



Estimating planktonic diversity through spatial dominance patterns in a model ocean



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ABSTRACT

In the open ocean, the observation and quantification of biodiversity patterns is challenging. Marine ecosystems are indeed largely composed by microbial planktonic communities whose niches are affected by highly dynamical physico-chemical conditions, and whose observation requires advanced methods for morphological and molecular classification. Optical remote sensing offers an appealing complement to these in-situ techniques. Global-scale coverage at high spatiotemporal resolution is however achieved at the cost of restrained information on the local assemblage.

Here, we use a coupled physical and ecological model ocean simulation to explore one possible metrics for comparing measures performed on such different scales. We show that a large part of the local diversity of the virtual plankton ecosystem – corresponding to what accessible by genomic methods – can be inferred from crude, but spatially extended, information – as conveyed by remote sensing. Shannon diversity of the local community is indeed highly correlated to a 'seascape' index, which quantifies the surrounding spatial heterogeneity of the most abundant functional group. The error implied in drastically reducing the resolution of the plankton community is shown to be smaller in frontal regions as well as in regions of intermediate turbulent energy.

On the spatial scale of hundreds of kms, patterns of virtual plankton diversity are thus largely sustained by mixing communities that occupy adjacent niches. We provide a proof of principle that in the open ocean information on spatial variability of communities can compensate for limited local knowledge, suggesting the possibility of integrating in-situ and satellite observations to monitor biodiversity distribution at the global scale.

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1. Introduction

The diversity of biological communities plays a key role for the homeostasis of the planet and for the resilience of ecosystem services of key relevance for human society (McGrady-Steed et al., 1997; Naem and Li, 1997). Biodiversity is unevenly distributed across the globe, and understanding its patterns is a central issue in ecology, as well as an important step for setting effective conservation priorities (Hutchinson, 1957; Gaston, 2000; Myers et al., 2000). On land, biodiversity studies of primary producers provide fundamental information on species distribution and on the ecological processes underpinning spatial changes in biodiversity (Jetz et al., 2009; Jenkins et al., 2013; Kerswell, 2006; Levin et al., 2003). Observation of spatial and temporal variations of biodiversity on land is relatively straightforward as terrestrial primary production is sustained by vascular plants, whose geographical position is not substantially modified during their life span, and between two subsequent measurements.

In contrast, in the open ocean, the observation and quantification of biodiversity patterns is more challenging, mostly because the whole trophic chain is sustained almost exclusively by microscopic, drifting photosynthetic organisms: the phytoplankton. Not only the physical localization of phytoplankton changes on a very rapid time scale with respect to the temporal resolution of biodiversity observations, but also the identification of species and the quantification of their abundance are problematic for microbial organisms (Achtman and Wagner, 2008; Konstantinidis et al., 2006; Giovannoni and Vergin, 2012).

Studies based on extremely time-consuming and expert-based morphological classification (Margalef, 1994; Irigoien et al., 2004) have been complemented in recent years by molecular techniques, thus substantially improving the resolution on the organisms composing microbial communities (Venter et al., 2004; Rusch et al., 2007; Bork et al., 2015). If it is now clear that the molecular diversity of planktonic communities is much larger than that revealed by morphological studies (Sunagawa et al., 2015; de Vargas et al., 2015) these in-depth analyses can still be obtained at the cost of a low spatio-temporal resolution. Even if some studies recently extended the temporal resolution of genomic-based community monitoring (Giovannoni and Vergin, 2012; Gilbert et al., 2012; Needham and Fuhrman, 2016), it is unconceivable

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to be able to observe plankton communities everywhere in the global ocean on the spatio-temporal scale of their variability.

Here, we use the ECCO2-Darwin model (Follows et al., 2007), which simulates simultaneously oceanic circulation and the ecology of a virtual plankton ecosystem, to explore to what extent classical indexes of local diversity can be captured by a metrics of patchiness of the dominant functional plankton group, the 'seascape index'. Whereas measures of local diversity require an extensive knowledge of the community, that can be best achieved by genomic methods, the seascape index is based on the shallowest possible description of the community – the dominant functional type – but compensates by integrating information on spatial patchiness.

Contrary to molecular and morphological in situ analysis, satellite-based observations indeed can only provide hints as to the properties of the phytoplankton community, based on what can be remotely sensed (pigments and bio-optical properties, mainly). However, they offer a spatio-temporal coverage hardly achievable – and certainly not at the global scale – by in situ sampling. Ocean color measures are now routinely exploited to monitor the global distribution of total chlorophyll and primary production (Joint and Groom, 2000), and will be soon empowered by hyperspectral captors. Such observations revealed that global chlorophyll patterns are strongly associated to physical features like eddies and fronts, indicating a strong structuring effect of the ocean transport on the phytoplanktonic community distribution (McGillicuddy, 2016; Sunagawa et al., 2015).

