



Review

Modelling plankton ecosystems in the meta-omics era. Are we ready?



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ABSTRACT

Recent progress in applying meta-omics approaches to the study of marine ecosystems potentially allows scientists to study the genetic and functional diversity of plankton at an unprecedented depth and with enhanced precision. However, while a range of persistent technical issues still need to be resolved, a much greater obstacle currently preventing a complete and integrated view of the marine ecosystem is the absence of a clear conceptual framework. Herein, we discuss the knowledge that has thus far been derived from conceptual and statistical modelling of marine plankton ecosystems, and illustrate the potential power of integrated meta-omics approaches in the field. We then propose the use of a semantic framework is necessary to support integrative ecological modelling in the meta-omics era, particularly when having to face the increased interdisciplinarity needed to address global issues related to climate change.

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1. Introduction

It is very likely that the ongoing wave of dramatic biodiversity loss, which seems to be comparable to the mass extinctions that occurred in the past, is being driven by human impact on the biosphere (Barnosky et al., 2011, Secretariat of the Convention on Biological Diversity). The scale of anthropogenic environmental perturbations has urged both the public and decision-makers to call for tools and approaches allowing the forecasting, management and mitigation of the continuing loss of biodiversity (Barnosky et al., 2011). Such a call can only be met with an integrated approach to understanding the mechanisms that regulate biodiversity, thus linking abiotic and biotic factors within conceptual models of ecosystems (Thuiller et al., 2013).

Since its inception, the study of ecology has focused on the interactions between organisms and between organisms and their environments (Haeckel, 1866). In any given ecosystem, populations of organisms compete and cooperate, forming ecological guilds which are traditionally characterized through metrics that estimate their phylogenetic and functional diversity alongside their response to disturbance. If collected with sufficient spatial and temporal resolution, these metrics permit a description of the way in which a given ecosystem follows a specific trajectory in the space of variables, or phase space, for example that of species abundance. Each trajectory would depend on the rates at which each species responds to the vast array of interactions and fluxes in an out of the system. Such a trajectory, although seldom mentioned as such, is what determines and is behind the more familiar term of 'ecosystem functioning'. The above implies that variation in biodiversity, which would alter the spectrum of biological units and consequently their interactions and functions, will naturally affect broader-scale ecosystem functioning (Krause et al., 2014; Tett et al., 2013; Crise et al., 2015). At times, the processes modulated by organisms in a given system are of interest, in which cases a functional diversity (FD) approach is adopted to understand ecosystem dynamics (Fig. 1a). The FD within an ecosystem would then be the assembly of functional traits of all the constituent organisms (Carmona et al., 2016) and summarize the community's metabolic or phenotypic capacities. However, most of these metrics only offer a loose approximation of the overall configuration of interactions within a community. Currently, a plethora of metrics is used to infer FD (for a review, see Mouchet et al., 2010), each of which has a different ability to describe the status of a system, depending on various aspects (e.g., if a process is dominated by disparate species, metrics emphasizing species richness or divergence may better predict functions affecting production than metrics emphasizing species evenness - Clark et al., 2012). Perhaps the main challenge in correctly estimating FD is the sheer complexity of many ecosystems. This is especially true in species-rich ecosystems, where accounting for and characterizing the role of all species is an immense and often unrealistic task. Compounding this challenge, many traits belong to uncharacterized or poorly understood species. Methods for estimating probable trait values for uncharacterized species have been proposed, based on statistical approaches (Madin et al., 2016; Májeková et al., 2016); however the quantification of the extent to which a given biological unit is performing one or more of its ecological functions at a specific time and in a specific environmental setting is hard to achieve. Nevertheless, in the past decade, research on ecosystem functioning has experienced a shift from a taxonomic to a functional perspective on its participant biotic components (Aerts and Honnay, 2011; Tett et al., 2013; Sutherland et al., 2013 - Fig. 1b).

This shift should be properly interpreted. The taxonomic approach, largely grounded in an evolutionary view, has assumed that by knowing the players it would be possible to determine their interactions and roles in an ecological network. In support of this view is the awareness that units of evolutionary selection are typically seen as organisms or ecological populations. However, this view is weakened by the fact that taxonomic identification, even at high resolution, does not necessarily reveal the functional spectrum of a given organism. The so-called

functional trait-based approach tries to fill this knowledge gap by linking phenotypic potential to organisms, populations, or entire communities regardless of their taxonomic identity. This approach should allow a more robust and process-oriented understanding of why community composition changes under the impact of perturbations and possibly predicts what will happen in future scenarios, including those driven by global climate change (Edwards et al., 2013).

2. Core challenges of modelling plankton in marine ecosystems

The ocean, which covers 72% of the Earth's surface, is believed to be responsible for ~46% of global primary production (Field et al., 1998). Recent estimates suggest a total photic-zone eukaryotic plankton richness of ~150,000 OTUs (De Vargas et al., 2015). Within this vast diversity of organisms primary production is carried out by autotrophic plankton and processed by a myriad of other planktonic organisms before being ultimately conveyed to larger metazoans or exported to the deep layers or to the ocean floor. The diversity of plankton and their internal dynamics are therefore key drivers of the functioning of marine ecosystems. In recent years, technical advances from various fields have been applied to the ocean sciences, broadening the range and the accuracy of measurements and allowing unprecedented interdisciplinary collaboration. An exceptional effort is now required to integrate the astonishing amount and variety of data available into a common framework to reduce gaps in our knowledge of plankton functional biology and ecology.

Novel methodological and technical developments, as well as efforts in cross-disciplinary community building, are enabling for the first time the global and integrated measurement of variables required to assess both biodiversity and FD. The relatively recent applications of sequencing techniques to biodiversity assays, combined with standardized sampling approaches, are revising our view of marine biodiversity (Leray and Knowlton, 2015; Kopf et al., 2015). DNA metabarcoding (e.g., Taberlet et al., 2012; Valentini et al., 2016) is allowing, en masse, species identification from environmental samples, but is often unable to link phylotypes to phenotypes; therefore, taxonomic and functional diversity remain decoupled. The above efforts call for advanced informatics, data mining and analysis, and integrative modelling centered on a common conceptualization and terminology. Modelling in particular, if intended in its wide meaning of reproducing and testing our perception of reality, is likely to play a crucial role as it stimulates hypothetical mechanistic reconstructions of observed dynamics providing the first support or the falsification of working hypotheses.

Despite the endeavors to define and quantify biological traits, extant plankton models typically explore the distribution and diversity patterns of micro-organisms (e.g., Follows et al., 2007) and have seldom exploited trait information. Notably, traits that are unrelated to trophic or defensive requirements, e.g., those controlling differences in plankton life strategies (Anderson, 2005), receive even less attention. These constraints result in a considerable under-representation of both organismal diversity (OD) and FD, and their impacts, in ecosystem models. The goal of the present review is to draft the state-of-the-art in both plankton ecological modelling and ocean meta-omics to pave the way to possible future directions for the integration of meta-omics data in a new generation of models.

To achieve this goal, we first discuss the key, though elusive, processes in plankton dynamics. In particular, we explore processes determining community structure and the short- and long-term succession of species. Secondly, we discuss the advantages and disadvantages of various numerical and statistical models. We then describe and evaluate novelties in meta-omics approaches to marine biological, functional and trophic diversity, highlighting their potential for being incorporated into models and for advancing our knowledge. We then explore the role of semantic technologies in promoting harmonized knowledge - and thus a basis for more interdisciplinary models - across the multiple often disparate domains investigating planktonic systems. Finally, we

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