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Increasing aridity affects soil archaeal communities by mediating soil niches in semi-arid regions

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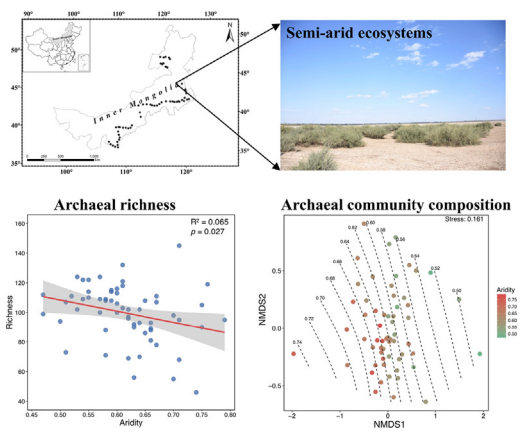
HIGHLIGHTS

- Increasing aridity diminished archaeal richness through improving soil electrical conductivity.
- Different archaeal taxa were present with different levels of aridity.
- Archaeal communities were mainly governed by niche-based processes along the aridity gradient.
- Increasing aridity altered archaeal community composition by changing soil total nitrogen.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil archaea plays a vital role in the functioning of dryland ecosystems, which are expected to expand and get drier in the future as a result of climate change. However, compared with bacteria and fungi, the impacts of increasing aridity on archaea in these ecosystems remain largely unknown. Here, soil samples were collected along a typical aridity gradient in semi-arid regions in Inner Mongolia, China, to investigate whether and how the increasing aridity affects archaeal communities. The results showed that archaeal richness linearly decreased with increasing aridity. After partialling out the effects of soil properties based on partial least squares regression, the significant aridity-richness relationship vanished. The composition of archaeal communities was distributed according to the aridity gradient. These variations were largely driven by the changes in the relative abundance of *Thaumarchaeota*, *Euryarchaeota* and unclassified phyla. Niche-based processes were predominant in structuring the observed archaeal aridity-related pattern. The structural equation models further showed that aridity indirectly reduced archaeal richness through improving soil electrical conductivity (EC) and structured community composition by changing soil total nitrogen (TN). These results suggested that soil salinization and N-losses might be important mechanisms underlying the increasing aridity-induced alterations in archaeal communities, and highlighted the importance of soil niches in mediating the indirect impacts of increasing aridity on archaea.

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1. Introduction

Drylands, including arid, semi-arid and dry-subhumid ecosystems, cover approximately 41% of Earth's land surface with over 38% of the global human population inhabited (Reynolds et al., 2007), and are supposed to be the most susceptible ecosystems to climate change (Maestre et al., 2012). As a consequence of climate-change-driven increases in temperature and frequency of drought events (Easterling, 2000), these areas will experience increasing aridity in the future as forecasted by climate models (Collins et al., 2014; IPCC, 2013). Microbial communities play key roles in soil nutrient cycles (Bardgett and van der Putten, 2014) that are tightly linked to many crucial ecosystem functioning based on plant productivity and soil fertility (Delgado-Baquerizo et al., 2014; Lamarque et al., 2011). Assessing their responses to increasing aridity is of particular importance for predicting alterations in ecosystem functioning under future climate scenarios and developing effective management strategies.

It used to be thought that archaea were only present in extreme environments, but growing evidence indicates that archaea are diverse and widespread on Earth (Schleper et al., 2005). Recently, the archaeal tree has been rapidly expanded with the discovery of new archaeal lineages at different taxonomic levels (Adam et al., 2017). Their crucial roles in mediating biogeochemical processes, such as breakdown of organic matter (Yu et al., 2018), sulfate reduction (Sorokin et al., 2017) and ammonia oxidation (Sauder et al., 2017) have also been well recognized in a wide range of ecosystems. Similarly to soil bacteria and fungi, archaea are also significant or even major components of belowground diversity (Chaban et al., 2006; Angel et al., 2010) and they are altogether responsible for nutrient cycles in terrestrial ecosystems (Kirk et al., 2004; Siles and Margesin, 2016). More importantly, archaeal populations such as ammonia-oxidizing archaea (AOA) preserve a high level of activity (Martens-Habbena et al., 2009; Verhamme et al., 2011) and are more responsible for nitrogen cycle in drylands (Adair and Schwartz, 2008; Valentine, 2007).

