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An Estimation of the Global Diversity and Distribution of the Smallest Eukaryotes: Biogeography of Marine Benthic Heterotrophic Flagellates

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Protists are ubiquitous, but the factors influencing their diversity and biogeography remain unclear. We use a comprehensive database on the marine benthic heterotrophic flagellate (HF) morphospecies to explore the worldwide patterns in their diversity and distribution in comparison with predictions of the Ubiquity model (UM) and Moderate Endemicity model (MEM). The number of known HF morphospecies was limited (even when considering the rates of descriptions), and the local-to-global diversity ratio was relatively high (10-25%). Regional diversity was highly correlated with the investigative effort, indicating considerable under-exploration. Regional endemics were few (not over 19% of total richness), and many morphospecies were widespread or even cosmopolitan. No obvious latitudinal trend in HF diversity was detected. By species composition, the regions were distinctly arranged into three groups according to cold, temperate and warm waters, but not in accordance with geographical distances. This distribution pattern was most likely explained by contemporary climate (temperature) but did not suggest clear geographical barriers for dispersal. Therefore, the HF are less concordant with the MEM predictions but closer to the UM than other (larger) protists. Molecular studies reveal significantly higher HF diversity; the distributional patterns obtained from genetic- and morphology-based data, however, complement but not generally contradict each other.
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Key words: Heterotrophic flagellates; diversity; distribution; biogeography.

Introduction

Global patterns in diversity and distribution are well studied for the macro-organisms, such as the insects, birds, and plants; while relatively little is known about microorganisms. Many issues in protist macroecology are subject to lively debate but are still unresolved, e.g., whether microbes are dispersed globally or whether they, like the macro-organisms, have historical biogeographies and follow the common rules. Two alternative views have been expressed on this point: **A**. Being highly abundant, commonly ubiquitous and dispersion-unlimited, the microbes follow the "everything is everywhere, but the environment

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Table 1. Selected predictions of two models for free-living protists (based on Finlay et al. 2004; Foissner 2008).

Features	Ubiquity model	Moderate endemicity model
Global number of morphospecies	Low	High
Relative number of endemics	Low	Moderate (~ 30%)
Proportion of the (known) global species pool found locally	High (> 10%)	Moderate
Large-scale distribution: role of geographical barriers (dispersal limitation) and historical contingencies, e.g., continental drift	Low	Moderate

selects" principle, and therefore are primarily cosmopolitan (in appropriate habitats), with an abrupt threshold discriminating them from macroorganisms ("Ubiquity model" (UM); Fenchel and Finlay 2004; Finlay et al. 1996); or **B**. Most species have a restricted distribution; therefore, patterns of their diversity follow the common macroecological trends ("Moderate Endemicity model" (MEM); Foissner 2004, 2008).

The models share some common features but disagree about the strength of discrepancy between micro- and macroorganisms. In Table 1, we listed some divergent predictions of the models, emphasizing those that could be verified on our data (see below). In recent years, the MEM model has become prevalent in studies of micrometazoans and some protists, e.g., tintinnids, testate amoebae and foraminifera (for examples, see Fontaneto 2011). However, many other groups are understudied, and the direct comparison of the two models is hampered by the lack of sufficient data.

In particular, very little is known about the distribution of heterotrophic flagellates (HFs) – the collective name for the extremely broad "motley crew" of small and most mobile eukaryotes with considerably different evolutionary origin, metabolism, and ecology. These protists are ubiquitous, occupy a variety of habitats and play an important role in aquatic systems (Leadbeater and Green 2000). Being the tiniest and most abundant eukaryotes, they are natural candidates for validating the above-mentioned models and for testing whether the organisms' size actually matters in relation to their biogeography. Nevertheless, no special issues were devoted to the HF in recent monographs (Foissner and Hawksworth 2009; Fontaneto 2011). The only study on the global diversity and geographical distribution of this group was conducted more than 15 years ago by Lee and Patterson (1998). They analyzed the composition of the free-living HF morphospecies in 31 marine and freshwater localities and found that the communities from similar habitats worldwide (e.g., freshwater or marine, and water column or sediments) appeared to be similar to one another, whereas the geographically proximate communities did not group together. Further studies (Al-Qassab et al. 2002; Lee 2015; Patterson and Lee 2000) also did not reveal specific geographic patterns but confirmed a wide distribution for many of the HF species.

Since the work of Lee and Patterson (1998), a considerable volume of new data on the HF diversity and distribution has appeared. The taxonomy of many HF groups was revised substantially, based on ultrastructural characteristics and molecular features. Recent molecular-based studies with modern sequencing techniques provided new insights into the diversity and biogeography of unicellular eukaryotes. Morphospecies were often found to be genetically diversified; many phylotypes were widely distributed, but some others showed ecologically and/or geographically restricted distributions (Bass et al. 2007; Bates et al. 2013). The potential mismatch between molecular and morphology-based distributional patterns is often noted but remains generally intractable, mainly due to the lack of suitable datasets for broad comparisons.

The aims of our study were 1) to compile the available data for the morphospecies of marine benthic HF and 2) using this most comprehensive worldwide data set, to investigate the patterns in HF diversity and distribution in comparison with other protists and with the predictions of the UM vs. MEM models.

Results

Species Richness

After quality control of the data to remove synonyms and obsolete names, 432 species (155 genera) of free-living heterotrophic flagellates

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