Continental-scale niche differentiation of dominant topsoil archaea in drylands

Running title: Topsoil archaeal niche differentiation in drylands

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Summary

Archaea represent a diverse group of microorganisms often associated with extreme environments. However, an integrated understanding of biogeographical patterns of the specialist *Haloarchaea* and the potential generalist ammonia-oxidizing archaea (AOA) across large-scale environmental gradients remains limited. We hypothesize that niche differentiation determines their distinct distributions along environmental gradients. To test the hypothesis, we use a continental-scale research network including 173 dryland sites across northern China. Our results demonstrate that *Haloarchaea* and AOA dominate topsoil archaeal communities. As hypothesized, *Haloarchaea* and AOA show strong niche differentiation associated with two ecosystem types mainly found in China’s drylands (i.e., deserts vs. grasslands), and they differ in the degree of habitat specialization. The relative abundance and richness of *Haloarchaea* are higher in deserts due to specialization to relatively high soil salinity and extreme climates, while those of AOA are greater in grassland soils. Our results further indicate a divergence in ecological processes underlying the segregated distributions of *Haloarchaea* and AOA. *Haloarchaea* are governed primarily by environmental-based processes while the more generalist AOA are assembled mostly via spatial-based processes. Our findings add to existing knowledge of large-scale biogeography of topsoil archaea, advancing our predictive understanding on changes in topsoil archaeal communities in a drier world.

Originality-Significance Statement

This work contributes to the current limited understanding on the large-scale biogeography of *Haloarchaea* and ammonia-oxidizing archaea (AOA) in drylands. Our study is original and significant, as it reveals a strong niche differentiation between these two dominant topsoil archaeal groups, primarily driven by habitat specialization associated with contrasting ecosystem types (i.e., deserts and grasslands) rather than small-scale microsites (i.e., bare ground and vegetated areas). Moreover, this work also provides new insights into the community assembly processes underpinning the distinct biogeographical patterns of *Haloarchaea* and AOA. It reveals that the distribution of *Haloarchaea* is mainly determined by environmental-based processes, while AOA are more influenced by spatial-based processes. These observations are important to understand future changes in key soil microbial taxa in drylands under climate change.

Introduction

Archaea is one of the most abundant and diverse groups of organisms on Earth, which can colonize a wide range of environments (Chaban *et al*., 2006). Moreover, there is a growing appreciation of the astonishing diversity, life history, and metabolic versatility of archaea, as well as their contributions to global biogeochemistry, particularly the carbon (C) and nitrogen (N) cycles (Offre *et al*., 2013; Baker *et al*., 2020). Despite their ecological importance, however, biogeographical patterns of archaea at large spatial scales remain relatively unexplored, particularly compared with those of bacteria and fungi. This limit of knowledge is therefore hampering our understanding of their ecology in natural ecosystems.

Previous large-scale studies on bacterial and fungal biogeography have collectively shown that diversity and community composition of these organisms are strongly partitioned by ecosystem types, biomes or geographic regions associated with particular environmental conditions. That is, there is a strong role for niche differentiation, which can be attributed to environmental filtering and/or biotic interactions (Fierer and Jackson, 2006; Lozupone and Knight, 2007; Tedersoo *et al*., 2014; Bahram *et al*., 2018; Delgado-Baquerizo *et al*., 2018; Egidi *et al*., 2019). Strong evidence, from experimental work and local studies, also support the existence of distinct adaptive strategies and metabolic lifestyles within contrasting archaeal types (Walsh *et al*., 2005; Jiang *et al*., 2007; Ke *et al*., 2014; Rath *et al*., 2019). However, empirical evidence from environmental gradients at large spatial scales is still limited.

We posit that niche differentiation can explain the distinct distributions of archaeal groups with contrasting traits (e.g., specialists vs. generalists) across large-scale environmental gradients (Barberán *et al*., 2012). For example, *Haloarchaea* are well-known specialist archaea inhabiting a specific and restricted range of environmental conditions (Auguet *et al*., 2010). Conversely, ammonia-oxidizing archaea (AOA) affiliated with the phylum *Thaumarchaeota* represent one of the most abundant and ubiquitous groups of archaea dominating most soil and aquatic systems (Francis *et al*., 2005; Leininger *et al*., 2006; Auguet *et al*., 2010; Bates *et al*., 2011). In particular, AOA have been suggested to be resistant to conditions of low energy availability (e.g., water and nutrient) such as those often found in arid ecosystems (Valentine, 2007; Adair and Schwartz, 2008; Bates *et al*., 2011; Trivedi *et al*., 2019). As such, AOA appear to be generalist archaea showing broader environmental tolerances than *Haloarchaea* (Erguder *et al*., 2009). Recent studies provide evidence for niche differentiation between AOA and their bacterial counterparts (ammonia-oxidizing bacteria; AOB) in dryland soils driven by the presence of perennial plants (Delgado-Baquerizo *et al*., 2013a; Trivedi *et al*., 2019), yet whether niche partitioning also occurs between AOA and *Haloarchaea* remains poorly understood.

