1   **Placing biodiversity in ecosystem models without getting lost in translation**

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10 **Abstract**

11 A key challenge to progressing our understanding of biodiversity's role in the sustenance of

12 ecosystem function is the extrapolation of the results of two decades of dedicated empirical

13 research to regional, global and future landscapes. Ecosystem models provide a platform for

14 this progression, potentially offering a holistic view of ecosystems where, guided by the

15 mechanistic understanding of processes and their connection to the environment and biota,

16 large-scale questions can be investigated. While the benefits of depicting biodiversity in such

17 models are widely recognized, its application is limited by difficulties in the transfer of

18 knowledge from small process oriented ecology into macro-scale modelling. Here, we build

19 on previous work, breaking down key challenges of that knowledge transfer into a tangible

20 framework, highlighting successful strategies that both modelling and ecology communities

21 have developed to better interact with one another. We use a benthic and a pelagic case-study

22 to illustrate how aspects of the links between biodiversity and ecosystem process have been

23 depicted in marine ecosystem models (ERSEM and MIRO), from data, to conceptualisation

24 and model development. We hope that this framework may help future interactions between

25 biodiversity researchers and model developers by highlighting concrete solutions to common

26 problems, and in this way contribute to the advance of the mechanistic understanding of the

27 role of biodiversity in marine (and terrestrial) ecosystems.

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29 Keywords: BEF; biogeochemical; ecosystem function; environmental forcing; functional

30 diversity; species richness; trait;

31

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 remains a key challenge of modern day ecology (Chapin, Sala et al. 1998; Sutherland, Freckleton et al. 2013). Two decades of experimental and observational research have advanced our understanding of the relationship between biodiversity, ecosystem processes and functioning ("BEF", Hooper, ChapinIII et al. 2005; Balvanera, Pfisterer et al. 2006; Hooper, Adair et al. 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, Duffy 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, Aiken 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, Pahlow et al. 2012), potentially providing a holistic view of ecosystems where the impacts of conservation, management, and global scenarios can be assessed (Barange 2003; Allen, Somerfield et al. 2007; Levin, Fogarty et al. 2009; Artioli, Blackford et al. 2014). 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, Harrison et al. 2005). However, its implementation is challenging and particularly so for highly dynamic marine ecosystems (Allen, Aiken et al.

66   2010). The difficulties of representing biological groups and structure in models has been
67   noted by Anderson (2005) and Flynn (2005), who took a critical look at the development of
68   plankton models over the past decades. Here, we build upon their work, expanding the focus
69   onto the more general engagement of modellers and ecologists (i.e. empiricists, experimental
70   and observational scientists) in marine BEF research. Collaborations in recent years have
71   brought advances towards a better integration and transfer of knowledge, from small process
72   oriented ecology into macro-scale modelling systems. Here, we provide a synthetic overview
73   of the key challenges for the further engagement between modellers and ecologists,
74   highlighting strategies that the two communities have developed to overcome them, and the
75   consequences of this engagement for the progress of the mechanistic understanding of BEF.
76   To illustrate this, we present two case-studies: a benthic example where data generated by the
77   Western Chanel Observatory has been used to include aspects of BEF in the European
78   Regional Seas Ecosystem Model (Blackford, Allen et al. 2004); and a pelagic example that
79   was used to implement BEF data from the Belgian coast using the MIRO model (Lancelot,
80   Spitz et al. 2005).
81
82   **1.1 *Translation across disciplines***
83   Traditionally, scientific programmes proceed from hypothesis to experimentation and
84   observation, and only then to modelling, almost always resulting in inadequate data to
85   properly model the system in question. Involving modellers and ecologists at the conceptual
86   planning stage has improved matters, but also serves to emphasise the disconnect that can
87   exist between the two communities. Often it transpires that each's conceptual understanding
88   of a given system is based on rather different bricks and mortar, i.e. the elements of the
89   system and their interactions. Breaking this conceptual barrier is key to real progress.
90
91   In ecology, BEF is perceived to be a complex link, confounded by variability in genetic
92   pools, phenotypical plasticity, species interactions, resource availability and response to
93   environmental variables (Stachowicz, Fried et al. 2002; Hillebrand, Bennett et al. 2008;
94   Hoffmann and Sgrò 2011). These aspects are not easily aggregated into functional typologies,
95   causality relationships and scenarios, which are necessarily employed in ecosystem
96   modelling to synthesise complex natural systems (Blackford, Allen et al. 2004; Chevin,
97   Lande et al. 2010). These two apparently conflicting views of biodiversity are not necessarily
98   bound to specific words or terms. Rather, they reflect the different aims and lines of work
99   typically undertaken by the two communities, which require a different structuring of natural