Despite the significance of soil archaea, previous studies conducted to determine the effects of increasing aridity on soil microbes have largely focused on bacteria and fungi. It is clear that soil bacteria and fungi respond to increasing aridity in terms of diversity, abundance, biomass and community composition (Chen et al., 2015; Fierer et al., 2012; Hu et al., 2014; Wang et al., 2015), and that aridity promotes these shifts by its effects on plant (Chen et al., 2015) or soil properties (Maestre et al., 2015; Yao et al., 2017). Compared to them, variations in soil archaeal communities resulting from increasing aridity have received much less attention. Limited studies reported that aridity was a significant factor influencing archaeal community composition (Angel et al., 2010; Shi et al., 2016; Wang et al., 2015) and taxa abundance such as *Thaumarchaeota*, *Crenarchaeota* (Auguet et al., 2010; Neilson et al., 2017), and *Euryarchaeota* (Auguet et al., 2010). For patterns of archaeal diversity, however, contradictory results have emerged from different works. Wang et al. (2015) reported that archaeal diversity was greatest in the driest regions, while Angel et al. (2010) proposed that archaeal diversity was not constrained by precipitation. These inconsistent results might be derived from molecular technology adopted in their studies either were low-resolution (Angel et al., 2010) or yielded relatively small numbers of reads (Wang et al., 2015). The lack of taxonomic resolution and precision might hamper the ability to disclose the specific taxa contributing to the observed community differentiation (Fortunato et al., 2013). In addition, although it has been broadly recognized that the niche-based processes and neutral processes simultaneously drive the microbial distribution patterns (Dumbrell et al., 2010; Langenheder and Székely, 2011), their relative influences vary across spatial and temporal scales (Stegen et al., 2012). To date, the primary ecological processes that govern the spatial variation in archaeal community composition along a large-scale aridity gradient have not been addressed.

Understanding the impacts of increasing aridity on soil archaea and the mechanisms underlying those impacts will allow us to better predict ecological systematic responses to climate change in a more holistic view of soil microbes. In this study, we examined whether and how increasing aridity affects archaea along a 1500 km aridity gradient in semi-arid regions in Inner Mongolia, China, which is characterized by contrasting aridity from west to east. A total of 60 samples were collected and high-throughput sequencing with focus on archaeal communities was performed to provide a higher resolution analysis. We hypothesized that (1) there would be a significant aridity-related pattern of archaeal diversity and community composition along the aridity gradient, which are mainly caused by the indirect effect of aridity; (2) there would be some specific taxa that are responsible for the increasing aridity-induced alterations in archaeal communities.

2. Materials and methods

2.1. Study area and sample collection

The current study was carried out in the Inner Mongolia in northern China, with an area of 1.18 million km^2 (Bai et al., 2008). This region is characterized by strong climate gradients (Liu et al., 2008) and provides ideal sites to examine how increasing aridity affects soil archaea. Thus, a 1500 km transect was established in this study, covering a longitude from 107.23 to 122.41°E and a latitude from 37.69 to 49.25°N (Fig. S1). The transect experienced semi-arid continental climate with limited precipitation and the aridity index (AI, the ratio of annual precipitation to annual potential evapotranspiration) ranging from 0.21 to 0.53. The sample collection took place from middle September to early October in 2016, and a total of 60 sites were selected through the entire transect (Fig. S1). The latitude and longitude for each site were recorded using a GPS device during the field work. Soil types of the study sites were arid, sandy, and belonged to desert soils (Bai et al., 2008; Wang et al., 2014). The ground surfaces were characterized by sparse shrubs (*Caragana microphylla Lam.*, *Artemisia ordosica* or *Salix psammophila*) and grasses (*Leymus chinensis*). At each site, an 8 m × 8 m large plot representative of the landscape and dominant vegetation was established. In order to facilitate the comparison between sites with different dominant vegetation, five 0.5 m × 0.5 m quadrats were then randomly placed in bare ground areas within each large plot as previously depicted by Bachar et al. (2010). In each quadrat, random soil samples (0–10 cm) were collected after removing litter and then were mixed thoroughly. Five soil subsamples collecting from quadrats in the same plot were pooled together and homogenized to make a composite sample and were passed through a 2 mm mesh for removing gravel and roots in the field. All soil samples were divided into two parts and sealed in sterilized sampling bags. One part was placed on ice, returned to laboratory as soon as possible and stored at −80 °C until DNA extraction. The other part was transported at ambient temperature and was used immediately for soil properties measurements upon arrival.

2.2. DNA extraction, Illumina sequencing and sequence analysis

The Power soil DNA Kit (MO BIO, Carlsbad, CA, USA) was used to extract total microbial DNA from 0.25 g soil per sample following the manufacturer's recommended instructions. The concentration and purity of the extracted DNA was assessed spectrophotometrically (Nanodrop2000, Thermo Scientific, Waltham, USA). The DNA of high quality was used for polymerase chain reaction (PCR) with the archaeal primer sets 524F10extF 5′-GYCAGCCGCCGCGGTAA-3′ and Arch958RmodR 5′-YCCGGCGTTGAVTCCAATT-3′ (Pires et al., 2012). PCR amplification was individually conducted for each DNA sample in 20-μL volumes including 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM deoxynucleoside triphosphate (dNTP) mix, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase (TeansGen), 0.2 μL of bovine serum albumin (BSA), 10 ng of template DNA and double-distilled H_2O. The PCR