Given the ecological significance of *Haloarchaea* and AOA, a comprehensive investigation of the ecological preferences of these archaeal groups across large-scale natural ecosystems is needed. We argue that *Haloarchaea* and AOA may differ in niche breadth and thus should show contrasting distributions across large-scale environmental gradients. *Haloarchaea*, as specialists, are expected to thrive in the extremes of environmental gradients, leading to restricted distributions as previously observed in communities of plants (Berdugo *et al*., 2019), invertebrates (Pandit *et al*., 2009), birds (Devictor *et al*., 2008), and bacterioplankton (Logares *et al*., 2013). In contrast, AOA are expected to be generalists with greater niche breadth. This is further expected to cause a tradeoff such that AOA are relatively weak competitors under environmental conditions where *Haloarchaea* are favoured, but AOA may inhabit a larger habitat range than *Haloarchaea* (*sensu* Fournier *et al*., 2020). However, given that AOA can tolerate a wide range of environmental conditions (Erguder *et al*., 2009) and are likely to coexist with *Haloarchaea* in some local environments (Auguet *et al*., 2010; Shi *et al*., 2016; Rath *et al*., 2019), it is not immediately clear how the biogeographies of these two archaeal groups will be related to each other across large-scale environmental gradients.

To test the hypotheses stated above, we use a continental-scale research network including 173 dryland sites across northern China (Fig. S1). These study sites cover > 3 500 000 km^2 and span a distance of 4 000 km from northeast to northwest of China, representing a wide range of environmental gradients including plant attributes, climatic conditions, and soil properties (Hu *et al*., 2021). Drylands across northern China are highly heterogeneous environments that are typically formed by two major ecosystem types (i.e., deserts and grasslands) (Chinese Academy of Sciences, 2001) (Fig. S1).

Several previous studies have suggested that ecosystem type plays a crucial role in structuring the composition of soil microbial communities from local to global scales (Bates *et al*., 2011; Chu *et al*., 2011; Griffiths *et al*., 2011; Delgado-Baquerizo *et al*., 2018; Egidi *et al*., 2019). Different ecosystem types reflect different environmental conditions; most directly relevant to the questions herein, the transitions from grasslands to deserts may represent an increase in the degree of habitat specialization of soil archaeal communities (Fig. S2). Specifically, deserts are generally considered as more extreme ecosystems that have higher soil salinity and pH and their climates are characterized by higher temperature and aridity and lower precipitation, as compared to grasslands. We therefore posit that niche differentiation between *Haloarchaea* and AOA in drylands across northern China is associated with ecosystem type (Fig. S2). More specifically, *Haloarchaea* are expected to be specialized to thrive in more extreme desert ecosystems but have a more restricted distribution in grasslands. Hence, we expect a stronger influence of environmental-based processes (e.g., environmental selection) over *Haloarchaea* (Pandit *et al*., 2009; Logares *et al*., 2013; Liao *et al*., 2016). Conversely, AOA are expected to be found in both deserts and grasslands but prefer the latter in which fitness advantages of *Haloarchaea* are largely reduced. Here, a stronger role of spatial-based processes (e.g., probabilistic dispersal) is expected because AOA, as generalists, are thought to be less influenced by environmental selection (Pandit *et al*., 2009; Langenheder and Székely, 2011; Liao *et al*., 2016) (Fig. S2). The coexistence of these two distinct ecosystem types in China's drylands provides a unique opportunity to test our hypotheses under field conditions, and to address a critical research gap in microbial ecology.

Results

Taxonomic composition of topsoil archaea

After correcting for the differences in sequencing depth, we retained 1 871 archaeal operational taxonomic units (OTUs). *Haloarchaea* and *Thaumarchaeota* dominated the topsoil archaeal communities in drylands across northern China, together accounting for 57% of the OTUs and 89% of 16S rRNA gene sequences (Fig. 1a). *Thermoplasmata*, deep-sea hydrothermal vent *Euryarchaeota* group (DSHVEG) and *Nanohaloarchaeota* were relatively diverse, encompassing between 4.5 and 22% of the OTUs, but less abundant (~10.5% of the sequences). Other high-rank archaeal taxa, including *Methanomicrobia*, *Lokiarchaeota*, *Aenigmarchaeota*, *Bathyarchaeota*, *Archaeoglobi* and *Methanobacteria*, represented a minor fraction of the archaeal communities

(~1.5% of the OTUs and < 0.05% of the sequences).

Haloarchaeal OTUs can be assigned to three major orders, with *Halobacteriales* being most abundant, followed by *Natrialbales* and *Haloferacales* (Fig. 1b,c). Thaumarchaeotal OTUs fell into three identifiable orders belonging to three AOA lineages: *Nitrosopumilales* of Group I.1a, *Nitrososphaerales* of Group I.1b, and *Nitrosocaldales* of HWCG-III, among which *Nitrososphaerales* accounted for > 99.9% of thaumarchaeotal sequences (Fig. 1b,c). Our network analyses showed that haloarchaeal and thaumarchaeotal OTUs tended to co-occur with others belonging to the same taxa and generated two independent clusters that had extremely few connections with each other (Figs. 1d, S3). Such a contrasting co-occurrence pattern indicates that OTUs affiliated with these two dominant archaeal taxa may differ in ecological preferences.

Niche breadth and ecological distributions of Haloarchaea and Thaumarchaeota

Both the Levins' index and the tolerance index were significantly higher for thaumarchaeotal OTUs than those of *Haloarchaea* (Mann-Whitney U test, both $P < 0.001$; Fig. 2a,b). Moreover, both the relative abundance and richness of *Haloarchaea* were much higher in deserts than in grasslands (Mann-Whitney U test, both $P < 0.001$; Fig. 2c–f). Conversely, *Thaumarchaeota* were distributed widely in both deserts and grasslands, but were more abundant and diverse in the latter (Mann-Whitney U test, both $P < 0.001$; Fig. 2c,d,g,h). Consistent results were observed for the sub-dataset (i.e., study sites without missing environmental data; see also Experimental Procedures) (Mann-Whitney U test, all $P < 0.01$; Fig. S4).

