

## ORIGINAL PAPER

# Distribution of Ciliates in Intertidal Sediments across Geographic Distances: A Molecular View



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**The estimation of the diversity and geographic distribution of protists in particular ciliates has long been an ongoing debate. We estimated the distribution of ciliates in intertidal sediments with geographic distance ranging from 10 cm to 1,000 km, using high-throughput DNA sequencing. Higher community similarity, in particular that of rare ciliate taxa, occurred between replicates than between sites. Statistical analyses showed that the community dissimilarities of both abundant and moderately abundant ciliates had correlations with geographic distance at the scales of 50 m, 200 km and 1000 km, indicating a distance-decay relationship. No significant correlation was observed for rare taxa. The analysis of Bray-Curtis similarity showed a higher pairwise community similarity in abundant taxa than in moderately abundant taxa, and that in rare taxa was the lowest. Abundant taxa usually can disperse in a wider range than rare taxa, though their distribution is restricted by distance to some extent. Rare taxa are potentially more sensitive to changing environments, but no distance-decay relationship could be observed. The data indicate contrasting patterns of geographic distribution of the abundant and rare ciliate taxa and a weak distance-decay relationship for relatively abundant taxa at a scale over 50 m.**

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## Introduction

Understanding the diversity of microorganisms and major factors structuring their distribution is a main goal in ecology. The estimation of the diversity and geographic distribution of protists, in particular ciliates, has long been an ongoing debate. It has been

claimed that free-living protists are cosmopolitan microbes that thrive anywhere in the world where their preferred habitats are realized. [Finlay \(2002\)](#) strongly indicated that the dispersal of free-living protists is rarely restricted by geographic barriers, and thus they tend to have a cosmopolitan distribution. The simple explanation is that protists are tiny (most less than 1 mm long) and so abundant that continuous large-scale dispersal sustains their global distribution ([Fenchel and Finlay 2004](#); [Finlay](#)

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2002; Finlay and Fenchel 2004). Finlay et al. (2006) further indicated that most protist morphospecies, even the ribotypes or rRNA sequence clusters of one morphospecies, have cosmopolitan distribution. A very recent study by Azovsky et al. (2016) revealed that many morphospecies of marine benthic heterotrophic flagellates were widespread or even cosmopolitan and regional endemics were few.

By contrast, Foissner (1999 and 2008) indicated that only a few species of protists are much more abundant, while the vast majority (>90%) have moderate or low abundance, and presented a moderate endemicity model for the distribution of most protists. Recently, the distribution of protists (less than 5  $\mu\text{m}$ ) at a regional scale (six French lakes) has been explained as a pattern of distance-decay relationship (Lepère et al. 2013). This study indicated that geographic distance seemed to restrict the distribution of protists. Although protist diversity patterns have been surveyed in different habitats, only a few studies have attempted to address the distribution of protists in relation to geographic distance (Lepère et al. 2013; Logares et al. 2014).

Ciliates, with their high diversity and wide distribution as well as a broad range of body size, are important arguments in the debate of protist diversity and distribution. Among the natural habitats of ciliates, intertidal sediments are known to contain a high abundance of ciliates, up to 2500 cells/ml (Musat et al. 2006; Wickham et al. 2000). The species richness of ciliates in the intertidal sediments is also pretty high. For instance, a total of 53 species were detected from only a volume of 0.2 ml intertidal sediment (Hamels et al. 2005). With their high abundance and species richness, intertidal ciliates are suitable for evaluating the distribution patterns of protists and the major factors regulating their dispersal (Foissner et al. 2008).

Previous studies on marine intertidal ciliates mostly adopted the classic morphological method, which was used to identify ciliates from the fixed samples (Du et al. 2012; Hamels et al. 2005; Wickham et al. 2000). Since most ciliates are fragile, fixative has negative effect on estimation of ciliate diversity and thus may result in underestimation of the diversity of fragile species. Application of molecular techniques might overcome the shortcomings of classic methods. Molecular methods can be useful to assess the diversity of ciliates and to provide additional insights into the biogeography of microbes (Foissner et al. 2008). The estimation of protist diversity based on the 18S rRNA gene sequencing has been successfully applied to marine and freshwater environments, uncovering

high diversity of ciliates (Coyne et al. 2013; Epstein and López-García 2008; Jousset et al. 2010; Lara and Acosta-Mercado 2012). More recently, the high-throughput sequencing method, which can process hundreds of thousands of sequences simultaneously, provides a practical and possibly more comprehensive approach to understand the diversity of ciliates (Gimmler and Stoeck 2015; Logares et al. 2014).

In this study, we utilized high-throughput DNA sequencing to investigate the ciliate diversity in intertidal sediments along the coastline of China across a broad geographic distance ranging from 10 cm to 1000 km. We aimed (i) to evaluate the potential distance-decay relationship of ciliates in intertidal sediments; and (ii) to estimate the variability of ciliate diversity and distribution in relation to geographic distance.

## Results

### Environmental Parameters

The median grain size of sediments ranged from 17.22  $\mu\text{m}$  at the site GXA to 612.77  $\mu\text{m}$  at the sites DSA-K and DSA-B (Table 1). The sediments collected from the QDW sites in the Yellow Sea were classified as the type of silty sand (St-S), those from the HKA, DSA-B and DSA-K sites in the East China Sea belonged to the type of sand (S), and the sediments from the DY sites in the Bohai Sea and the GXA sites in the East China were classified as the type of silt (St). The content of the sediment total organic carbon (TOC) from DSA-K was the highest, followed by those from QDW and GXA, and the TOC contents from DY, HKA and DSA-B were lower than 1%. The highest content of the sediment chlorophyll a was obtained from the silty sediment site GXA, and relatively low contents were detected from the sandy sediment sites DSA-B, DSA-K and HKA (Table 1).

### Overview of High-throughput Sequencing Data

After mapping tags to ciliate related OTUs, a total of 419,092 tags ranging from 30,898 at site DSA-K to 56,081 at site GXA, with an average of 38,099 tags for each site, were kept for further analyses. Based on a similarity of 97%, a total of 483 different ciliate OTUs were obtained from the 11 sites. The number of OTUs obtained from each site varied from 81 to 170, with an average of 115 (Table 2). The proportion of abundant OTUs at each site was on average 12% (ranging from 5% to 20%), and

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