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### Supporting Online Material

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## Controls on Diatom Biogeography in the Ocean

Pedro Cermeño<sup>1,†</sup> and Paul G. Falkowski<sup>1,2,\*</sup>

The extent to which the spatial distribution of marine planktonic microbes is controlled by local environmental selection or dispersal is poorly understood. Our ability to separate the effects of these two biogeographic controls is limited by the enormous environmental variability both in space and through time. To circumvent this limitation, we analyzed fossil diatom assemblages over the past ~1.5 million years from the world oceans and show that these eukaryotic microbes are not limited by dispersal. The lack of dispersal limitation in marine diatoms suggests that the biodiversity at the microbial level fundamentally differs from that of macroscopic animals and plants for which geographic isolation is a common component of speciation.

Unlike terrestrial ecosystems, the oceans are an interconnected geophysical fluid that potentially allows planktonic organisms to disperse globally. Owing to their dispersal ability, microbial species exhibit a broad spatial distribution, which has led to the hypothesis that, below 1 mm body size, “everything is everywhere, but the environment selects” (1–3). However, several studies have questioned this idea, arguing that, like macroscopic animals and plants, microorganisms can exhibit biogeographic patterns and macroevolutionary trajectories linked not only to present-day environmental conditions but also to historical contingency and dispersal limitations (4–7). If marine planktonic microbes were limited by dispersal, the spatial range of species’ distributions should be constrained to a geographic area near the center of their origin, and, therefore, the degree of community similarity should gradually

decay with geographic distance (8, 9). However, because geographic distance is often correlated with specific environmental characteristics, disentangling the relative influence of these two factors on community divergence represents a major challenge in elucidating whether or not marine planktonic microbes are limited by dispersal (6, 10).

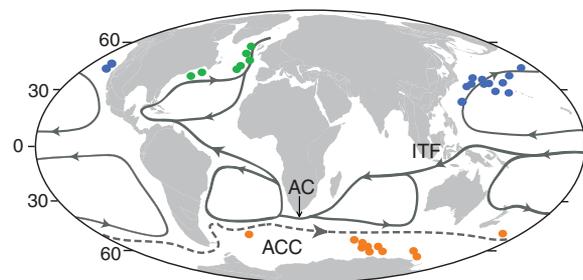
Using fossil diatom assemblages from far distant regions and contrasting open ocean environments, we tested the importance of environmental selection and dispersal limitation on the spatial distribution of marine diatom morphospecies. Owing to the relatively similar physicochemical

conditions between sites very far apart in the ocean, our analysis represents an ideal study case. Furthermore, the fossil record provides a time-averaged view of the effect of environment on past biological communities, reducing the range of extrinsic environmental variables that must be considered as causative factors.

Fossil assemblages of marine diatoms were extracted from the Neptune database, a global record of microfossil occurrences reported by the Deep Sea Drilling Project and Ocean Drilling Program (11). Our complete data set consisted of 225 assemblages containing 307 morphologically defined species (70 genera) from the early Pleistocene (~1.5 million years ago (Ma)) to the present (table S1). The analysis included assemblages typical of north temperate habitats from the Atlantic and Pacific Oceans, and high-latitude environments in the Southern Ocean from the Atlantic, Pacific, and Indian sectors and Antarctic waters (Fig. 1).

On time scales encompassing speciation, adaptive radiation, and long-term regime shifts such as historical climate change, the temporal turnover of community composition may bias our analysis, making it difficult to find biogeographical patterns. To set up the time scale of the analysis, we first quantified the change in floristic composition of diatom assemblages through time using the Jaccard index, a measure of similarity

**Fig. 1.** Paleogeographic reconstruction for Early Pleistocene (~1.8 Ma) showing locations of Deep Sea Drilling Project and Ocean Drilling Program sites used in this study. The pattern of major surface water current systems is shown schematically. The most likely dispersal routes between northern temperate habitats in the Atlantic and Pacific Oceans are (i) via the Indonesian through-flow (ITF) and Agulhas current (AC), (ii) a route to the North through the Arctic Ocean, or (iii) a route to the South within the Antarctic circumpolar current (ACC). Color code denotes different oceanic regions. These patterns of water mass circulation have persisted, albeit with substantial regional variations during the period of study. The figure is modified from Sexton and Norris (19).