To ensure that merging data across vegetated and non-vegetated microsites (i.e., vegetated areas and bare ground; see also Experimental Procedures) was not influencing our results, we examined the niche breadth of *Haloarchaea* and *Thaumarchaeota* for these two potentially different niches separately. Further, we compared both the relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* between the two microsites. Our results showed consistently higher values of the Levins' index and the tolerance index for *Thaumarchaeota* than those of *Haloarchaea* in both the microsites (Mann-Whitney U test, all $P < 0.001$); however, the two indices had no differences between vegetated and bare ground microsites for both the archaeal groups (Mann-Whitney U test, all $P > 0.05$) (Fig. S5). Moreover, we also showed similar relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* between vegetated areas and bare ground (Mann-Whitney U test, all $P > 0.05$; Fig. 2c,d,i–l). The similarities in both niche breadth and distribution patterns across the two microsites can be, at least partially, attributed to the relatively homogeneous soil properties and nutrient contents between the microsites (Fig. S6).

Environmental predictors of distributions of Haloarchaea and Thaumarchaeota

Random forest models identified electrical conductivity, a common indicator of salinity (soil dissolved salt), as the most important and significant predictor for the distributions of *Haloarchaea* and *Thaumarchaeota* (Fig. S7). Ecosystem type (deserts = 1 vs. grasslands = 0) was also identified as a major predictor in all models. Partial Spearman's correlations further confirmed positive relationships between ecosystem type and the relative abundance and richness of *Haloarchaea* after controlling for spatial influences (Fig. 3). Accordingly, we also found negative relationships of ecosystem type with both thaumarchaeotal attributes. Given that deserts (4576.2 ± 1594.3 μS cm^{-1}; $N = 82$) had a significantly higher soil electrical conductivity than grasslands (300.4 ± 112.2 μS cm^{-1}; $N = 51$) (Fig. S8), our results indicated that changes in soil salinity associated with different ecosystem types largely explain the changes in the large-scale distribution patterns of *Haloarchaea* and *Thaumarchaeota* (Fig. 3). Similarly, higher relative abundance and richness of *Thaumarchaeota* in grasslands could be partially attributed to grassland soils having relatively higher total N [0.22 ± 0.02 g kg^{-1} ($N = 82$) and 1.47 ± 0.18 g kg^{-1} ($N = 51$) for deserts and grasslands, respectively] and ammonium [3.11 ± 0.59 mg kg^{-1} ($N = 82$) and 4.76 ± 0.51 mg kg^{-1} ($N = 51$) for deserts and grasslands, respectively] —in these nutrient poor ecosystems—, and plant species richness [5.5 ± 0.5 ($N = 82$) and 24 ± 2 ($N = 51$) for deserts and grasslands, respectively] (Figs. S8, S9). These three variables all showed positive associations with thaumarchaeotal richness and relative abundance, which is likely due to the direct mechanistic connection *Thaumarchaeota* have with N cycling (Fig. 3).

Furthermore, the contrasting distribution patterns of *Haloarchaea* and *Thaumarchaeota* between deserts and grasslands could also be mediated by certain climatic factors (Fig. 3). For instance, mean annual temperature (MAT), mean diurnal temperature range (MDTR), isothermality and aridity, which were higher in desert ecosystems (Fig. S9), were positively associated with haloarchaeal attributes. Conversely, negative correlations were found between both thaumarchaeotal attributes and MDTR, isothermality and aridity. Interestingly, our results revealed strong and negative correlations among haloarchaeal and thaumarchaeotal attributes (Fig. 3).

Ecological preferences of Haloarchaea and Thaumarchaeota

Our mapping effort based on results from four ecological clusters of haloarchaeal and thaumarchaeotal OTUs sharing ecological preferences further supported a strong influence of niche differentiation (Figs. 4a,b, 5a,b). *Haloarchaea* were assigned exclusively to the desert and high-salinity clusters (331 and 561 OTUs, respectively), whereas *Thaumarchaeota* were included in all clusters but more frequently present in the grassland (80 vs. 57 OTUs) and low-salinity (122 vs. 2 OTUs) clusters. Our continental maps accounted for 70 to 94% of the spatial variation in these clusters. Also, strong relationships of ecosystem type and electrical conductivity with the relative abundance of corresponding clusters indicated that these were reasonably well-defined and ecologically meaningful clusters (Figs. 4a,b, 5a,b). Overall, our maps provided predictions on the regions where the four ecological clusters were expected to be most abundant. As expected, an opposing spatial distribution pattern was found between the desert and grassland clusters and between the high- and low-salinity clusters. For example, the high-salinity cluster showed a narrower distribution compared with the desert cluster and was particularly abundant in the most arid desert regions (e.g., Taklamakan, Kumtag and Qaidam Deserts) where their soils are often hypersaline. However, the low-salinity cluster revealed a similar distribution with the grassland cluster and had greater relative abundance in moist grassland regions (e.g., central and eastern Inner Mongolia) known for their relatively low-salinity soils. Our network analyses showed that nodes within the same ecological clusters were more connected, indicating that haloarchaeal and thaumarchaeotal OTUs sharing a particular ecological preference tended to co-occur with each other (Figs. 4c,d, 5c,d, S10).

