



Placing biodiversity in ecosystem models without getting lost in translation



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ABSTRACT

A key challenge to progressing our understanding of biodiversity's role in the sustenance of ecosystem function is the extrapolation of the results of two decades of dedicated empirical research to regional, global and future landscapes. Ecosystem models provide a platform for this progression, potentially offering a holistic view of ecosystems where, guided by the mechanistic understanding of processes and their connection to the environment and biota, large-scale questions can be investigated. While the benefits of depicting biodiversity in such models are widely recognized, its application is limited by difficulties in the transfer of knowledge from small process oriented ecology into macro-scale modelling. Here, we build on previous work, breaking down key challenges of that knowledge transfer into a tangible framework, highlighting successful strategies that both modelling and ecology communities have developed to better interact with one another. We use a benthic and a pelagic case-study to illustrate how aspects of the links between biodiversity and ecosystem process have been depicted in marine ecosystem models (ERSEM and MIRO), from data, to conceptualisation and model development. We hope that this framework may help future interactions between biodiversity researchers and model developers by highlighting concrete solutions to common problems, and in this way contribute to the advance of the mechanistic understanding of the role of biodiversity in marine (and terrestrial) ecosystems.

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1. Introduction

Biodiversity, the variety of life across organisational levels, is a fundamental attribute of all natural ecosystems (Heywood, 1995). Its role in supporting fluxes of energy and matter (i.e. ecosystem processes and functions), and the benefits we derive from them, was clearly recognised more than 20 years ago at the 1992 Earth Summit in Rio de Janeiro (Solbrig, 1991). However, understanding and predicting how the functioning of the global ecosystem will respond to unprecedented accelerated biodiversity change as a result of human impact remain a key challenge of modern day ecology (Chapin et al., 1998; Sutherland et al., 2013). Two decades of experimental and observational research have advanced our understanding of the relationship between biodiversity, ecosystem processes and functioning ("BEF", Balvanera et al., 2006; Hooper et al., 2005, 2012). But extrapolation of these empirical findings to the larger landscape is difficult, because experimental BEF research often operates at relatively low temporal and spatial scales (Cardinale et al., 2012).

Ecosystem models are synthetic mathematical descriptions of ecosystem processes joined together, guided by a mechanistic understanding of their regulating environmental drivers and biota, which

can be used to project changes in the bulk properties of an ecosystem (Allen et al., 2010). In this way, ecosystem models provide a platform where empirical findings can be used to investigate large-scale questions. Such models can thus be used to investigate BEF and its drivers at large scales (Norberg, 2004; Prowe et al., 2012), potentially providing a holistic view of ecosystems where the impacts of conservation, management, and global scenarios can be assessed (Allen et al., 2007; Artioli et al., 2014; Barange, 2003; Levin et al., 2009). The use of these models therefore provides an invaluable aid in our ability to project possible states of future marine ecosystems under conditions not currently observed and changes imposed by rare events (if constrained by suitable experimental data). This is because observational knowledge is bound within present and past system conditions (Barnsley, 2007).

The benefits of representing biodiversity in ecosystem models are well recognised, with recent work focusing on the evolution of communities (Loreau, 2010 and references therein). The main aim of describing biodiversity structure in models should be to improve model skill for processes of interest (Le Quéré et al., 2005). However, its implementation is challenging and particularly so for highly dynamic marine ecosystems (Allen et al., 2010). The difficulties of representing biological groups and structure in models have been noted by Anderson (2005) and Flynn (2005), who took a critical look at the development of plankton models over the past decades. Here, we build upon their work, expanding the focus onto the more general engagement of modellers

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and ecologists (i.e. empiricists, experimental and observational scientists) in marine BEF research. Collaborations in recent years have brought advances towards a better integration and transfer of knowledge, from small process oriented ecology into macro-scale modelling systems. Here, we provide a synthetic overview of the key challenges for the further engagement between modellers and ecologists, highlighting strategies that the two communities have developed to overcome them, and the consequences of this engagement for the progress of the mechanistic understanding of BEF. To illustrate this, we present two case-studies: a benthic example where data generated by the Western Channel Observatory has been used to include aspects of BEF in the European Regional Seas Ecosystem Model (Blackford et al., 2004); and a pelagic example that was used to implement BEF data from the Belgian coast using the MIRO model (Lancelot et al., 2005).

1.1. Translation across disciplines

Traditionally, scientific programmes proceed from hypothesis to experimentation and observation, and only then to modelling, almost always resulting in inadequate data to properly model the system in question. Involving modellers and ecologists at the conceptual planning stage has improved matters, but also serves to emphasise the disconnect that can exist between the two communities. Often it transpires that each's conceptual understanding of a given system is based on rather different bricks and mortar, i.e. the elements of the system and their interactions. Breaking this conceptual barrier is key to real progress.