<sup>1</sup>Environmental Biophysics and Molecular Ecology Program, Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901, USA. <sup>2</sup>Department of Earth and Planetary Science, Rutgers University, 610 Taylor Road, Piscataway, NJ 08854, USA.

\*To whom correspondence should be addressed. E-mail: pedro@uvigo.es (P.C.); falko@marine.rutgers.edu (P.G.F.)  
†Present address: Departamento de Ecología y Biología Animal, Universidad de Vigo, 36310 Vigo, Spain.

that emphasizes compositional changes (Fig. 2 and table S2) (12). The results reveal a slow and gradual decay of community similarity over the past 1.5 million years (My) of Earth's history (Fig. 2 and table S2). The pattern is consistent throughout the oceanic regions considered in the analysis. Using these data, we estimate a turnover time for these communities in the range of 2 to 8 My. For the purpose of our analysis, a time frame spanning 0.5 My satisfied the assumption of contemporaneity, that is, less than 15% reduction in community similarity.

For each time interval defined, the fossil assemblages were plotted simultaneously in a two-dimensional space according to their floristic similarity, using nonmetric multidimensional scaling (Fig. 3A and fig. S1). The analysis reveals a clear biogeographic differentiation between communities occupying temperate regions in the Northern Hemisphere and high-latitude environments in the Southern Ocean from the Atlantic, Indian, and Pacific sectors, and Antarctic waters; these communities share very few common species (Fig. 3B). In contrast, despite geographic/oceanographic barriers to dispersal, changes in community composition through time, and the disparity of data sources, far distant communities in north temperate regions of the Atlantic and Pacific Oceans exhibit remarkable similarities (Fig. 3B). Closer inspection of our database shows that, excluding poorly represented species (i.e., less than five occurrences in the global database), these oceanic regions respectively share ~95% and 75% of their total species pool.

Our sampling strategy allows comparison across large differences in longitude, separated by continents, and between large gradients in latitude with no land masses hindering dispersal. We assume that, to first order, the northern temperate habitats of the Atlantic and Pacific Oceans have been characterized by comparable environmental conditions over the past 1.5 My. In contrast, there are clear environmental differences between northern temperate habitats and the Southern Ocean sites considered in this analysis (13). At latitudes higher than ~45°S, the contemporary Southern Ocean is dominated by cold and nutrient-rich water masses comprising the Antarctic circumpolar current, which is delimited on its northern flank by the sub-Antarctic polar front (Fig. 1). In contrast to their northern hemispheric counterparts, where phytoplankton growth primarily is limited by nitrate, this oceanic region is characterized by strong iron limitation. Iron is an essential component of photosystems, and its limitation has been shown to influence the distribution of marine diatom species (14).

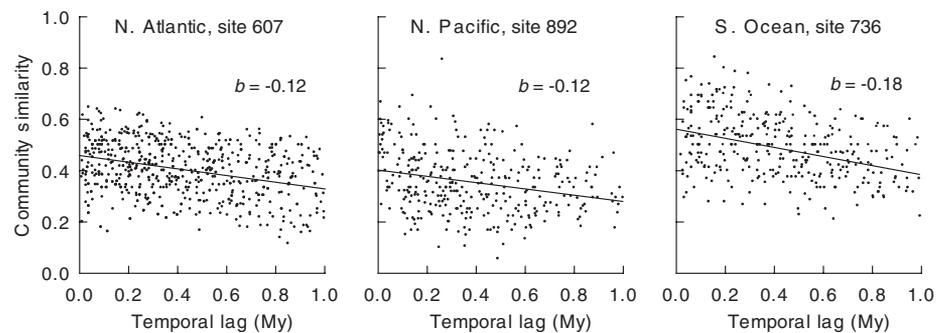
The proximity in the ordination space of fossil assemblages associated with northern temperate environments in the Atlantic and Pacific Oceans, and their separation from the Southern Ocean communities (Fig. 3), indicates that environmental conditions primarily control the global biogeography of marine diatom assemblages. These results, however, do not exclude spatial constraints

such as the geographic configuration of continents as relevant controls on species distribution. To further constrain the importance of geographic distance and dispersal limitations, we compared the differences in floristic composition within and between different oceanic regions. Here, our hypothesis presumes that the effect of dispersal limitation increases with geographic distance; that is, community dissimilarities should progressively increase from regional to global data sets. However, the analysis reveals that the taxonomic differences between far distant assemblages from north temperate regions in the Atlantic and Pacific Oceans are not significantly different from those observed within each oceanic region/basin (Fig. 3B).