Ecological processes governing the assembly of Haloarchaea and Thaumarchaeota

Relative contributions of major ecological processes structuring community assembly differed between *Haloarchaea* and *Thaumarchaeota* (Fig. 6). *Haloarchaea* were associated with a greater influence of homogeneous selection (41.8%) than *Thaumarchaeota* (3.5%). By contrast, a greater contribution from ecological drift enabled by dispersal limitation was observed for *Thaumarchaeota* (58.6%) than for *Haloarchaea* (23.9%). In sum, *Haloarchaea* were largely driven by environmental-based processes, as expected for specialists, while *Thaumarchaeota* were primarily assembled by spatial-based processes, as expected for generalists. Also, consistent results were observed when the vegetated and bare ground microsites were analyzed separately. That is, the relative influences of different community assembly processes were similar between the two microsites for both *Haloarchaea* and *Thaumarchaeota* (Fig. S11). Together with our results above (Figs. 2c,d,i–l, S5), the consistency in assembly processes across the two microsites further indicates that merging data across the microsites should not affect the conclusions of this study.

Discussion

Our results showed that topsoil archaeal communities across China's drylands were dominated by *Haloarchaea* and AOA, and aligned with our hypotheses and suggested that *Haloarchaea* tended to be specialists governed by environmental-based processes whereas AOA were generalists governed by spatial-based processes. We also observed that relative to grasslands, desert soils had higher relative abundance and richness of *Haloarchaea* and lower relative abundance and richness of AOA. Our findings provided strong evidence for niche differentiation between these two archaeal groups across large-scale environmental gradients, primarily driven by habitat specialization associated with contrasting ecosystem types.

Our results indicate that niche specialization of *Haloarchaea* to salt is likely a key determinant of the clear differentiation of *Haloarchaea* and AOA observed between deserts and grasslands, which can be linked to their highly specialized osmoadaptive strategy. The most prevalent strategy for osmoadaptation performed by *Haloarchaea* is "salt-in", which involves the accumulation of potassium ions to balance osmotic pressure and maintain their requirements for salts to maintain growth and structural stability (Oren, 2008). Because this strategy requires extensive adaptation of the intracellular enzymatic machinery to high salt concentrations (Oren, 2008, 2013), *Haloarchaea* generally can't thrive in low-salinity environments but thrive only under extreme conditions with high salinity (Oren, 1994; Walsh *et al*., 2005; Jiang *et al*., 2007; Auguet *et al*., 2010; Rath *et al*., 2019; Zhang *et al*., 2019). Niche specialization to salt endows *Haloarchaea* with a competitive advantage over the more generalist AOA in deserts, where high soil salinity selectively enriched *Haloarchaea* which then may outcompete AOA due to their relatively low-salinity tolerance (*sensu* Fournier *et al*., 2020). Salinity-driven competitive suppression was observed previously between *Haloarchaea* and *Thaumarchaeota* and other archaeal taxa (Walsh *et al*., 2005; Jiang *et al*., 2007; Shi *et al*., 2016; Rath *et al*., 2019). Competitive suppression associated with salinity is further supported by the strong negative correlations between haloarchaeal and thaumarchaeotal attributes along the salinity gradient across our study sites (see Fig. S12). Furthermore, nitrification is generally inhibited at high salt concentrations (Oren, 1994), thereby putting AOA at a further competitive disadvantage in desert soils. We infer that the lower relative abundance and richness of AOA in deserts is likely due to both competitive interactions and direct negative effects of soil salinity on the availability of ammonium, the main inorganic N source for AOA (Mosier and Francis, 2008; Moin *et al*., 2009; Delgado-Baquerizo *et al*., 2013a).

Grasslands contrast with deserts in many ways, such as grassland soils having lower salinity, higher N availability, and supporting higher plant diversity. The lower salinity in grassland soils likely changes the competitive dynamics to facilitate AOA, with additional influences from N availability and plants. Specifically, in the transitions from deserts to grasslands as salinity decreases and N availability increases, AOA become more competitive over *Haloarchaea*. We must note that, however, as N availability keeps increasing AOA will be outcompeted by AOB (Delgado-Baquerizo *et al*., 2013a; Trivedi *et al*., 2019). Thus, our results suggest that the relationship between N availability and the relative abundance and richness of AOA may be unimodal and further modified by salinity. In general, AOA tend to dominate in soils with ammonium concentrations below 15 mg kg^{-1}, whereas AOB become more competitive when ammonium concentrations are above 100 mg kg^{-1} (Pester *et al*., 2011). However, for this study the N availability in grasslands is just high enough to favor AOA but not so high to select for AOB

(Fig. S8). Moreover, soil AOA have been found to have a specific association with plant roots (Simon *et al*., 2000; Ke *et al*., 2013, 2014), and their abundance and diversity have been reported to be influenced greatly by root exudates (Sliwinski and Goodman, 2004; Simon *et al*., 2005; Chen *et al*., 2008), indicating a profound plant–soil–AOA interaction. Because plant species generally differ in both the composition and amount of root exudates (Grayston *et al*., 1998), individual plant species may select for specific AOA communities in soil via bottom-up forces (Nicol *et al*., 2005). As a result, the higher plant diversity of grasslands may combine with lower salinity and higher N availability, relative to deserts, to facilitate higher relative abundance and richness of soil AOA.

