</i> Stapf;<br><i>Reaumuria soongarica</i> (Pall.) Maxim.; |
| Alpine desert (AD)               | 35.886°N, 94.595°E | 3544–3564     | 9          | <i>Kalidium foliatum</i> (Pall.) Moq.;   |
| Alpine grassland (AG)            | 35.127°N, 93.043°E | 4243–4818     | 39         | <i>Reaumuria kaschgarica</i> Rupr.;  |
| Secondary alpine grassland (SAG) | 33.746°N, 92.145°E | 4576–4759     | 21         | <i>Leymus chinensis</i> (Trin. ex Bunge) Tzvelev;  |
| Alpine meadow (AM)               | 31.975°N, 91.524°E | 4526–4901     | 48         | <i>Salsola abrotanoides</i> Bunge;<br><i>Kalidium foliatum</i> (Pall.) Moq.;                                       |
| Meadow-grassland ecotone (MGE)   | 30.469°N, 91.093°E | 4296–4301     | 9          | <i>Krascheninnikovia ceratoides</i> (Linn.) Gueldenst.;  |
| Shrub grassland (SG)             | 30.041°N, 90.594°E | 4249–4567     | 18         | <i>Reaumuria kaschgarica</i> Rupr.;  |
|                                  |                    |               |            | <i>Leontopodium pusillum</i> (Beauv.) Hand.-Mazz.;   |
|                                  |                    |               |            | <i>Stipa purpurea</i> Griseb.;   |
|                                  |                    |               |            | <i>Potentilla bifurca</i> Linn.;   |
|                                  |                    |               |            | <i>Anemone imbricata</i> Maxim.;   |
|                                  |                    |               |            | <i>Potentilla fruticosa</i> var. <i>pumila</i> Hook. f.;   |
|                                  |                    |               |            | <i>Hippophae tibetana</i> Schldl.;   |
|                                  |                    |               |            | <i>Stellera chamaejasme</i> L.;  |
|                                  |                    |               |            | <i>Astragalus polycladus</i> Bur. et Franch.;  |
|                                  |                    |               |            | <i>Carex montis-everestii</i> Kükenth.;  |
|                                  |                    |               |            | <i>Kobresia littledalei</i> C. B. Clarke;  |
|                                  |                    |               |            | <i>Potentilla anserina</i> Linn.;  |
|                                  |                    |               |            | <i>Heteropappus semiprostratus</i> Griens.;  |

heterogeneity is the primary factor underlying microbial spatial differentiation (Nemergut et al., 2011), assuming similar microbial communities exist in similar environments. Others have shown that the similarity of communities could be explained by geographic distance rather than by environmental heterogeneity (Green and Bohannan, 2006). Even when environmental conditions are comparable across regions, a distance-decay relationship has emerged, which suggests a dispersal limitation (Langenheder et al., 2006; Lear et al., 2014).

Competition may also be an important force that influences community structure and dynamics (Mayfield and Levine, 2010). Ecologists appreciate that competition and environmental processes act simultaneously as suggested by the existence of trade-offs between stress tolerance and nutrient competition. However, little attention has been paid to the relative contributions of competition, abiotic factors and spatial processes. Phylogenetic approaches using a null community aim to separate the processes of competition and abiotic filtering (de Bello et al., 2012), the distinction of which is frequently fuzzy. For example, both abiotic environmental filtering and competition can result in phylogenetically clustered patterns (Goberna et al., 2014a), but such clustering has traditionally been ascribed to environmental filtering alone (Mayfield and Levine, 2010). For macroorganisms, Zhang et al. (2015) showed that competition was more important than regional climate in determining long-term changes in tree mortality. In a phylogenetic analysis of microbial communities, Goberna et al. (2014a) showed that competition was most important under high resource availability while abiotic filtering was most important during periods of high environmental stress. Thus, we examined the interplay among environmental filtering, spatial processes and competition, as well as their relative importance in shaping the biogeography of taxonomic structure of bacterial communities.

The Tibetan plateau is sometimes described as the “roof of the world”, characterized by harsh environmental conditions (e.g., high UV, low humidity, low oxygen tensions, etc.) and unique flora and fauna (Guo et al., 2011). In recent decades, this plateau has been threatened by climate change (Li and Tang, 1988; Klein et al., 2004; Déry and Brown, 2007) as shown by the reduction in alpine tundra area (Walker et al., 2001), accompanied by variation in both soil biogeochemical processes and the structures of various biological communities (Klein et al., 2004, 2007). However, little is known about the

geographic distribution of soil bacterial communities on the plateau, which are important for multiple ecosystem processes. In four mountainous grasslands on the plateau, the effects of climate change were determined using soil microbial structural genes (N and C-cycling genes) and space-for-time substitution (Yang et al., 2013). In another study the distributions of archaea and bacteria were reported to be mainly driven by soil geochemical factors such as pH and SOC across three Tibetan climatic zones (Wang et al., 2014). A baseline survey of soil bacterial distributions at a larger geographic scale would be extraordinarily valuable in understanding how climate change will alter several ecosystem functions in the Tibetan ecosystems.

In this study, we performed a baseline survey of bacterial communities of the Tibetan Plateau using high throughput sequencing. With these data we aimed to elucidate how environmental filtering, spatial process and biotic competition interplay to affect soil bacterial communities and to determine the relative importance of each of their contributions to community variation.

## 2. Materials and methods

### 2.1. Sampling description

This study was part of a comprehensive biodiversity investigation of the Tibetan Plateau. We established 22 transects from Golmud (94.89°E, 36.42°N) in Qinghai, to Lhasa (91.00°E, 29.60°N) in Tibet (elevation: 3000–4900 m; geographical distance > 1000 km), China. The transects covered seven vegetation types (Gobi desert, alpine desert, alpine grassland, secondary alpine grassland, alpine meadow, meadow-grassland ecotone, shrub grassland) of the Tibetan Plateau (Table 1 and Fig. 1). A total of 150 sampling sites were randomly chosen. The number of sampling sites per vegetation type is given in Table 1. At each of these sample sites, 1 m × 1 m sampling plots were established. Five soil cores (depth 40 cm, diameter 4 cm) were taken in each sampling plot and pooled to form a single independent sample in August 2013. The pooled soil samples were sealed in plastic bags and refrigerated, immediately transported to the laboratory and sieved to 2 mm to remove most roots and stones. Soil samples were preserved at –80 °C for molecular analysis. Sub-samples of each soil sample were collected and air-dried for physio-chemical analysis. The longitude,

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