Studies in freshwater ecosystems have demonstrated that geographical factors such as the fractal-like nature of drainage basins, the distance between lakes, or the availability of habitat primarily control the regional- to global-scale biogeography of diatom morphospecies (7, 15, 16). However, unlike freshwater ecosystems such as rivers and lakes, where the distribution of species is strongly constrained by habitat connectivity, the mutual contiguity of oceanic water masses

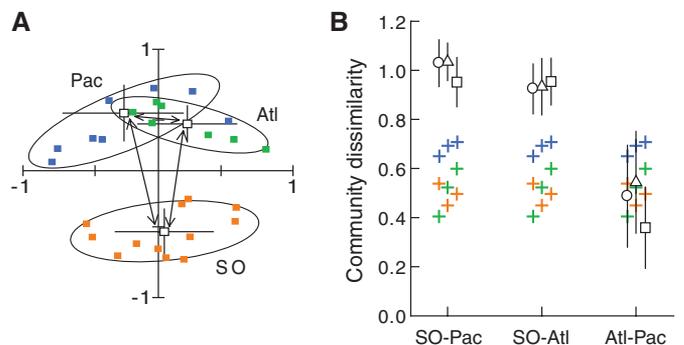
appears to be an effective conduit for global dispersal of marine planktonic microbes over evolutionary time (17–19). Far from the long-standing view that open ocean habitats are stable and uniform, mesoscale and submesoscale mixing processes, which are a highly important mode of energy dissipation in open ocean (20), mediate the intrusion of nutrient-rich deep waters into the euphotic zone and, hence, contribute to the widespread dispersal of marine planktonic diatoms. Furthermore, the circulation of surface ocean water masses and the strength of oceanic fronts may change in response to medium/long-term climatic variations, seasonal cycles, and transient events such as storms, temporarily opening alternative routes to seed dispersal.

Increasing evidence indicates that marine diatom morphotypes may be composed of several genetically distinct “cryptic” species characterized by subtle morphological differences (21, 22). This represents a potential caveat of our study, which is based on species defined by obvious morphological criteria. However, if dispersal overwhelmed the biogeographic effects of genetic divergence between populations, we would expect to find similar distribution patterns regard-



**Fig. 2.** Temporal decay of community similarity through the Pleistocene. Each point represents a single pairwise comparison between fossil diatom assemblages separated in time. The maximum temporal lag considered here is 1 My.  $b$  is the slope of the ordinary least square linear regression model. The plots are for different sites in the North Atlantic, North Pacific, and Southern Ocean (see also table S2).

**Fig. 3.** Inter- and intra-oceanic differences in community composition. **(A)** Representative illustration of floristic relationships among oceanic regions obtained by using nonmetric multidimensional scaling. Orange, blue, and green symbols are for Southern Ocean, North Pacific, and North Atlantic, respectively. Open squares are the mean coordinates in the ordination diagram for each oceanic region. Error bars represent  $\pm 1$  SD. The Euclidean distance between data points is an estimate of community dissimilarity (i.e., the longer the arrow, the larger the difference between communities). **(B)** Mean ( $\pm 1$  SD) community dissimilarities between oceanic regions. Circles, triangles, and squares are different geological time intervals analyzed; 0 to 0.5, 0.5 to 1, and 1 to 1.5 Ma, respectively. Color crosses are mean community dissimilarities within each oceanic basin. Inter- and intra-oceanic mean community dissimilarities were estimated using a Monte Carlo simulation model (100 trials of the multidimensional scaling) and randomized combinations of among 15 to 50 communities (see also fig. S1).



less of the level of taxonomic resolution. In this regard, genetic analyses have shown the existence of widespread, although disjunct, distribution patterns for several cryptic species of the marine diatom *Skeletonema* (23). Similar results have been reported for other microbial plankton groups, such as picoeukaryote algae and foraminifera (17, 24). Alternatively, our results could reflect the convergence or parallelism of morphological traits among genetically unrelated taxa in disjunct oceanic regions.