100 complexity for synthesis. Consequentially, the same words can be used by the two
101 communities to describe very different structural elements, representing very distinct degrees
102 of complexity, in support of different aims. For example, ERSEM has been successfully
103 implemented in the last decade using three functional groups to represent sedimentary fauna
104 ("meiofauna", "suspension feeders" and "deposit feeders") that are seen as being sufficient to
105 describe the influence of these organisms on the bulk properties of the processes represented
106 in the model (Blackford, Allen et al. 2004). However, a benthic ecologist unfamiliar to
107 macro-scale modelling may find this structure to be an over-simplistic misrepresentation of
108 the natural diversity of these communities, within which large numbers of functional groups
109 can be identified within taxa (e.g. Tyler, Somerfield et al. 2012; Faulwetter, Markantonatou et
110 al. 2014). Hence, the first and foremost challenge to successfully depict biodiversity in an
111 ecosystem model is the translation of the BEF attribute a modeller may want to include in a
112 model structure (e.g. "macrofauna diversity", "plankton diversity", and the process mediated
113 by this) and the complexity underlying that relationship, as seen by the ecologist.

114

115 A good translation of concepts requires a clear definition of terminology. Modellers and
116 ecologists share a set of common words, but their meaning is not always identical in the two
117 communities. Clear, common definitions of biodiversity, parameters, state variables,
118 processes, functions (and more) need therefore to be established across disciplines and in
119 practice, at least, early on in research projects. In this way, the probability that data
120 collection, analysis and model structure are well matched is optimised. Furthermore, the
121 modeller needs to be guided in the direction of important, at times diffuse, non-parametric
122 understanding of the problem, the direction of processes and their drivers, and functional
123 grouping that may be of relevance to the model. The ecologist will require specific
124 information about what are the particular processes and relationships between them that are
125 of interest, what are the state variables in the model, what parameters need constraining, what
126 type of data are required and at what resolution. When the translation of terminology and
127 concepts is successful, ecologists are therefore well positioned to inform and provide data
128 about the key attributes that the model aims to represent. Alternatively, failure can stifle the
129 adequate bounding of the problem, and therefore the identification of the steps necessary to
130 generate solutions (Jeffers 1978). In such cases, modellers are provided with data which they
131 cannot use (Miller 2004), modelling outputs are seen with suspicion (Anderson 2005) and
132 effort is wasted (Flynn 2005).

133

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, Somerfield et al. 2007; de Mora, Butenschön 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, that 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 (Somero 2010; Hoffmann and Sgrò 2011).

 Dispersal influences local species composition, directly affecting three well understood drivers of the BEF link: selection effects, complementarity in resource use, and species interactions (Loreau and Hector 2001; Hooper, ChapinIII et al. 2005). 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, Lande 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 (Norberg 2004; Pörtner, Peck et al. 2012; Murray, Widdicombe et al. 2013). When trade-offs influence individual fitness, genetic change may also occur

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168 (Somero 2010), with concurring changes in phenotypical distributions and therefore the
169 contribution of communities to ecosystem processes.

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171 Our understanding of how plasticity and genetic change enable marine organisms to cope
172 with chronic exposure to combinations of global stressors is limited. This is because our
173 current knowledge is predominantly based on experimental work that focused on short-term
174 responses of single species to individual stressors (Wernberg, Smale et al. 2012). How
175 multiple stressors impact single species, functional guilds and whole communities in the
176 long-term thus remains largely unquantified. Additionally, species interactions add
177 significant complexity to the shaping of the BEF link but are not always quantified in
178 biodiversity research (Cardinale, Duffy et al. 2012). In particular, their importance across
179 life-stages has been recognised, but more work is still needed (Estes, Terborgh et al. 2011;
180 Harley 2011; Russell, Harley et al. 2012).

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182 In present day ecosystem modelling, there is thus a need to translate observed mechanisms
183 (short-term, single species) into conceptual models that include combinations of species and
184 environmental gradients not yet observed (multiple stressors, long-term, interacting species).
185 This is an important example of the challenge inherent to the integration of knowledge gained
186 in small scaled empirical research into macro-scale modelling. There is no clear solution to
187 this issue beyond the need to integrate additional knowledge once it becomes available. A
188 degree of caution is thus required in the interpretation of such work, but awareness about the
189 assumptions made at each stage (i.e. model traceability) should provide the basis of any
190 model development. Further investigation of species interactions, plasticity, and genetic
191 change as drivers of BEF in long-term and multi-stressor experiments, could therefore
192 significantly help build a common way forward for the implementation of important
193 biodiversity concepts into ecosystem modelling.

