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In-depth analysis of core methanogenic communities from high elevation permafrost-affected wetlands

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ABSTRACT

The organic carbon of permafrost affected soils is receiving particular attention with respect to its fate and potential feedback to global warming. The structural and activity changes of methanogenic communities in the degrading permafrost-affected wetlands on the Tibetan Plateau can serve as fundamental elements for modelling feedback interaction of ecosystems to climate change. Hence, we aimed at anticipating if and how the rapid environmental changes occurring especially on the high altitude Tibetan platform will affect methanogenic communities. We identified methanogenic community composition, activity and abundance in wetland soils with different hydrological settings, permafrost extent and soil properties and pinpoint the environmental controls. We show that despite a pronounced natural gradient, the Tibetan high elevation wetland soils host a large methanogenic core microbiome. Hydrogenotrophic methanogens, in particular *Methanoregula*, and H_2-dependent methanogenesis were overall dominant although acetoclastic methanogens in addition to hydrogenotrophs were among the dominating taxa in a minerotrophic fen. Tracing the *Methanoregula* community of the Tibetan Plateau using public databases revealed its global relevance in natural terrestrial habitats. Unlike the composition, the activity and abundance of methanogens varied strongly in the studied soils with higher values in alpine swamps than in alpine meadows. This study indicates that in the course of current wetland and permafrost degradation and the loss in soil moisture, a decrease in the methane production potential is expected on the high Tibetan Plateau but it will not lead to pronounced changes within the methanogenic community structure.

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1. Introduction

The Qinghai-Tibet Plateau (QTP), also known as Tibetan Plateau, is the largest altitudinal permafrost unit on Earth. The lower elevation areas (<4000 m) are influenced by seasonally frozen ground, while on the high altitude plateau permafrost is more developed in depth, continuity and coverage (Zhou et al., 2000). The plateau is warming at a rate approximately two times higher than the global average since the 1950s (IPCC, 2007), and even faster at higher elevations (Wei and Fang, 2013). Permafrost degradation has occurred on the plateau during the last few decades, manifested by areal decrease of continuous and discontinuous permafrost, thinning of permafrost, shrinkage of isolated patches of permafrost and changes into seasonally frozen ground (Cheng and Wu, 2007; Jin et al., 2009; Wu et al., 2015). Around 18.6% of its permafrost has degraded in the past 30 years and up to 46% permafrost will disappear in 100 years (Cheng and Wu, 2007; Cheng and Jin, 2013). Degradation of permafrost has led to a

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lowering of ground water levels, shrinking lakes and wetlands, and changes of grassland ecosystems from alpine meadows to steppes (Jin et al., 2009; Cheng and Jin, 2013).

Besides rivers and lakes, wetlands such as alpine swamps and meadows are fed mainly through precipitation and occur together with frozen ground. Alpine swamps and meadows occupy a large area of the eastern plateau (Zhou et al., 2000; Wang et al., 2016). While water in alpine meadows flows slowly through shallow flooded zones, the water in swamps is typically stagnant (Wang et al., 2016). The Tibetan wetlands altogether occupy 50% of the total wetland area of China (Ding and Cai, 2007), with the majority (85%) distributed in the headwater regions of the Yangtze and Yellow Rivers at higher elevations (>4000 m) and the Zoige (Ruoergai) Peat Plateau at lower altitudes (<4000 m; Zhang et al., 2011). It was estimated that 7.4 Pg C was stored at the top one meter of the whole alpine grasslands (Yang et al., 2008). Although there is no specific carbon estimate for the Tibetan wetlands, the soil organic density of wetlands was in general far higher than that of the alpine steppe and of the plateau's average, highlighting the alpine wetlands as important carbon pool with the potential for positive climate feedback (Ding and Cai, 2007; Yang et al., 2008; Ding et al., 2016). As a result of climate warming and permafrost degradation, the area of Tibetan wetlands reduced by about 8% from 1970 to 2006 (Zhao et al., 2015). Due to hydrological deterioration, degeneration from wetlands to meadows or from meadows to steppes have been observed at local scales (Jin et al., 2009; Brierley et al., 2016), which has subsequently impaired their roles in regulating the flow of rivers and carbon stores (Cheng and Jin, 2013).

The greenhouse gas methane is a major end product of the microbial degradation of organic matter under anaerobic conditions. Wetlands contribute 70% to the global total emission of methane and therefore are a major research focus (Bridgham et al., 2013). Moreover, ice core records showed that the variations in the atmospheric CH_4 content were consistent with the areal change of wetlands (Blunier et al., 1995). The methane fluxes on the Tibetan wetlands range from 9.6 to 214 mg CH_4 m^{-2} d^{-1} (Jin et al., 1999; Hirota et al., 2004; Cao et al., 2008; Chen et al., 2013) and are generally comparable to Arctic permafrost regions (Wille et al., 2008; Sachs et al., 2010; also see Fig. S1). Both alpine swamps and meadows are thus potential hotspot of methane emission on the plateau.

