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.

2010). The difficulties of representing biological groups and structure in models has 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 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 Chanel Observatory has been used to include aspects of BEF in the European Regional Seas Ecosystem Model (Blackford, Allen et al. 2004); and a pelagic example that was used to implement BEF data from the Belgian coast using the MIRO model (Lancelot, Spitz 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 (Stachowicz, Fried et al. 2002; Hillebrand, Bennett et al. 2008; Hoffmann and Sgrò 2011). 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, Allen et al. 2004; Chevin, Lande 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

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

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

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).

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.

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

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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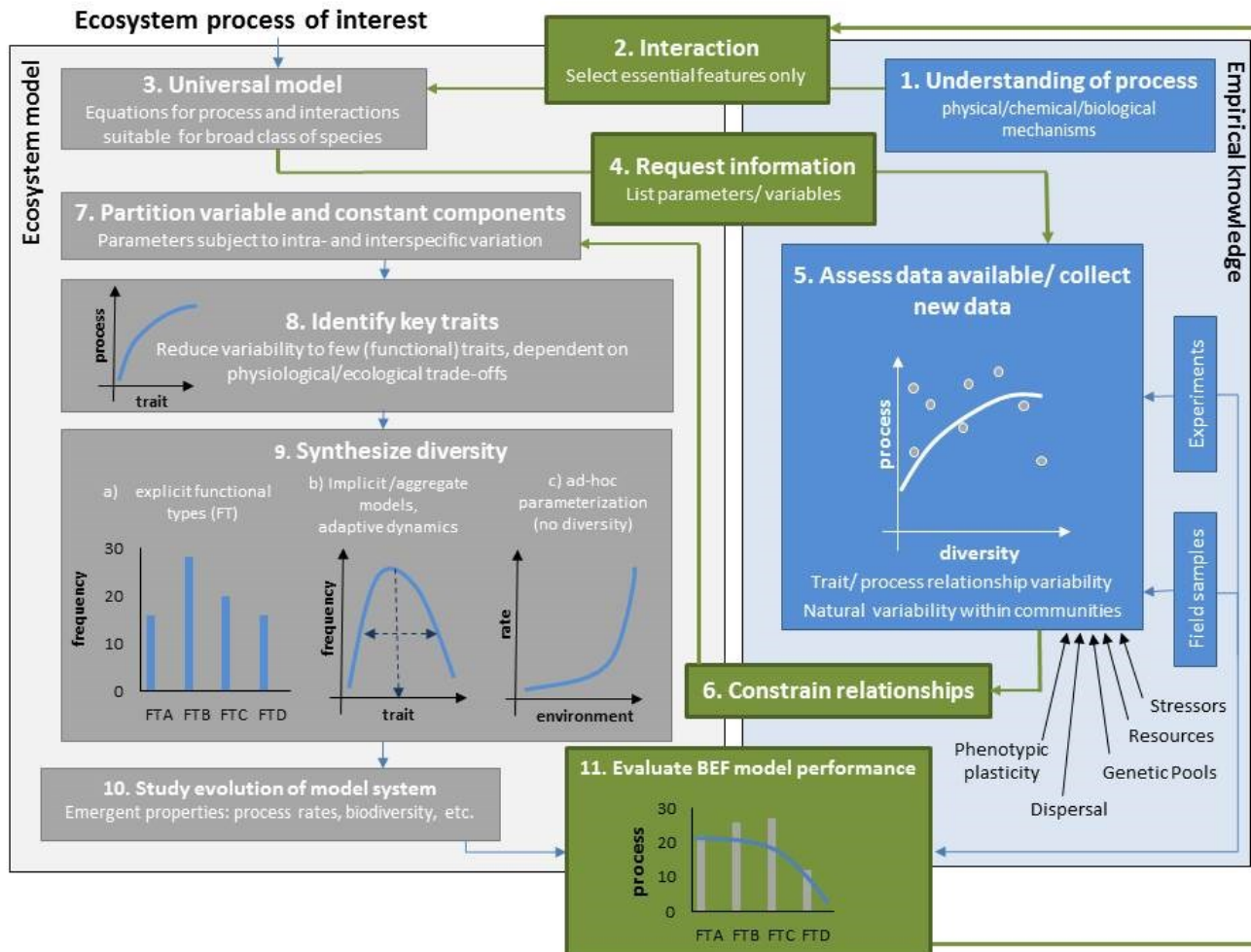
Figure 1: Conceptualising biodiversity in an ecosystem model. Schematic representation of the steps carried out by modeller and ecologist during the process of representing BEF in an ecosystem model, under a specific research question. The two parties are perceived to be engaging at any given point in 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.