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195 Testing of specific formulations of the BEF link using ecosystem models can help to
196 elucidate poorly understood underlying ecological mechanisms, as done in other fields
197 (Loreau 1998; Polimene, Archer et al. 2012; Prowe, Pahlow et al. 2012). Low model skill
198 could, in such cases, help to highlight deficiencies in the functional structure used, lack of
199 understanding of physiological mechanisms (e.g. plasticity), and an inappropriate degree of
200 complexity in the interconnection of model components (e.g. species, functional groups,
201 trophic levels). Model parameters can also be optimised where observational/experimental

202	data are available. This approach enables a direct quantification of the variation in the data
203	not explained by the model, highlighting aspects of model structure needing refinement, even
204	before the drivers of variation are fully understood (Butenschön, Polimene et al. 2010; Ward,
205	Friedrichs et al. 2010). Thus, limited understanding of particular aspects of the BEF link
206	should not hinder the ambition to include it in ecosystem models. Rather, these can be used to
207	test hypotheses, elucidate areas of uncertainty and, correspondingly, help identify future areas
208	for BEF research.
209

210	## 2. *Conceptualising BEF in models*

211	The complexity of the BEF link often seems incompatible with the degree of simplification
212	needed by ecosystem models that deal with physical processes at high resolution.
213	Computational resources have historically posed an upper limit on model detail, enforcing a
214	balance between modelled complexity and resolution. Consequently, detail was typically
215	expanded only where there was both a need to improve emergent properties and adequate
216	data for parameterisation. In the present day, computational power has become less limiting;
217	and so the practical dialogue between modellers and ecologists about what degree of
218	complexity should be included in models has become possible. Currently, complexity
219	associated with biological systems is omitted if its impact on model performance is deemed
220	acceptable and model structure remains plausible. As with any model, there is thus a delicate
221	balance to be struck between the inherently synthetic structure of an ecosystem model and
222	capturing enough detail about nature to bring model predictions close to the ecosystem's true
223	state (Einstein 1934; Bruggeman and Kooijman 2007; Allen, Aiken et al. 2010). What degree
224	of complexity associated with biodiversity (and biological structure in general) is deemed as
225	essential depends upon the model purpose, the research question, and the degree to which the
226	BEF aspect at stake is understood. The latter is thus seen as the starting point of the process
227	of conceptualising BEF in macro-scale models, which is tentatively depicted in figure 1. We
228	provide this diagram as a means to break down the complex interaction between modeller and
229	ecologist faced with the task of including some aspect of BEF in an ecosystem model, as
230	described in the following.
231

232	The need for simplicity, and the widespread appreciation that the interaction of organisms
233	with their environment are determined by traits, underpin the widespread use of functional
234	typologies in ecosystem modelling (Anderson 2005). By definition, traits are well-defined,
235	measurable properties of organisms that, when linked to ecosystem processes and function,

can be used to investigate the functional impacts of changes in biodiversity (i.e. "functional traits", McGill, Enquist et al. 2006; Petchey and Gaston 2006). Functional diversity, i.e. "number, type and distribution of functions performed by organisms within an ecosystem" (Díaz and Cabido 2001) thus provides a tangible strategy to synthesize biodiversity in ecosystem models (box 9a in Fig.1). This approach invites explicit formulations to be made about what species do in ecosystems, their relationship with environmental gradients and therefore niche space, trade-offs, interactions and performance currencies (McGill, Enquist et al. 2006; Litchman, Klausmeier et al. 2007). For these reasons, representing functional diversity in models has received large interest, despite often not being named explicitly as such (Baretta, Ebenhöh et al. 1995; Le Quéré, Harrison et al. 2005). Such representations of functional diversity may be good depictions of the "natural ecology" of the groups represented (i.e. defined via traits that reflect response to the environment), but are more often better at representing the impact of groups on ecosystem processes (i.e. effect traits, Chown, Gaston et al. 2004). Nevertheless, their implementation in models brings a new set of challenges to the modeller-ecologist dialogue: what traits underly a specific process of interest; how do they relate to physiology and trade-offs; and what is their natural variability across levels of organisation, that within and between species. Unfortunately, even in well studied systems, knowledge about the most basic traits is often limited to a small proportion of species (Tyler, Somerfield et al. 2012). This can be problematic, because the observation of a small number of species may lead to incorrect conclusions about the contribution of specific traits toward a specific process (Flynn 2005; Le Quéré, Harrison et al. 2005). There is clearly a need to improve the availability of functional trait information for marine ecosystems, and significant efforts have been made in recent years (Brey 2001; Bremner, Rogers et al. 2006; MarLIN 2006; Bruggeman 2011; Barton, Pershing et al. 2013; Queirós, Birchenough et al. 2013; Faulwetter, Markantonatou et al. 2014 and others).