Further, we emphasize that the observed ecosystem type-associated niche differentiation may not be independent of climate, which is a major aspect of the Earth system that affects the structure and functioning of drylands (Maestre *et al*., 2016; Berdugo *et al*., 2020). Our results indicate that climatic factors could mediate the degree of habitat specialization of *Haloarchaea* to desert ecosystems indirectly via influences on soil salinity. For example, the high temperature, low precipitation and extreme temperature fluctuations typical of desert ecosystems could increase salinity via soil drying and accumulations of inorganic minerals (e.g., halite, gypsum, and carbonates) (Pointing and Belnap, 2012; Delgado-Baquerizo *et al*., 2013b; Genderjahn *et al*., 2018). Our results support this, as soil salinity was found to be positively correlated with MAT, MDTR, isothermality and aridity across our studied sites (see Fig. S13). On the other hand, we found negative correlations of MDTR, isothermality and aridity with total soil N, ammonium, and plant species richness (see Fig. S13). These results coincide with previous studies indicating that both increasing aridity and temperature variability decreased soil N availability and plant diversity in drylands worldwide (Delgado-Baquerizo *et al*., 2013b, 2016a; Zhang *et al*., 2018; Berdugo *et al*., 2020), and also explain the observed negative associations of aridity and temperature variability with the relative abundance and richness of AOA. Taken together, our results suggest that future changes in temperature and/or precipitation regimes could modify the distributions of the main topsoil archaeal groups in drylands across northern China.

One goal of understanding drivers of microbial community composition is to use that knowledge to better understand differences in the spatial distributions of different microbial taxa and ecologically coherent groups. To this end, we used high-resolution maps to visualize the spatial distributions of *Haloarchaea* and AOA sharing ecological preferences for deserts and grasslands as well as for high or low salinity. Just like those atlases for preferences of dominant soil microbial taxa at continental and global scales (Delgado-Baquerizo *et al*., 2018; Egidi *et al*., 2019; Jiao *et al*., 2019), our results suggest that there are predictable clusters of co-occurring dominant archaeal groups in dryland soils across northern China. As hypothesized, our continental atlases and co-occurrence networks confirm the importance of ecosystem type and specialization to specific environmental factors in determining the biogeographical patterns of *Haloarchaea* and AOA in drylands.

Given the identities of *Haloarchaea* and AOA as specialists and generalists, respectively, the distinct continental atlases also imply that their distribution patterns could be underpinned by contrasting community assembly processes (Pandit *et al*., 2009; Hanson *et al*., 2012; Stegen *et al*., 2013, 2015). Our results confirm this, and are consistent with earlier findings that habitat specialists were more strongly structured by environmental factors, whereas the distribution of habitat generalists was more influenced by spatial-based processes (Pandit *et al*., 2009; Langenheder and Székely, 2011; Logares *et al*., 2013; Liao *et al*., 2016; Malard *et al*., 2019). These results also confirm that *Haloarchaea* have strict requirements for specific environmental conditions (e.g., high salinity and extreme climates) (Oren, 1994), while AOA have a wide environmental tolerance and high resistance to environmental stresses and therefore could colonize diverse ecological niches (Erguder *et al*., 2009).

Moreover, we argue that the segregated distributions of *Haloarchaea* and AOA should be taken into consideration when predicting changes in the functioning of drylands in a changing world, given their strong links with multiple ecosystem functions including organic matter decomposition, C fixation, N cycling and climate regulation (Chaban *et al*., 2006; Offre *et al*., 2013; Baker *et al*., 2020; Hu *et al*., 2021). For example, AOA may contribute to rapid nutrient cycles and therefore to high plant productivity in grassland ecosystems (Wardle *et al*., 2004; Offre *et al*., 2013; Trivedi *et al*., 2019), whereas *Haloarchaea* may contribute to the slow decomposition of recalcitrant organic matter and therefore to soil C sequestration in desert ecosystems (Oren, 1994; Wardle *et al*., 2004; Chaban *et al*., 2006; Auguet *et al*., 2010).

The fact that *Haloarchaea* and AOA did not show niche differentiation across small-scale vegetated and bare ground microsites is surprising, as the two microsites are typically considered as contrasting niches that are reported to support different soil microbial communities as well as the segregated distributions of AOA and AOB (Delgado-Baquerizo *et al*., 2013a; Trivedi *et al*., 2019). Dryland plant patches often can accumulate and capture soil resources under their canopies, leading to the formation of the so-called fertile islands, which largely contribute to variation in the abundance, diversity, and composition of soil microbial communities compared to adjacent bare areas (Ochoa-Hueso *et al*., 2018). However, we found no significant differences in soil salinity, N availability, or other soil nutrients between the two microsites (see Fig. S6). Therefore, the lack of clear differentiation between *Haloarchaea* and AOA across the two microsites can by partially explained by the lack of the fertile island phenomenon and the relative homogeneity in soil properties between the microsites studied here.

In conclusion, our results support the hypothesis of the ecosystem type-associated niche differentiation for *Haloarchaea* and AOA, which are the two dominant topsoil archaeal groups found in drylands across northern China. This indicates that the relative contributions of these archaeal groups to ecosystem functioning are likely to vary systematically across China's drylands, and potentially beyond. This understanding of the habitat preferences of *Haloarchaea* and AOA is critical for predicting the responses of their spatial distributions to ongoing global change and the resulting ecological consequences. Given the more deterministic assembly of *Haloarchaea* compared with that of AOA, we argue that environmental impacts on the biogeography and functional contribution of *Haloarchaea* will be more predictable than for AOA.

Experimental Procedures

Field survey and sampling

Field data and soil samples were collected from 173 dryland sites located in five provinces of northern China (Fig. S1). Vegetation survey and soil sampling were conducted between June and September from 2015 to 2017 according to the well-established standardized protocols as described by Hu *et al*. (2021) (see Supporting Experimental Procedures for more details). In brief, 6–21 topsoil samples (0–20 cm depth) per site were collected under the canopies of the dominant plant species and in bare areas devoid of vegetation, and 1 155 samples were taken and analyzed in total.

