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Global biogeography of marine fungi is shaped by the environment

Kaho H. TISTHAMMER^{a,*}, Gerald Manuel COBIAN^b, Anthony Stuart AMEND^c

^aKewalo Marine Laboratory, University of Hawaii at Manoa, United States

^bDepartment of Botany, University of Hawaii at Manoa, United States

^cDepartment of Botany; Ecology, Evolution and Conservation Biology Program, University of Hawaii at Manoa, United States

ARTICLE INFO

Article history:

Received 9 July 2015

Revision received 27 August 2015

Accepted 31 August 2015

Available online 1 October 2015

Corresponding editor:

Felix Bärlocher

Keywords:

Global scale

Microbial biogeography

RDA

Fungal community dissimilarity

Biodiversity

Sediment

ABSTRACT

Fungi are essential components of marine ecosystems, yet very little is known about their global distribution and diversity in the marine environment. In this study, we analyzed marine fungal community structure at a global scale using the International Census of Marine Microbes dataset. Marine fungal communities sampled from both the water column and sediments were compared. Based on the sequences of the nuclear ribosomal small subunit V9 region, 2200 operational taxonomic units (OTUs) were identified at 97% similarity. There was a significant distinction between the pelagic and benthic communities, with 15.4% OTUs shared between the two realms. Environmental factors, particularly sample depth, oxygen, and nitrate, strongly correlated with the fungal community composition and explained more variance than did geographic distance. This study represents the first global-scale analysis of marine fungal community structure, and highlights potential opportunities for research in marine fungal ecology and biogeography.

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Introduction

Marine fungi are both diverse and important components of ocean ecosystems; however, they are understudied compared to other micro-organisms. Multiple lines of evidence indicate that fungi are critical and abundant components of nutrient cycling dynamics (Raghukumar 2004; Orsi et al., 2013a, b), exert top down control on phytoplankton communities (Gutierrez et al., 2011), are essential to marine food webs (Kagami et al., 2007; O'Rorke et al., 2013), and are symbiotic with marine macro-organisms (Yarden, 2014). It is clear that

fungi are present, active and potentially significant players in marine biological processes across realms (Raghukumar 2004; Richards et al., 2012).

Diverse fungal assemblages have been enumerated from nearly every marine habitat searched, including open water (Gao et al., 2010), deep sea and hydrothermal vents (Bass et al., 2007; Edgcomb et al., 2011), anoxic environments (Jebaraj et al., 2010), wood substrata in the ocean (Rämä et al., 2014; Pang and Mitchell, 2005), as pathogens of macroorganisms (Nagahama et al., 2003), associated with healthy corals, sponges and other marine invertebrates (Amend et al., 2012;

* Corresponding author.

E-mail address: kahot@hawaii.edu (K.H. Tisthammer).

<http://dx.doi.org/10.1016/j.funeco.2015.09.003>

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Yarden, 2014), and on various marine plants and algae (Zucaro et al., 2008; Jones and Pang, 2011). However, little is known about the basic biogeographic patterning of marine fungi, and to what extent these habitats share fungal taxa.

Relative to fungi, patterns and processes of marine bacteria biogeography are better documented. Repeatedly, depth gradients (Giovannoni and Stingl, 2005; DeLong et al., 2006), habitat type (Zinger et al., 2011), and climate (Barberán and Casamayor, 2010) have been shown to contribute to biogeographic patterns in these microbes. Differences between sediment and water column bacteria are particularly stark. Zinger et al. (2011) found that bacterial communities of water column and sediment realms share only 7.1% of taxa on average. Comparatively rich, standardized datasets have enabled robust biogeographic inferences on a truly global scale, including the prevalence of macroecological patterns such as Rapoport's rule (Amend et al., 2013), latitudinal diversity gradients (Sul et al., 2013), isolation by distance and distance decay of community similarity patterns (Zinger et al., 2014).