If information on the distribution of traits of interest in the studied ecosystem is available, the subsequent question is how this diversity should be represented in the model, i.e. how to reduce the observed biodiversity into groups of species that share common trait values. These groups are referred to as functional groups, or types (box 9a, Fig.1) and functional typologies are employed in nearly all ecosystem models, in one way or another. The decision about which functional typology to use is a common cause of disagreement between modeller and ecologist, requiring a very clear understanding of the purpose of the model by both sides, and therefore of the compromises required. The strategies employed to define where that

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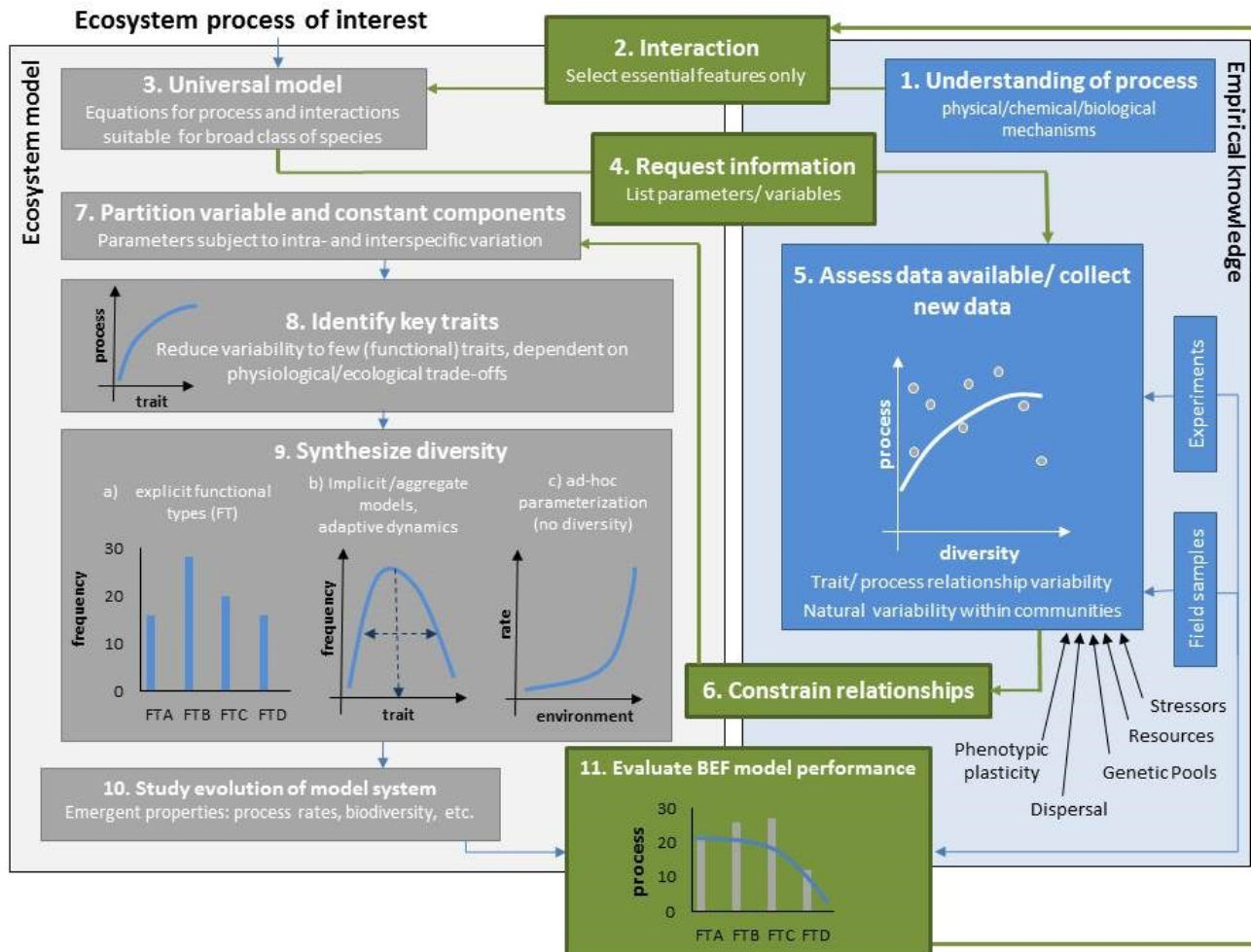
Figure 1: Conceptualising biodiversity in an ecosystem model. Schematic representation of the steps carried out by modeller and ecologist during the process of representing BEF in an ecosystem model, under a specific research question. The two parties are perceived to be engaging at any given point in the process, but the need for that engagement to be efficient is particularly relevant in the steps illustrated by green boxes.

