ARTICLE IN PRESS

Applied Soil Ecology xxx (xxxx) xxx-xxx



Contents lists available at ScienceDirect

Applied Soil Ecology



journal homepage: www.elsevier.com/locate/apsoil

Biogeographical patterns of soil microbial community as influenced by soil characteristics and climate across Chinese forest biomes

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ARTICLE INFO

Keywords: Microbial biomass Soil microbial community structure Latitudinal variation Soil nutrient Climate Plant functional traits

ABSTRACT

Soil microorganisms form an important component of the Earth's biosphere and play an integral role in carbon, nitrogen and phosphorus cycling. Several biotic and abiotic factors affect the biogeographical distributions of soil microbial biomass (MB) and communities on geographical scales; however, the extent to which soil microbial communities are influenced by these factors is not yet clear. We examined and compared the biomass and structure of soil microbial communities within and between nine mature undisturbed forest ecosystems along the 3700-km North-South Transect in Eastern China (NSTEC). The results showed that soil MB and phospholipid fatty acids (PLFAs) increased with latitude. The structure of the microbial communities in warm temperate, subtropical and tropical forests. The mean annual temperature, soil organic carbon, soil total nitrogen and soil easily soluble phosphorus were the main predictors of latitudinal variance in the soil microbial communities. Soils within the same climatic types had similar properties, and soil MB and PLFAs seemed to change along gradients in the various forest types along the NSTEC. Microbial communities showed spatial traits and litter quality. The results suggested that soil microbes could improve the ecosystem models so that they simulate the microbial mechanisms of carbon (C) and nutrient cycling.

1. Introduction

Soil microorganisms play a pivotal role in the earth's biogeochemical cycles (Falkowski et al., 2008; Tu et al., 2016). While we know that soil microbial communities vary across geographical space, with possible consequences for geochemical cycling, we have limited information about the biogeographical distribution of these communities. It restricts our ability to simulate and predict the microbial mechanisms that control carbon (C), nitrogen (N) and phosphorus (P) cycling. As highlighted by Luo et al. (2016), information about the large-scale distributions and structures of soil microbial communities would help reduce the uncertainties associated with earth system models. We therefore need an improved appreciation of the spatial patterns of, and the factors that control, soil microbial biomass (MB) and communities (Balser and Firestone, 2005).

Microbial biomass, an important living part of soil organic matter, is mainly comprised of soil C and N. Numerous studies have confirmed that spatial variations in soil MB are the result of spatial heterogeneity in soil properties and climate conditions (Marinari et al., 2006; Xu et al., 2013). These spatial variations in soil MB among biomes reflect its ability to respond rapidly to environmental change (Marinari et al., 2006); for example, soil MB increases as latitude increases, and also as soil organic C density and below-ground plant biomass increase (Xu et al., 2013; Li et al., 2014). Soil MB mainly consists of bacteria, archaea and fungi with diameters of less than 500 µm. Different microbial species are involved in a range of ecosystem functions. For example,

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https://doi.org/10.1016/j.apsoil.2017.11.019

Received 19 June 2017; Received in revised form 13 November 2017; Accepted 19 November 2017 0929-1393/ © 2017 Elsevier B.V. All rights reserved.

most bacteria do not, but fungi do, exude enzymes for decomposing complex C compounds. Therefore, information about the spatial distribution of soil microbial biomass at the regional scale is needed to support examinations of soil microbial biogeography (Martiny et al., 2006) and for global nutrient cycling (Allison et al., 2010).

Similar to macro-organisms, soil microbes can be used as indicators of biogeography because of their diversity, functional traits, dispersal ability and density (Fierer et al., 2007; Tu et al., 2016; Zhou et al., 2016). For example, Tu et al. (2016) reported that the different forests along a latitudinal gradient harbored markedly different soil diazotrophic communities and that the biogeographic patterns of the soil communities resembled those of the plants and animals. The variations in the diversity and richness of soil bacterial communities along climatic gradients (Zhou et al., 2016) and between ecosystem types (Fierer and Jackson, 2006) also highlight spatial patterns in soil microbes. While earlier studies have highlighted variations in the structures of microbial communities with latitude (Zhou et al., 2008; Ghiglione et al., 2012; Tedersoo and Bahram, 2014), we still do not have a clear picture of how soil microbial communities vary along geographical gradients or which factors control geographical patterns at different scales. The structures of microbial communities are intimately linked to their roles in ecological processes, and these relationships are one of the central issues in ecological theory (Loreau et al., 2001; Talbot et al., 2014). With an improved understanding of the geographical patterns in the structures of soil microbial communities, we could predict the functional attributes or functional diversity of these soil microbial communities (Cao et al., 2016); this would represent an important step towards the development of a generalized framework for simulating and predicting microbial mechanisms that contribute to ecosystem functioning at the regional scale.