To test the niche-differentiation hypothesis proposed (Fig. S2), we classified all study sites into deserts and grasslands, the two most representative ecosystem types occurring in drylands across northern China, using China's vegetation atlas at a scale of 1:1 000 000 (Chinese Academy of Sciences, 2001) combined with our field observation. Each site grouped into a certain ecosystem type was considered as a replicate. Totally, we had 112 replicates collected in deserts and 61 collected in grasslands (Fig. S1).

Molecular analyses

Topsoil archaeal diversity and community composition were assessed using Illumina-based sequencing. Genomic DNA from each of topsoil samples (N = 1 155) was extracted from 0.5 g of defrosted soils using the PowerSoil® DNA Isolation Kit following manufacturer's protocols, and pooled at site level, ultimately resulting in 173 composite DNA samples under the canopies of vegetation and in bare ground, respectively.

The primer pair ARC344F (5′-ACGGGGYGCAGCAGGCGCGA-3′) and ARC915R (5′-GTGCTCCCCCGCCAATTCCT-3′) was used to amplify the V3−V5 regions of the archaeal 16S rRNA gene. While amplicon sequencing can always introduce some biases, the primer pair used here is a set of archaeal universal primers and to our best knowledge has not been reported to be biased towards any archaeal taxa. We therefore infer that the higher relative abundance of *Thaumarchaeota* than *Haloarchaea* observed in this study (Fig. 1a) is not expected to be the result of a bias in the primers towards the *Thaumarchaeota*. PCR reaction system and thermal cycling conditions are described in Supporting Experimental Procedures. Amplicons were gel-purified using the AxyPrep DNA Gel Extraction Kit and paired-end sequenced (2 × 300 bp) on an Illumina MiSeq platform at the Majorbio Bio-pharm Technology Co., Ltd. (Shanghai, China). Resulting sequences were processed by using the QIIME package (Caporaso *et al.*, 2010) (see Supporting Experimental Procedures for more details of the bioinformatic analyses). OTUs not assigned at kingdom level or identified as non-archaeal organisms were removed and the OTU table was subsequently rarefied to the lowest number of sequences (10 707) found within an individual sample. Our resampled dataset included a total of 1 871 archaeal OTUs. Raw sequencing data of the archaeal 16S rRNA gene have been deposited in the NCBI Sequence Read Archive under BioProject accession number PRJNA608843.

Soil physicochemical analyses

All topsoil samples (N = 1 155) were subjected to physicochemical analyses of pH, electrical conductivity, organic C, total N, total phosphorus (P), available P, ammonium and nitrate contents using standard laboratory methods as described in Supporting Experimental Procedures. It should be noted that topsoil samples were collected under the canopies of vegetation and in bare ground in each site; thus, the site-level measurements of all the soil physicochemical properties analyzed here were obtained by using a weighted average of the mean values observed in vegetated areas and bare ground by their respective cover (Maestre *et al*., 2012; Delgado-Baquerizo *et al*., 2013b).

Data acquisition from public databases

For all the sites surveyed, we gathered 20 standardized climatic variables (Table S1) related to temperature, precipitation and solar radiation from the Worldclim database (Fick and Hijmans, 2017). We obtained the aridity index and potential evapotranspiration from the Global Aridity Index and Potential Evapotranspiration Climate database (https://doi.org/10.6084/m9.figshare.7504448.v3). Note that we used 1 – aridity index as our surrogate of aridity level in all cases. In addition, we used normalized difference vegetation index (NDVI) as a metric for net aboveground primary productivity as explained in recent studies in drylands (Delgado-Baquerizo *et al*., 2016b, 2018). NDVI data were obtained from the moderate resolution imaging spectroradiometer aboard NASA’s Terra satellites (https://neo.sci.gsfc.nasa.gov/). We used the average NDVI values during our sampling dates as a proxy for net aboveground primary productivity at the site level as described by Delgado-Baquerizo *et al*. (2016b, 2018). Finally, we obtained information on soil texture (percentage of clay, silt and sand) from the SoilGrids system (https://soilgrids.org/).

Pre-selection of multicollinearity free environmental variables

After data collection, we maximized the number of study sites without missing environmental data, ultimately generating a sub-dataset (N = 133) that included 82 desert sites and 51 grassland sites. For this sub-dataset, we excluded those environmental variables that were strongly correlated with each other (Pearson's $r > 0.8$) within either climatic or soil variables as they may cause multicollinearity problems in subsequent analyses (Maestre *et al*., 2012; Delgado-Baquerizo *et al*., 2017). Based on these analyses, we retained 9 out of 22 climatic variables (Fig. S14) and 11 out of 12 soil variables (Fig. S15) that were not strongly correlated with the rest ($r < 0.8$) for our statistical analyses.

Phylogenetic analyses

We constructed a phylogenetic tree for OTUs belonging to the *Haloarchaea* and *Thaumarchaeota* to visualize their taxonomic affiliations (Fig. 1b). Representative sequences from haloarchaeal (N = 863) and thaumarchaeotal (N = 208) OTUs were multiple aligned using the MEGA7 program (Kumar *et al*., 2016) and filtered to remove uninformative regions. An approximately maximum-likelihood tree was then constructed with the FastTree 2 (Price *et al*., 2010) based on the generalized time-reversible model of nucleotide evolution and visualized with the interactive tool Evolview (Subramanian *et al*., 2019).