274   compromise lies are varied, but are often balanced by the following five factors (in no

275   particular order). First, every newly identified functional type requires a specific model

276   structure and parameterisation. This places great demand on the quantity and quality of

277   empirical information required to constrain the model (boxes 4 to 6 in Fig.1), and as seen,

278   functional trait information is often scarce. Second, increased complexity in functional

279   typology may increase model instability (Denman 2003), although it may also increase the

280   applicability of a model to a wider range of systems (i.e. increase model portability, Law and

281   Blackford 1992; Friedrichs, Dusenberry et al. 2007). Third, expansion of the number of

282   functional types may come at a non-negligible computational cost, and as a result, the

283   functional typology chosen may become too artificial, clumping together very distinct types

284   of organisms (Anderson 2005) . Fourth, increased model complexity can lead to increased

285   difficulty in the assessment of the meaningfulness of modelling outputs (both in quantity and

286   quality, fig 1, arrow from box 11 to 2). Fifth, the specific purpose of the model (i.e. the

287   research question) should direct this decision.

288

289   As illustrated in figure 1, the choice of particular functional typology (box 9a in Fig.1) can be

290   informed based on *a-priori* ecological understanding and/or the availability of data on key

291   functional traits within a particular study system (box 5 in Fig.1). The difficulty associated

292   with this pre-determination of (often low) functional diversity in models, and the decision

293   about which functional types are dominant, can be circumvented by an alternative trait-based

294   stochastic approach (fig.9b). In this case, large numbers of functional groups are defined

295   initially based on a small number of traits, which are perceived to be essential to predict a

296   particular process, and explicitly linked to physiology, trade-offs and ecology in the model. A

297   self-organising process is then allowed to take place over time. This process consists of

298   functional types interacting in a prescribed way (e.g. via competition for a specific resource)

299   during simulations, leading to a decrease in the number of (surviving) functional types over

300   time ("stochastic" approach, Follows, Dutkiewicz et al. 2007). This approach has been used

301   to predict with great consistency geographical habitat, rank abundance and physiological

302   specialisation of functional types of phytoplankton (Bruggeman and Kooijman 2007;

303   Follows, Dutkiewicz et al. 2007), showing great potential for other areas of biodiversity

304   research. This approach appeals for its simplicity and economy of parameters, which may be

305   constrained using specific values for each functional group, or be characterised by a given

306   mean and dispersion (box 9b in figure 1). It may, however, be restricted to systems where a

307   BEF relationship is well understood.

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The use of continuous trait space (the semi-explicit approach in box 9b, by which a community has a distribution for each trait that is made up by the distribution of individual functional types) has merit for its simplicity of parameter use, flexibility and elegance of emulation of changes in community structure (e.g. body size, Bruggeman and Kooijman 2007). It may, however, be difficult to implement with non-quantitative traits, like type of larval development, or sediment re-working mode. In such cases, use of different models may be a better approach to characterise the contribution of individual functional groups to a specific BEF relationship, challenging usage in ecosystem models with possible unwanted complexity.

Whether one general, semi-explicit model is used to describe the trait/process relationship, or whether different models per functional type are used explicitly, is thus a point for consideration (box 9, Fig. 1). In practice, models of the more complex ecosystems are likely to adopt elements of both functional type and trait-based representations of biodiversity (boxes 9a and b). While these approaches may be desirable, our limited understanding of the role of biodiversity in mediating function, or a hereto limited ability to translate such understanding to macro-scale modelling, means that it is actually not uncommon for such representation to be done implicitly (box 9c in figure 1). That is, in such cases, the representation of biodiversity is by-passed (box9c), leading to an undesirable representation of processes that ignores the contribution of biological variability to these. As such, many models have been better at implementing the "EF" in BEF than the "B".

Once the model structure is defined, the model runs can be evaluated against empirical data (box 11) and the results interrogated. Evaluation of the model against observational data limits the assessment to present and past system conditions and experimental data may be more suitable to evaluate model simulations of future states, not presently observed. If the skill of the model is unsatisfactory, it is thus necessary to re-iterate the cycle of interaction (box 2), considering the refinement of the model and traits considered (boxes 2 and 3), a re-evaluation of the suitability of the data and evaluation method used (boxes 5 and 11, Allen and Somerfield 2009; de Mora, Butenschön et al. 2012) and/or the request of additional data (box 4). Here too, the definition of what level of skill is acceptable (box 11) depends on the purpose of the model and the research question to hand.