Both space and environment also play a role in determining fungal community composition in the ocean. Studies of wood-inhabiting marine fungi show that community composition is driven by water temperature and salinity (Booth and Kenkel, 1986), as well as log attachment (whether secured or free-floating) and location (Rämä et al., 2014). A study of five subsurface sediments showed a high correlation between site physiochemical characteristics (dissolved inorganic carbon, total organic carbon and sulfide) and active fungal community composition as inferred from RNA analysis, suggesting a link between nutrients and fungal community composition (Orsi et al., 2013b). In a study of fungal communities associated with sea-cucumber aquaculture, both realms (benthic and water column) and sampling date significantly differentiated community composition (Guo et al., 2015).

Whereas both geographic distance and habitat are important predictors of fungal community composition it has not been determined which contributes more strongly to community differences. Of the handful of studies that have examined marine fungal community composition and community similarity patterns, the majority are limited to geographic scales <1000 km such as a depth gradient across 100 s of km within the North Pacific Gyre (Gao et al., 2010), fungal communities in the East (Zhang et al., 2014), or Central Indian Oceans (Singh et al., 2011). Fewer studies have examined fungal communities at greater geographic extent, and these have focused on specific habitats or substrata such as hydrothermal vent regions (e.g. Le Calvez et al., 2009, and Edgcomb et al., 2011), or Mangroves (Shmit and Shearer, 2003; Sarma, 2012). Further, differences in sampling methodology and primer choice among researchers have made robust synthetic analysis of fungal communities challenging. Analysis of fungal distributions based on taxonomy provide evidence for both narrow endemism (Sarma, 2012) and ubiquitous generalists (Hughes, 1986; Shearer et al., 2006; Amend et al., 2012; Richards et al., 2012; Amend, 2014), providing few clues as to which patterns predominate overall at the community level. To date, little is known about global biodiversity patterns and whether taxa overlap across habitats.

In this study we analyze a fungal community sequence dataset derived from the standardized collection by International Census of Marine Microbes (ICoMM) project (Amaral-Zettler et al., 2010). ICoMM was established in 2004 to facilitate the inventory of marine microbial diversity by cataloging all known diversity of marine single-cell organisms and exploring unknown microbial diversity. ICoMM provides one of the most geographically extensive datasets of marine microbial communities to date, enabling studies on the global distribution patterns of marine bacterial communities (see Zinger et al., 2011; Amend et al., 2012; Sul et al., 2013). Here, we use the dataset containing the eukaryotic environmental samples, processed in a single laboratory, using identical loci and protocols (Amaral-Zettler et al., 2009) and replicated amongst 56 water and sediment samples collected from various research groups from around the world's oceans. Previous analyses of portions of this dataset have focused on protists (Lie et al., 2014). Marine fungal community distributions have not been examined specifically from this dataset, and this study was the first attempt to understand them at a global scale.

The aims of our study were to determine whether community composition differs between fungal communities in sediments and the water column, to correlate composition with abiotic environmental variables, and to determine the extent to which realm, environment and distance shape fungal community dissimilarity patterns. We limited our analyses to fungal communities that are "free-living" (not associated with macroscopic host organisms) in marine sediments and water columns. We predicted that patterns of marine fungal biogeography would follow similar patterns to those detected amongst marine bacteria, and correlate with: (a) physiochemical characteristics of the environment, (b) geography, and (c) realm. We hypothesized that, similar to marine bacteria, fungal communities would more strongly correlate with environmental factors compared to geographic distance. Using a large, diverse and standardized dataset, we hoped to provide insight into the various factors that shape these diverse, little-studied assemblages.

Methods

The ICoMM data set

All samples were downloaded from the marine microbial database (MICROBIS, website: <http://icomm.mbl.edu/microbis>), which provides public access to the results of the ICoMM project (Amaral-Zettler et al., 2010), as well as detailed information about sampling sites and their associated projects and attributes. The dataset contains DNA sequence data from 454-sequencing technology, in which identical PCR, sequencing and bioinformatic processing were employed to ensure standardization. An ~65 bp fragment of the Eukaryotic nuclear ribosomal small subunit V9 region was amplified using 1380F/1389F and 1510R primers as described in Amaral-Zettler et al. (2009). Operational taxonomic units (OTUs) were determined at 97% similarity level. 2200 OTUs pertaining to Kingdom Fungi (2.7% of all OTUs in the dataset) were retained in a site-by-taxon matrix (Table S1). Taken together, 42 pelagic

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