Network analyses

We conducted correlation network analyses to explore the co-occurrence pattern of haloarchaeal and thaumarchaeotal OTUs (Fig. 1d). For co-occurrence network construction, we first calculated all possible Spearman's rank correlations (ρ) among OTUs. We focused only on positive correlations as they provide information on haloarchaeal and thaumarchaeotal OTUs that may have similar ecological preferences (Delgado-Baquerizo *et al*., 2018). We considered a co-occurrence to be robust if the Spearman's correlation coefficient (ρ) was both > 0.65 and statistically significant ($P < 0.00001$) (Delgado-Baquerizo *et al*., 2018). The final network was visualized with the interactive platform gephi (https://gephi.org/). We then tested whether haloarchaeal and thaumarchaeotal OTUs tend to co-occur with others within the same taxa or not. To achieve this, we fitted a power law model to determine the degree distributions of *Haloarchaea* and *Thaumarchaeota* in the constructed co-occurrence network (Banerjee *et al*., 2018) (Fig. S3).

Statistical analyses

We estimated niche breadth for each of haloarchaeal and thaumarchaeotal OTUs using the Levins' index (Levins, 1968) and the tolerance index (Dolédec *et al*., 2000). The Levins' index estimates niche breadth in terms of the number of sites where an OTU was detected, while the tolerance index estimates niche breadth in terms of the environmental (including plant species richness, NDVI, and the multicollinearity free climatic and soil variables as determined above) tolerance of OTUs. These indices were calculated using the spaa and ade4 packages in R (http://cran.r-project.org/), and their differences between haloarchaeal and thaumarchaeotal OTUs were evaluated using the non-parametric Mann-Whitney U test (Figs. 2a,b, S4a). Low values of the indices correspond to specialists and high values to generalists. Further, we used the Mann-Whitney U test to compare the differences in both the relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* between deserts and grasslands (Figs. 2e–h, S4d–g). These analyses were conducted for both the full dataset and the sub-dataset, except that the tolerance index was calculated exclusively for the sub-dataset.

Next, we performed random forest models to identify the major statistically significant predictors of the relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* (Fig. S7). Variables used for random forest models comprised the multicollinearity free environmental variables (Figs. S14, S15), plant species richness, NDVI and ecosystem type (coded as a categorical variable with two levels: 1 = deserts and 0 = grasslands). These analyses were carried out using the R package rfPermute. Then, we conducted non-parametric partial Spearman's rank correlations to explore the net associations of haloarchaeal and thaumarchaeotal attributes with ecosystem type, climatic factors, plant attributes and soil properties after accounting for their simultaneous correlations with space (latitude and longitude). We included exclusively in these analyses those variables that were identified as main statistically significant predictors of haloarchaeal and thaumarchaeotal attributes from random forest models (Fig. S7). Furthermore, we also considered the partial correlations among haloarchaeal and thaumarchaeotal attributes. Information on partial Spearman's correlations was visualized using the R package corrplot (Fig. 3). To facilitate the interpretation of results for partial correlation analyses, we used the Mann-Whitney U test to assess the differences in climatic factors, plant attributes and soil properties between deserts and grasslands (Figs. S8, S9).

To further evaluate our ecosystem type-associated niche-differentiation hypothesis (Fig. S2), we conducted Spearman's correlations ($P < 0.05$) to group haloarchaeal and thaumarchaeotal OTUs into two ecological clusters with shared habitat preferences for deserts and grasslands. Similarly, given the key role of soil salinity in determining the niche differentiation (Figs. 3, S7, S8), we identified another two ecological clusters for high salinity and low salinity. We then calculated the standardized (z-score) relative abundance of each of the four ecological clusters per sample. We further used the Cubist regression models to predict the continental-scale distributions of relative abundance of the four ecological clusters in drylands across northern China as described previously (Delgado-Baquerizo *et al.*, 2018) (see also Supporting Experimental Procedures for more details). Predictions on the continental-scale distributions of the four ecological clusters were done on an approximate 10 km resolution grid (Figs. 4a,b, 5a,b). The accuracy of our predictions (R^2) was evaluated using a training subset (75%) and a test subset (25%) of the data. These analyses were performed using the R package Cubist, and all maps were visualized in ArcGIS 10.2. We also constructed correlation networks to elucidate the co-occurrence pattern of haloarchaeal and thaumarchaeotal OTUs sharing ecological preferences (Figs. 4c,d, 5c,d) and evaluated whether those OTUs within a particular ecological cluster tend to co-occur more often (Fig. S10), as described above. These analyses were performed exclusively for the sub-dataset.

Finally, we inferred the relative influences of major environmental-based and spatial-based processes on the community assembly of *Haloarchaea* and *Thaumarchaeota* using a null-modeling-based quantitative framework (Stegen *et al.*, 2012, 2013, 2015) (Fig. 6a; see also Supporting Experimental Procedures for detailed principles and calculations). The relative influences of these processes were estimated separately for *Haloarchaea* and *Thaumarchaeota* (Fig. 6b,c). Before analyses, the OTU tables were rarefied to 500 and 5 000 sequences per sample for *Haloarchaea* and *Thaumarchaeota*, respectively.