As a sequence of explicit steps, we hope that the framework described here may help other researchers interested in this type of cross-discipline work by objectively defining the tasks

342 involved in the process, highlighting particular stages when strategic decisions need to be
343 made (e.g. boxes 9 and 11), and alternative routes forward. This definition of the different
344 stages of the process is therefore aimed to provide a tangible route through which the
345 identification of key data and methodological requirements can be carried out, facilitating the
346 identification and resolution of limitations to progress.
347

348 **2.1** *Case-studies from the Eastern Atlantic Region*
349 Here, we provide two case studies, using figure 1 as a means to illustrate the steps involved in
350 the engagement of modeller and ecologist in ecosystem model development for the specific
351 purpose of depicting a BEF link. We use a benthic and a pelagic example, and two distinct
352 ecosystem models, to highlight that even in different areas of BEF research this engagement
353 has significant commonalities.
354

355 *2.1.1 Benthic case-study*
356 Bioturbation, the mixing of sediment and particulate materials carried out by sedimentary
357 organisms during foraging, feeding and burrow maintenance activities (Richter 1936; Rhoads
358 1974; Volkenborn, Polerecky et al. 2010) has a regulatory role in marine sedimentary
359 oxygen, pH and redox gradients, metal cycling, sediment granulometry, pollutant release,
360 macrofauna diversity, bacterial activity and composition, and carbon and nitrogen cycling
361 (Queirós, Birchenough et al. 2013 and references therein). This process has thus been
362 included in new developments of the European Regional Seas Ecosystem Model (ERSEM,
363 Blackford, Allen et al. 2004), to improve the model's ability to simulate benthic infauna and
364 their role in the regulation of benthic-pelagic nutrient fluxes. Using figure 1, bioturbation is
365 thus the ecosystem process of interest, and various possible general descriptions of the
366 bioturbation process have been considered (boxes 1, 2 and 3, Crank 1979; Soetaert, Herman
367 et al. 1996; Maire, Duchene et al. 2006; Schiffers, Teal et al. 2011). Information was
368 requested from the ecologist community at Plymouth Marine Laboratory (box 4) and a
369 dedicated research program has thus been undertaken as part of the monitoring program at the
370 Western Chanel Observatory (box 5). This data collection was guided (box 1) by early
371 dialogue between ecologist and modeller about partitioning of variability (box 7) associated
372 with seasonality (Maire, Duchêne et al. 2007) and habitat type in the study system
373 (Mermillod-Blondin and Rosenberg 2006). For example, to illustrate box 5, we have found
374 that the intensity of bioturbation (traditionally described through the calculation of the
375 biodiffusion coefficient, Guinasso and Schink 1975) decreases with the number of species in

the community, which is lowest at the end of winter and highest in late summer (Queirós, Stephens et al. *in review*). We also found that different functional groups of bioturbator species within the community contribute to this type of local transport differently (Queirós, Stephens et al. *in review*).This process would correspond to boxes 5 and 6 in figure 1. The explicit need to synthesise this information for conceptualisation in ERSEM (box 6, fig.1) has led to the understanding that the tendency in the bioturbation literature towards labelling of distinct processes (biodiffusive transport, bioturbation depth, bioturbation potential) under the common designation of "bioturbation" is misleading from a mechanistic point of view. This is because those different components have distinct environmental driver and response pathways (Queirós, Stephens et al. *in review*). Therefore, labelling them under the same term ("bioturbation") does not contribute towards a better mechanistic understanding of the contribution of burrowing fauna to the mediation of biogeochemical processes. Hence, in this case, the need for synthesis of empirical data with the aim of model development (box 6, fig.1) helped to highlight a shortcoming in our understanding of bioturbation as a multi-faceted process (c.f. Kristensen, Penha-Lopes et al. 2012).This information is now being used to improve bioturbation trait descriptions in the model (boxes 7 to 9). An evaluation strategy has been formulated, and new model structure implementations will be validated against the data (boxes 10 and 11). The explicit representation of biodiversity in the BEF relationship will be implemented in the subsequent model structure development. In its present form, the representation of bioturbation is still better represented by box 9c, and is currently being evaluated against seasonal response in infaunal biomass and benthic-pelagic nutrient fluxes (box 11).

2.1.2 Pelagic case-study

Diatoms play a crucial role in marine ecosystems and biogeochemical cycles (Sarthou, Timmermans et al. 2005; Armbrust 2009). They exhibit remarkable diversity in many traits including size. In the English Channel-North Sea region alone, field sampling programs indicate that diatom species span nearly seven orders of magnitude in cell volume (Rousseau, Leynaert et al. 2002; Widdicombe, Eloire et al. 2010). Significantly, this variability has a seasonal component: the community mean cell volume (log-transformed, biovolume-weighted) in this region reaches a minimum in late spring (6,000 μm^3 at the Western Channel Observatory, 10,000 μm^3 in the Belgian Coastal Zone) and a maximum in autumn (70,000 μm^3 in the WCO, 200,000 μm^3 in the BCZ).