In ecology, BEF is perceived to be a complex link, confounded by variability in genetic pools, phenotypical plasticity, species interactions, resource availability and response to environmental variables (Hillebrand et al., 2008; Hoffmann and Sgrò, 2011; Stachowicz et al., 2002). These aspects are not easily aggregated into functional typologies, causality relationships and scenarios, which are necessarily employed in ecosystem modelling to synthesise complex natural systems (Blackford et al., 2004; Chevin et al., 2010). These two apparently conflicting views of biodiversity are not necessarily bound to specific words or terms. Rather, they reflect the different aims and lines of work typically undertaken by the two communities, which require a different structuring of natural complexity for synthesis. Consequentially, the same words can be used by the two communities to describe very different structural elements, representing very distinct degrees of complexity, in support of different aims. For example, ERSEM has been successfully implemented in the last decade using three functional groups to represent sedimentary fauna (“meiofauna”, “suspension feeders” and “deposit feeders”) that are seen as being sufficient to describe the influence of these organisms on the bulk properties of the processes represented in the model (Blackford et al., 2004). However, a benthic ecologist unfamiliar to macro-scale modelling may find this structure to be an over-simplistic misrepresentation of the natural diversity of these communities, within which large numbers of functional groups can be identified within taxa (e.g. Faulwetter et al., 2014; Tyler et al., 2012). Hence, the first and foremost challenge to successfully depict biodiversity in an ecosystem model is the translation of the BEF attribute a modeller may want to include in a model structure (e.g. “macrofauna diversity”, “plankton diversity”, and the process mediated by this) and the complexity underlying that relationship, as seen by the ecologist.

A good translation of concepts requires a clear definition of terminology. Modellers and ecologists share a set of common words, but their meaning is not always identical in the two communities. Clear, common definitions of biodiversity, parameters, state variables, processes, functions (and more) need therefore to be established across disciplines and in practice, at least, early on in research projects. In this way, the probability that data collection, analysis and model structure are well matched is optimised. Furthermore, the modeller needs to be guided in the direction of important, at times diffuse, non-parametric understanding of the problem, the direction of processes and their

drivers, and functional grouping that may be of relevance to the model. The ecologist will require specific information about what are the particular processes and relationships between them that are of interest, what are the state variables in the model, what parameters need constraining, what type of data are required and at what resolution. When the translation of terminology and concepts is successful, ecologists are therefore well positioned to inform and provide data about the key attributes that the model aims to represent. Alternatively, failure can stifle the adequate bounding of the problem, and therefore the identification of the steps necessary to generate solutions (Jeffers, 1978). In such cases, modellers are provided with data which they cannot use (Miller, 2004), modelling outputs are seen with suspicion (Anderson, 2005) and effort is wasted (Flynn, 2005).

1.2. Running before we can walk: poorly understood aspects of BEF

Model development begins with a thorough understanding of the processes at play, and challenges arise when this knowledge is limited (Flynn, 2005). The degree to which a model replicates patterns observed in the real world (i.e. model performance, or skill) is an indication of the adequacy of this understanding. Performance can be assessed with suitably scaled, independent data and statistical methods (Allen et al., 2007; de Mora et al., 2012). At the same time, the ecosystem model should be challenged by expert knowledge in order to check if the mechanisms driving the model response are correctly represented and to assess the reliability of the model to project the ecosystem outside of the observed state. However, currently, several aspects that control the BEF link remain poorly understood, posing interesting challenges to model development.

The response of a species population to a changing environment is constrained by the ability to track optimum habitats. This tracking may involve migration to more suitable environments via dispersal. Alternatively, the potential to adapt to the new local environment depends on two other processes, which operate on different time scales: i) plasticity, the development of a different phenotype resulting from regulation of physiology or behaviour by the environment; and ii) genetic change, whereby environmental pressures influence variation in prevailing phenotypes via selection (Hoffmann and Sgrò, 2011; Somero, 2010).

Dispersal influences local species composition, directly affecting three well understood drivers of the BEF link: selection effects, complementarity in resource use, and species interactions (Hooper et al., 2005; Loreau and Hector, 2001). In principle, dispersal is amenable to conceptualisation in models, via well-established population dynamics formulations. On the other hand, plasticity and genetic change are more subtle modifiers of BEF, with potentially complex effects on its variability (Chevin et al., 2010). Plasticity is directly related to trade-offs: the energetic accounting at the organism level that determines the allocation of resources to processes driven by environmental forcing (like thermal tolerance). In this case, resources may be directed towards pathways that enable persistence in the new environment at the expenses of other organismal processes, like growth, reproduction and foraging behaviour (Pörtner and Knust, 2007). Changes in organismal processes consequentially impact upon the ecosystem processes they mediate, like primary production, and bioturbation (Murray et al., 2013; Norberg, 2004; Pörtner et al., 2012). When trade-offs influence individual fitness, genetic change may also occur (Somero, 2010), with concurring changes in phenotypical distributions and therefore the contribution of communities to ecosystem processes.

Our understanding of how plasticity and genetic change enable marine organisms to cope with chronic exposure to combinations of global stressors is limited. This is because our current knowledge is predominantly based on experimental work that focused on short-term responses of single species to individual stressors (Wernberg et al., 2012). How multiple stressors impact single species, functional guilds and whole communities in the long-term thus remains largely

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