The structuring effect of ocean dynamics over remotely sensed planktonic organisms appears to apply also when the planktonic community is described in further detail than chlorophyll. Some algorithms, like for instance PHYSAT, allow to statistically associate the bio-optical properties of the water backscatter spectrum to the phytoplanktonic group that dominates the community (Alvain et al., 2008; Alvain et al., 2012). Dominant groups estimated in this way are typically organized in patches whose boundaries are set by horizontal stirring (d'Ovidio et al., 2010). If the highly dynamical nature of such structures poses a challenge to the mapping of phytoplanktonic biogeography, it also prompts mixing of communities that are separated by dynamical barriers like jets and eddies, thus effectively enhancing diversity (Clayton et al., 2013; Lévy et al., 2015). At scales smaller than the mesoscale (10–100 kms), turbulence may convert a heterogeneous region with patches of different communities into a more homogeneous water mass with increased local diversity. Based on this hypothesis, an attempt has been made to define a planktonic diversity proxy based on the observation of water-leaving radiance heterogeneity (De Monte et al., 2013). Such proxy provides consistent views of macroecological patterns, such as the classical scalings of diversity distribution in temperature and latitudinal gradients (Irigoin et al., 2004; Fuhrman, 2009; Martiny et al., 2013; Chust et al., 2013; Beaugrand et al., 2013). However, the evaluation of patterns of satellite-derived diversity against in situ observations is – in spite of the rapidly growing amount of molecular observations – a daunting task. When focusing on specific locations and time, observations are sparse, and when available do not yield yet the statistical power needed to overcome errors and fluctuations in local estimates.

For this reason, we resorted to use a biophysical ocean simulation for quantifying how much and where the diversity of a virtual phytoplankton community can be explained by a seascape index like that accessible by remote sensing. The advantage of this approach lies in the possibility of accessing simultaneously different ecosystems' statistics, together with their environmental context at the global scale. In the MIT ECCO2-Darwin model, accurate and quantitative ocean mesoscale-resolving physical dynamics is coupled with phytoplankton ecology to a detail previously unattained by global-scale simulations (Follows et al., 2007). Recently, this model has provided a reliable virtual testbed for studying the processes that underlie global diversity patterns of oceanic primary producers, and for addressing the structuring role of physical determinants, notably transport and mixing induced by mesoscale

turbulence (Clayton et al., 2013; Lévy et al., 2015; Barton et al., 2010; Lévy et al., 2014; Dutkiewicz et al., 2009).

We first show that, for the virtual ocean of the ECCO2-Darwin model, the seascape index reflects to a large extent the variation in local diversity, even if the latter is computed at a 'taxonomic' resolution higher than that used for the spatial index.

Then, we compare the performance of the seascape index across locations of the global ocean with different physical environments, so as to infer where the satellite-based information may be more usefully applied to mapping and monitoring diversity variations.

2. Methods

2.1. Coupled physical and ecological model of the global ocean

Our analysis is based on numerical simulations from the ECCO2-Darwin model, which is an ocean global circulation model (MITgcm (Marshall et al., 1997; Menemenlis et al., 2008)) coupled with a plankton virtual ecosystem (Follows et al., 2007; Beaugrand et al., 2013; Barton et al., 2010; Dutkiewicz et al., 2009). The physics of ocean circulation is simulated with an eddy-permitting grid of 1/6 of degree horizontal resolution and with 50 vertical levels ranging in thickness from 10 m near the surface to approximately 450 m at a maximum model depth of 6150 m. The model has been run for 8 nominal years, from 1992 to 1999, and we considered data from the last 3 years.

The ecological component describes 78 virtual types of phytoplankton, belonging to 5 distinguished 'functional groups' (diatom analogs, two *Prochlorococcus* analogs, small photo-autotrophs and large eukaryotes), and two zooplankton predators. The physiological features of each virtual type are attributed, at the beginning of the simulation, in the form of parameters that are randomly drawn from a range of realistic values. The biogeography of the types is an emergent property of the simulation and results from the combined effects of adaptation to the local environmental conditions, competition, predation and dispersal by oceanic currents.

The virtual types play, in this context, the same role as species (for macro-organisms) or clusters of sequences (e.g. OTUs, for microorganisms) in community ecology. At a coarser 'taxonomic' resolution, the types are arranged in functional groups according to the set of parameters, that is the 'phenotype', they possess (Follows et al., 2007). These functional groups roughly correspond to classifications of the community components in broad clusters sharing either phylogenetic or functional features.

In this study, we consider only the surface layer, which is the region available to remote detection. At any location of the surface layer, we retrieve from the model the biological and physical parameters: abundance of every virtual type and of every functional group (hereafter, we denote 'dominant group' the group to which the most abundant type of the local assemblage belongs), total chlorophyll ($\mu\text{g/l}$), Sea Surface Temperature ($^{\circ}\text{C}$), Eddy Kinetic Energy (m^2/s^2) and nutrients concentration (nitrites, nitrates, ammonium, silicates, phosphorous, iron).

More details of the model including comparisons with biogeographical observations can be found in Follows et al. (2007); Barton et al. (2010); Dutkiewicz et al. (2009).

2.2. Local diversity indexes

The local diversity index is evaluated at two levels of 'taxonomic resolution', one at the level of phytoplankton types (78 types) and one at the level of phytoplankton functional groups (5 groups). The former best reflects the measures obtained by in situ sampling and DNA sequencing. The latter is computed on the same observable, the functional group, that is available for the evaluation of dominance patterns.

Local diversity is estimated through a metrics commonly used in community ecology, the Shannon index (Shannon, 1948; Haegeman et al., 2013). This index provides information on number and abundance

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