Spatial variations in soil microbial communities may be affected by biotic and abiotic factors (Fierer and Jackson, 2006; Cao et al., 2016). and the influences of these factors may vary at regional, continental and global scales (Tu et al., 2016). Previous studies reported that the composition and diversity of microbial communities were positively correlated with soil pH (Shen et al., 2013), carbon/nitrogen ratio (C/N) (Fierer and Jackson, 2006), multiple year mean annual temperatures (MAT) and precipitation (MAP) (De Vries et al., 2012; Tedersoo et al., 2012; Cao et al., 2016; Tu et al., 2016). Plant functional traits have also been reported to modify soil microbial communities by altering the quantity and quality of nutrient inputs (Orwin et al., 2010), and soil physical and chemical properties (Brussaard et al., 2007; Thoms et al., 2010). The LDMC and the leaf C/N ratio, combined with tree growth rates, had a positive influence on the abundances of specific microbial functional groups (Pei et al., 2016). However, most previous investigations of the relationships between plant functional traits and microbial communities have only considered a few plant species traits, so our understanding of the relative importance of the different traits is limited. The main controls on geographical patterns of soil microbes remain unclear, because, to date, few researchers have dealt adequately with the individual and interactive effects of climate, plant functional traits and soil substrate availability on soil microbial communities at the large scale.

The North-South Transect of Eastern China (NSTEC) extends from a cold-temperate coniferous forest in the north to a tropical rain forest in the south, and includes almost all forest types in the Northern Hemisphere (Zhang and Yang, 1995) (Fig. 1 and Table 1). This transect therefore provides the optimal setting for investigations of geographical patterns of microbial communities and their responses to environmental change at the large scale. In this study, we determined the compositions of soil microbial communities using phospholipid fatty acids (PLFAs) and examined the effects of climate, soil conditions, plant functional traits and litter properties on the structures of soil microbial communities across nine mature undisturbed forest ecosystems at different latitudes along the 3700-km NSTEC. The aims of this study were to determine (1) the latitudinal patterns of soil MB and different groups

of microbial PLFAs; and (2) the relationships between climate, soil properties, plant functional traits, litter properties and microbial PLFA biomass at the large scale.

2. Materials and methods

2.1. Study area

The NSTEC is the 15th standard transect of the International Geosphere-Biosphere Program (IGBP). It extends from Hainan Island in the south to the northern border of China, and includes 25 provinces and approximately 1/3 of China. Because of the influence of the eastern Asian monsoon, the climate along the NSTEC differs from the climates experienced at similar latitudes in Europe and North America, and is characterized by clear latitudinal gradients in temperature and precipitation. Different types of zonal forest ecosystems are distributed along the NSTEC from north to south, including cold-temperate coniferous forests, temperate mixed forests, warm-temperate deciduous broad-leaved forests, subtropical evergreen broad-leaved forests and tropical monsoon rainforests (Zhang and Yang, 1995; Yu et al., 2006).

We selected nine forest ecosystems along the NSTEC, namely Huzhong (HZ), Liangshui (LS), Changbai (CB), Dongling (DL), Taiyue (TY), Shennong (SN), Jiulian (JL), Dinghu (DH) and Jianfeng (JF) (18°44′-51°46′ N, 128°53′-108°51′E) (Fig. 1, Table 1). Together, they span 33° of latitude from 18 to 51 °N and extend over a distance of more than 3700 km. These ecosystems represent the primary zonal forest ecosystems in China, i.e. temperate coniferous forest, broad-leaved Korean pine forest, deciduous broad-leaved forest, evergreen broadleaved forest, monsoon evergreen broad-leaved forest and tropical rain forest. Our study forests were natural and had not been subjected to logging or harvesting activities in the last hundred years. According to the U.S. soil taxonomy, the main soils in the forests were Spodosols (HZ), Albi-Boric Argosols (LS and CB), Alfisols (DL and TY), Inceptisols (SN) and Ultisols (JL, DH and JF) (Table 1, Soil Survey Staff, 2010). The soils in HZ, LS, CB and TY were silt; those in SN, JL, DH and JF were silt loams, and the soil in DL was sandy loam (Soil Survey Staff, 2010).

2.2. Soil sampling

Soil samples were collected from four random plots in each study site in July and August 2013. The plots measured 30 \times 40 m, and were separated from adjacent plots by a 10 m buffer zone. The four plots at each site had identical vegetation. Mineral soil samples were collected from the soil surface (up to 10 cm deep) at between 30 and 50 points in each plot along an S-shape using a coring device with a diameter of 6 cm. The above-ground standing biomass, dead plant parts and litter were removed from each sampling point before extracting the sample. The soil samples from each plot were pooled together as a composite sample. Visible roots and residues were removed before the fractions of each sample were homogenized. We stored the samples at 4 °C in a portable refrigerator during field sampling. Once back at the laboratory, the fresh soil samples were immediately sieved through a 2-mm mesh and were subdivided into two subsamples. One subsample was stored briefly at 4 °C until analysis for soil physical and chemical properties. Another was stored briefly at -20 °C until analysis for phospholipid-derived fatty acids (PLFAs).

2.3. Soil analyses

2.3.1. Soil chemical analyses

Soil pH was measured on a soil to water suspension at a ratio of 1:2.5 *v*:*v* using a pH digital meter (Iovieno et al., 2010). Soil moisture (SM) was measured gravimetrically on 20 g of fresh soil that had been oven-dried at 105 °C to constant weight as soon as we returned to the laboratory. Soil temperature (ST) was measured *in situ* with a rectangular geo-thermometer. Soil organic carbon (SOC), total N (TN), litter

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