Methanogenic archaea (methanogens) are responsible for the biological production of methane (methanogenesis). They commonly use H_2/CO_2 (hydrogenotrophic) and acetate (acetoclastic) as substrates under anaerobic conditions (Wagner and Liebner, 2009). Methanogens on the Tibetan Plateau were studied in lakes (Liu et al., 2013) and wetland soils (Zhang et al., 2008; Deng et al., 2014; Cui et al., 2015; Tian et al., 2015). Most previous studies on wetlands were confined to the Zoige Plateau on the eastern margin of the plateau at lower elevation (3400–3600 m a.s.l.). In this region methanogenic community structure, in contrast to methane production, is little responsive to temperature increase and seasonal change (Cui et al., 2015). Methanogenic communities on swamps and meadows at the high plateau platform (>4000 m), however, remain poorly investigated despite their supposedly large relevance for the greenhouse gas (GHG) budget of the entire Tibetan Plateau. Also, anticipating if and how the rapid environmental changes presently occurring on the high Tibetan altitude platform will propagate into methanogenic communities is important.

This study is based on the assumption that methanogenic archaea respond to permafrost degradation, shrinkage of wetlands and extension of meadows. We expect that meadows differ from wetlands in displaying lower methanogenic activities and abundances, and significantly different composition in methanogenic communities. The objective of this research is to identify methanogenic community composition, activity and abundance in wetland soils with different hydrological settings (swamp and meadow), permafrost extent and soil properties, and to pinpoint the underlain environmental controls. Thereby, this study is the first to assess methanogenic communities on the Tibetan Plateau via deep sequencing on the functional gene of methanogenesis (methyl coenzyme M reductase A, *mcrA*) with a specific attention on the direct and indirect interactions between microbial taxa coexisting in the environment.

2. Material and methods

2.1. Study site and sample collection

The study sites on the northeastern Tibetan Plateau were selected along the air mass trajectory of the eastern Asian monsoon, by taking account of frozen ground, elevation and hydrology. Four sites were sampled in August 2012 when the active layer reached its maximum thaw depth: Huashixia (HUA), Donggi Cona Lake (DCL), Gande (GAN), and Haibei Station (HAI; Fig. 1). The variability of soil properties between each site was analyzed through a principal component analysis (PCA). Three of the sites are located above 4000 m while HAI is located at an elevation of approximately 3200 m similar to the Zoige wetland. HUA and DCL are located in the discontinuous permafrost region, whereas GAN and HAI are underlain by seasonally frozen ground (SFG). The sites DCL and HAI are swamp wetlands, while GAN and HUA are alpine meadows. For each research site, a series of soil profiles were described along an elevation gradient. The description of the HUA catena has been published recently (Dörfer et al., 2013). Of each catena, the profile which was most relevant for methanogenesis in terms of water level and soil moisture was selected for this study.

The DCL profile is located on a lakeshore wetland which derived from aeolian sediments. The sampling site at HUA is located on a patch of an alpine meadow near the Huashixia Permafrost Station. Laminated sandy or clayish sediments in yellowish and greyish were visible at this site where the discontinuous permafrost starts approximately at 80 cm below the surface. According to the Maduo climate station (98°12′ E, 34°54′ N, 4300 m a.s.l.) monitoring between 1953 and 2010, the mean annual air temperature (MAAT) near DCL and HUA is −4.1 °C with a mean annual precipitation (MAP) of 326 mm and most precipitation occurring in summer (280 mm, May to October). The GAN site is close to a small creek in a valley which is affected by deep seasonally frozen ground. The soil texture mainly consists of silt and clay. The MAAT at the GAN site is −2.2 °C, and the monthly average air temperature ranges from −15.2 °C (January) to 8.6 °C (July), with a MAP of around 550 mm in the period 1994 to 2010. Site HAI is a swamp affected by seasonally frozen ground where peat layer is visible in the entire profile. The MAAT at the Haibei weather station (37°29' - 37°45′N, 101°12' - 101°23′E, 2900–3500 m a.s.l.) is −1.7 °C with a maximum of 27.6 °C and a minimum of −37.1 °C in the period from 1989 to 2010. The MAP is around 500 mm with 80% within the growing season from May to September. The vegetation is generally dominated by sedges (*Kobresia* and *Carex*) with different coverage and density over different study sites.

At all study sites, soil profiles were excavated down to the permafrost table (approx. 50–70 cm) or to the water table (approx. up to 200 cm). After soil profile description, soil samples were taken in parallel for DNA extraction, methane production incubation and soil property analysis from the middle of each horizon. The samples were labeled with starting site name followed by increasing numbers indicating horizons from top to bottom, e.g.

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