Despite enormous environmental variability linked to glacial-interglacial climates of the Pleistocene, our analysis reveals that marine diatom communities have evolved slowly through gradual changes over the past 1.5 My of Earth's history (Fig. 2 and table S2). These patterns of community stability for extensive periods of geological time are probably associated with the great dispersal ability of marine diatoms (25, 26) and highlight the potential of microbial plankton communities for recovering from past and future climatic variations. This conclusion implies that there are few or no biogeographical traces of historical climate change in contemporary communities of marine diatoms.

Models of evolution of species commonly assume that tectonic barriers and water mass fronts act as effective isolating mechanisms (9). This is a necessary condition that precedes the delineation of biogeographic provinces *sensu stricto* (6, 9) and controls the development of global species richness. Our analysis, however, indicates that, even at the largest spatial scale, the geographic distribution of marine planktonic diatoms does

not seem to be limited by dispersal. These results, together with recent genetic evidence for high rates of inter- and intra-oceanic gene flow in planktonic protists and widespread oceanic distributions of cryptic "sibling" species (17, 23, 27), suggest that the geographic isolation of marine diatoms cannot be maintained for long periods. Our results strongly support the hypothesis that environmental selection rather than dispersal dominates diatom community structure. To the extent that marine diatoms are a model microbial taxonomic group, our results imply that the biodiversity and macroevolutionary patterns at the microbial level fundamentally differ from those of macroscopic animals and plants, negating the idea that all living things follow similar ecological and evolutionary rules (6).

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#### Supporting Online Material

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Materials and Methods

Fig. S1

Tables S1 and S2

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## A Constant Flux of Diverse Thermophilic Bacteria into the Cold Arctic Seabed

Casey Hubert,<sup>1\*</sup> Alexander Loy,<sup>2</sup> Maren Nickel,<sup>1</sup> Carol Arnosti,<sup>3</sup> Christian Baranyi,<sup>2</sup> Volker Brüchert,<sup>1†</sup> Timothy Ferdelman,<sup>1</sup> Kai Finster,<sup>4</sup> Flemming Mønsted Christensen,<sup>4,5</sup> Júlia Rosa de Rezende,<sup>1,5</sup> Verona Vandieken,<sup>1‡</sup> Bo Barker Jørgensen<sup>1,5</sup>

Microorganisms have been repeatedly discovered in environments that do not support their metabolic activity. Identifying and quantifying these misplaced organisms can reveal dispersal mechanisms that shape natural microbial diversity. Using endospore germination experiments, we estimated a stable supply of thermophilic bacteria into permanently cold Arctic marine sediment at a rate exceeding  $10^8$  spores per square meter per year. These metabolically and phylogenetically diverse *Firmicutes* show no detectable activity at cold in situ temperatures but rapidly mineralize organic matter by hydrolysis, fermentation, and sulfate reduction upon induction at 50°C. The closest relatives to these bacteria come from warm subsurface petroleum reservoir and ocean crust ecosystems, suggesting that seabed fluid flow from these environments is delivering thermophiles to the cold ocean. These transport pathways may broadly influence microbial community composition in the marine environment.

Microbial diversity surveys have revealed that species richness is determined by many low-abundance taxa—the so-called rare biosphere (1–3). In the ocean, certain

members of this relatively unexplored biosphere comprise a dormant microbial “seed bank” that can be transported passively over great distances (1). Quantitatively tracking the migration of in-

dicator taxa can highlight key factors that influence patterns of biogeography and may help evaluate the extent to which microorganisms exhibit a cosmopolitan distribution (4). Endospore germination allows certain bacteria to persist as dormant cells in hostile environments, explaining discoveries of viable thermophilic *Firmicutes* in inhospitably cold habitats (5–10). Quantitative studies of this phenomenon are scarce, and the origin and distribution of thermophiles in cold environments remain enigmatic (6–11). Thermophilic sporulating taxa such as certain *Desulfotomaculum* spp. may constitute only 0.001% of marine microbial populations (8, 12). Like the rare taxa, spores are less prone to viral lysis or predation, and are not detected by traditional diversity surveys (1, 2). A spore-forming *Desulfotomaculum* strain that can only grow between 26°C and 47°C was recently isolated from permanently cold Svalbard fjord sediment in the Arctic (10). The present study assessed thermophile diversity, abundance, and distribution in Svalbard sediments to reveal insights into mechanisms governing biogeography in the marine environment.

Pristine sediment was sampled from Smeerenburgfjorden (80°N; fig. S1) and incubated over an experimental temperature range (13), which revealed two distinct sulfate-reduction regimes