409 Calculations based on allometric relationships suggest that the observed one order of
410 magnitude variation in mean diatom size is likely to coincide with a change of at least 35 %
411 in traits related to resource acquisition and grazer susceptibility (Terseleer, Bruggeman et al.
412 Submitted). In turn, these traits affect carbon export and energy transfer to higher trophic
413 levels. Thus, changes in diatom community composition, quantified by changes in mean cell
414 size, can exert a major impact on ecosystem functioning. Nevertheless, marine ecosystem
415 models used for this region generally do not resolve diatom diversity (Baretta, Ebenhöh et al.
416 1995; Lancelot, Spitz et al. 2005; Le Quéré, Harrison et al. 2005). Their diatom
417 parameterizations are invariant across the seasons, and cannot reflect the plasticity of the
418 diatom community that results from changes in community composition and biodiversity.

419 To address this, Terseleer, Bruggeman et al. (Submitted) add diatom diversity to the marine
420 ecosystem model MIRO (Lancelot, Spitz et al. 2005). The universal diatom model in figure 1
421 (boxes 1-3) is in this case based on the original MIRO implementation (Lancelot, Spitz et al.
422 2005), which interacts with several ecosystem components through nutrient uptake, light
423 dependency, and consumption by copepods. To quantify the variation in diatom functional
424 traits (boxes 4-5), measured trait values are collected from literature (Taguchi 1976; Ingrid,
425 Andersen et al. 1996; Sarthou, Timmermans et al. 2005; Litchman, Klausmeier et al. 2007;
426 Marañón, Cermeño et al. 2013). This compilation suggests that several diatom traits are
427 subject to significant interspecific variability. These traits include maximum growth rate,
428 nutrient half-saturation, light affinity, and susceptibility to copepod grazing (box 7). Much of
429 the variability in these functional traits is captured by allometric relationships that link the
430 trait value to cell size. That is, variability in many functional processes (y-axis in box 5) can
431 be linked to variability in a single trait (x-axis in box 5): size. Based on this conclusion,
432 modelled diatoms are characterised by their cell volume alone, which sets the value of all
433 other traits (box 8). The composition of the diatom community is now completely described
434 by its size distribution. To include this distribution in the model (box 9), a computationally
435 efficient, aggregate approach is used that only tracks key statistics of the community (total
436 biomass, mean and variance of cell volume, Norberg, Swaney et al. 2001, box 9b). Notably,
437 this explicitly includes a measure of functional diversity, in the form of the variance of the
438 cell volume, and its link to ecosystem functioning.

439 After calibration to measured nutrients (dissolved inorganic nitrogen, phosphorous, silicate)
440 and biomasses of several functional types (diatoms, *Phaeocystis*, nanoflagellates, copepods,
441 microzooplankton, bacteria) in the Belgian Coastal Zone (BCZ), the model correctly captures
442 both the magnitude and seasonality of diatom size (which was not used during calibration):

15

443   low grazer concentrations in early spring favour a community of small, fast-growing diatom

444   species, which are replaced by larger species as grazing pressure increases over summer.

445   Bottom-up and top-down selection pressures peak during and just after termination of the

446   spring bloom (May-June), causing a minimum in size diversity in early summer that recovers

447   only in late autumn-winter. The model also predicts the viable size range for the BCZ region

448   (400 to 10^7 μm^3), which approximates the range of sizes observed in the field (78 to 1.4×10^7

449   μm^3). Additionally, representation of the size distribution modestly improves model

450   predictions for bulk variables including nutrient concentrations and plankton biomass (boxes

451   10-11).

452

453   **3. Future direction: what do we still need?**

454   For the purpose of this discussion we have portrayed the ecologist and modelling

455   communities as distinct groups. However, in practise, the two communities represent

456   different points on a continuum, ranging from ecologists with no modelling expertise at one

457   end, to mathematicians and physicists with limited ecological understanding at the other.

458   Most ecologists and modellers fall somewhere between the two extremes. Initiatives aimed to

459   promote communication across this continuum, e.g. open-source ecosystem models (ERSEM,

460   http://www.shelfseasmodelling.org/index-en) are leading to an increase in a centre-ground

461   population of model-savvy ecologists and ecologically competent modellers. This central

462   dialogue is of utmost importance, ensuring that expertise generated at the ends of the

463   continuum is integrated by the community, and used in model development. It is precisely

464   this dialogue that the current paper addresses.

465

466   Transference of knowledge is taking place, and ecosystem models are being developed with

467   increasingly better depictions of BEF. The associated challenges of communication have

468   been discussed here, but it cannot be stressed enough how paramount to the process it is for

469   ecologist and modellers to invest time and effort to insure that that communication across the

470   continuum is effective. Clarification of terminology and concepts that are mutually

471   understood are key to any subsequent work, and researchers should be quick to raise

472   questions where doubt remains. Use of this common language typically follows a learning

473   curve, so early stage failures should be weighted accordingly.