We must note, however, that the vegetated and bare ground microsites typically found in drylands may represent distinct niches and therefore harbor significantly different soil microbial communities (Delgado-Baquerizo *et al*., 2013a; Trivedi *et al*., 2019). Thus, merging these two small-scale contrasting microsites could affect the large-scale patterns of the ecosystem type-associated niche differentiation of *Haloarchaea* and *Thaumarchaeota*. To address this, we also evaluated the niche breadth, ecological distributions, and relative importance of those community assembly processes of the two archaeal groups for vegetated areas and bare ground separately. This set of analysis revealed no significant differences in all of these aspects between the two microsites for both *Haloarchaea* and *Thaumarchaeota* (Figs. 2c,d,i–l, S5, S11). Combining data across the two microsites should not, therefore, influence the conclusions of our study.

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Figure legends

Fig. 1 Taxonomic composition of topsoil archaea in drylands across northern China. a Percentage of OTUs and relative abundance of 16S rRNA gene sequences representing high-rank archaeal taxa. **b** Phylogenetic tree of haloarchaeal and thaumarchaeotal OTUs. Taxonomic affiliations of *Haloarchaea* and *Thaumarchaeota* are presented at the end of the branch (Ring 1). Branches are colored by these two archaeal taxa (blue for *Haloarchaea* and red for *Thaumarchaeota*). **c** Taxonomic composition of *Haloarchaea* and *Thaumarchaeota*. *Nitrososphaerales* affiliated with the lineage Group I.1b accounts for > 99.9% of thaumarchaeotal sequences. The remaining haloarchaeal and thaumarchaeotal OTUs assigned to the least abundant taxa are not shown on bars (including *Nitrosocaldales* < 0.001%, *Nitrosopumilales* = 0.02%, unidentified *Haloarchaea* < 0.001%, and unidentified *Thaumarchaeota* = 0.01%). **d** Co-occurrence network with nodes (OTUs) colored by *Haloarchaea* and *Thaumarchaeota*. The network diagram includes 1 071 nodes with 9 167 significant edges (ecological connections among OTUs). The size of the nodes is proportional to the number of edges they contain.

Fig. 2 Niche breadth of *Haloarchaea* and *Thaumarchaeota* and their ecological distributions in deserts and grasslands as well as in bare ground and vegetated areas. a, **b** Boxplots of the niche breadth for each of haloarchaeal and thaumarchaeotal OTUs estimated using the Levins' index and the tolerance index, respectively. **c**, **d** Relative abundance (**c**) and percentage of OTUs (**d**) of 16S rRNA gene sequences representing the *Haloarchaea*, *Thaumarchaeota* and the remaining archaea in deserts, grasslands, bare ground and vegetated areas, respectively. **e**–**l** Boxplots of the relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* in deserts and grasslands (**e**–**h**) as well as in bare ground and vegetated areas (**i**–**l**). **a**–**l** These results are shown for the full dataset, except that the tolerance index is calculated for the sub-dataset. Significant differences between boxes are determined using the non-parametric Mann-Whitney U test. Significance levels are: ns, not significant ($P > 0.05$); ***$P < 0.001$.

Fig. 3 Partial Spearman's correlation matrix of the main determinants of ecological distributions of *Haloarchaea* and *Thaumarchaeota*. Partial Spearman's correlations of the relative abundance and richness of *Haloarchaea* and *Thaumarchaeota* with ecosystem type, climatic factors, plant attributes and soil properties after controlling for spatial influence (latitude and longitude). The variables that are identified as significant predictors of haloarchaeal and thaumarchaeotal attributes from random forest models are included in these analyses. The size and color of the squares are proportional to partial correlation coefficients as shown in the scale bar. Blue and red colors represent significant positive and negative correlations, respectively. na, not applicable (non-significant predictors of haloarchaeal and thaumarchaeotal attributes from random forest models); ns, not significant (P > 0.05); ATR, annual temperature range; MTWQ, mean temperature of wettest quarter; PS, precipitation seasonality; PDM, precipitation of driest month; PSR, plant species richness.

Fig. 4 Predicted distributions and co-occurrence patterns of haloarchaeal and thaumarchaeotal OTUs with shared habitat preferences. a, **b** Predicted continental-scale distributions of relative abundance of the two ecological clusters of haloarchaeal and thaumarchaeotal OTUs sharing habitat preferences for deserts and grasslands in drylands across northern China, respectively. R^2 denotes the percentage of variation explained by the models. The scale bar depicts the standardized relative abundance (z-score) of each ecological cluster. The inset shows relationship between ecosystem type and the z-score of each ecological cluster. **c**, **d** Co-occurrence networks with nodes colored by the ecological clusters and taxa, respectively. The size of the nodes is proportional to the number of edges they contain.

Fig. 5 Predicted distributions and co-occurrence patterns of haloarchaeal and thaumarchaeotal OTUs with shared salinity preferences. a, **b** Predicted continental-scale distributions of relative abundance of the two ecological clusters of haloarchaeal and thaumarchaeotal OTUs sharing environmental preferences for high salinity and low salinity, respectively. The inset shows relationship between the standardized relative abundance (z-score) of each ecological cluster and soil salinity, indicated as log-transformed electrical conductivity. **c**, **d** Co-occurrence networks with nodes colored by the salinity clusters and taxa, respectively. **a**–**d** Other details as in Fig. 4.

Fig. 6 Relative influences of ecological processes mediating the community assembly of *Haloarchaea* and *Thaumarchaeota*. a The null-modeling-based analytical framework for estimating relative influences of multiple environmental-based and spatial-based processes structuring microbial community assembly proposed by Stegen *et al*. (2012, 2013, 2015). βNTI, β-nearest taxon index; RC_{bray}, Bray–Curtis-based Raup–Crick. **b, c** Relative contributions of the five ecological processes governing community turnover of *Haloarchaea* and *Thaumarchaeota*, respectively.