474

475   With regard to the data required for future ecosystem model development that includes BEF,

476   several aspects deserve consideration. While issues of data availability concerning trait

477 information and less understood aspects of BEF have already been considered here, there is a
478 much wider need for contextualising information associated with any empirical dataset that
479 should preclude the inclusion of BEF understanding in an ecosystem model. Because
480 ecosystem models are mathematical descriptions of how a number of ecosystem processes
481 relate to each other, to biological systems and the environment, model development requires
482 that basic information associated with system conditions is considered when relationships are
483 constrained (box 6, figure 1). For instance, a dataset describing how competition between two
484 functional types of plankton for a specific resource changes in relation to a stressor (e.g.
485 ocean acidification) is of little use if no other information is provided about very basic, yet
486 key, regulating parameters such a light, temperature, season, and nutrient availability.
487 Without such data, this very relevant information about one specific box in the ecosystem
488 model cannot be adequately linked to other model components (like environmental forcing,
489 or nutrient fluxes). Furthermore, while relevant to any model development, contextual
490 information is crucial specifically for observational BEF findings because species will have
491 undergone selective processes (species sorting) that influence which traits are present within
492 natural communities, and thus the performance of individual organisms towards processes
493 (Norberg 2004). Provision of this contextualizing information (or meta-data) can be improved
494 if ecologists more frequently consider future uses of their data beyond their particular
495 discipline, and particularly, ecosystem-level applications. Here too, engagement between
496 modellers and ecologists early on in projects (including the writing stage) is key to greater
497 awareness.

498

499 On the same level, mechanistic understanding – that at the core of macro-scale modelling -
500 requires information about process history. I.e. high quality and high frequency
501 measurements of the particular BEF link of interest and of the conventional environmental
502 parameters associated with it. This type of work contrasts with the outputs of traditional
503 (observational and experimental) research which, being limited by funding constrains, is
504 often only able to provide a snapshot of processes and their support in biodiversity. Lack of
505 information about process history leads to a type of model development that imposes
506 particular conditions to force specific responses, rather than representing mechanisms that
507 cause responses. Those would (ideally) emerge from the model. Repeated, comparable
508 measurements of specific BEF links across time and a range of conditions are thus of great
509 use to modellers. Unfortunately, funding bodies may be keener to lend support to novel areas
510 of research and less inclined to fund what may be perceived as a repetition of a previous body

511 of work. One possible alternative route is meta-analysis, the quantitative assessment of large
512 numbers of studies at once (Hedges, Gurevitch et al. 1999). This approach has become a
513 successful framework to scrutinise and synthesise ruling principles uncovered by empirical
514 ecological science in the last decade, and such work has started to emerge in the BEF
515 literature (Cardinale, Matulich et al. 2011; Hooper, Adair et al. 2012). Meta-analysis can help
516 to identify drivers of BEF relationships that are not apparent in single system studies,
517 providing an objective route to compare the results of different studies under a common
518 question(Hooper, Adair et al. 2012). This approach may therefore become an important
519 alternative intermediate source of mechanistic BEF information for model developers in the
520 near future, helping to separate evidence from judgement, given the necessary caution for the
521 interpretation of such summary approaches (Dupont, Dorey et al. 2010; Hendriks and Duarte
522 2010). Consideration of this approach should take place explicitly during model development
523 (steps 1 or 4, Fig.1).

524

525 A remaining hurdle for the inclusion of realistic descriptions of biodiversity in macro-scale
526 models is our limited understanding of the role of multi-functionality in BEF (Hector and
527 Bagchi 2007; Hiddink, Davies et al. 2009; Gamfeldt, Snäll et al. 2013). Multi-functionality is
528 relevant to the current discussion because of the need to summarise biodiversity into a finite
529 number of traits or functional types in models. From the point of view of advancing the
530 mechanistic understanding of how biodiversity contributes to ecosystem processes and
531 function, Leibold's concept of "impact niche", the sum of the roles a species has in an
532 ecosystem (Leibold 1995), is thus of great relevance. However, we have very little
533 information about how traits that are relevant to one process may influence another because
534 very few studies have measured the direct contributions to multiple processes simultaneously.
535 Future representations of biodiversity in ecosystem models where a number of processes are
536 described should therefore aspire to at least interrogate the role of multi-functionality in BEF.
537 This too is a gap that empirical science can help to fill. However, considering the complexity
538 of the modeller-ecologist interaction, other poorly understood aspects of BEF and data
539 requirements for single processes; it seems that this gap may be one that will remain for some
540 time to come.

541

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555

556 **Author contributions**

557 AMQ, JB, NS, YA, MB, JCB and SW conceived the rationale for the manuscript. AMQ, JB

558 and NS wrote the manuscript. All authors contributed to the text.

559

560 **Conflicts of interest**

561 None stated.

562

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