308

309   The use of continuous trait space (the semi-explicit approach in box 9b, by which a

310   community has a distribution for each trait that is made up by the distribution of individual

311   functional types) has merit for its simplicity of parameter use, flexibility and elegance of

312   emulation of changes in community structure (e.g. body size, Bruggeman and Kooijman

313   2007). It may, however, be difficult to implement with non-quantitative traits, like type of

314   larval development, or sediment re-working mode. In such cases, use of different models may

315   be a better approach to characterise the contribution of individual functional groups to a

316   specific BEF relationship, challenging usage in ecosystem models with possible unwanted

317   complexity.

318

319   Whether one general, semi-explicit model is used to describe the trait/process relationship, or

320   whether different models per functional type are used explicitly, is thus a point for

321   consideration (box 9, Fig. 1). In practice, models of the more complex ecosystems are likely

322   to adopt elements of both functional type and trait-based representations of biodiversity

323   (boxes 9a and b). While these approaches may be desirable, our limited understanding of the

324   role of biodiversity in mediating function, or a hereto limited ability to translate such

325   understanding to macro-scale modelling, means that it is actually not uncommon for such

326   representation to be done implicitly (box 9c in figure 1). That is, in such cases, the

327   representation of biodiversity is by-passed (box9c), leading to an undesirable representation

328   of processes that ignores the contribution of biological variability to these. As such, many

329   models have been better at implementing the "EF" in BEF than the "B".

330   Once the model structure is defined, the model runs can be evaluated against empirical data

331   (box 11) and the results interrogated. Evaluation of the model against observational data

332   limits the assessment to present and past system conditions and experimental data may be

333   more suitable to evaluate model simulations of future states, not presently observed. If the

334   skill of the model is unsatisfactory, it is thus necessary to re-iterate the cycle of interaction

335   (box 2), considering the refinement of the model and traits considered (boxes 2 and 3), a re-

336   evaluation of the suitability of the data and evaluation method used (boxes 5 and 11, Allen

337   and Somerfield 2009; de Mora, Butenschön et al. 2012) and/or the request of additional data

338   (box 4). Here too, the definition of what level of skill is acceptable (box 11) depends on the

339   purpose of the model and the research question to hand.

340   As a sequence of explicit steps, we hope that the framework described here may help other

341   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

376 the community, which is lowest at the end of winter and highest in late summer (Queirós,

377 Stephens et al. *in review*). We also found that different functional groups of bioturbator

378 species within the community contribute to this type of local transport differently (Queirós,

379 Stephens et al. *in review*).This process would correspond to boxes 5 and 6 in figure 1. The

380 explicit need to synthesise this information for conceptualisation in ERSEM (box 6, fig.1) has

381 led to the understanding that the tendency in the bioturbation literature towards labelling of

382 distinct processes (biodiffusive transport, bioturbation depth, bioturbation potential) under the

383 common designation of "bioturbation" is misleading from a mechanistic point of view. This

384 is because those different components have distinct environmental driver and response

385 pathways (Queirós, Stephens et al. *in review*). Therefore, labelling them under the same term

386 ("bioturbation") does not contribute towards a better mechanistic understanding of the

387 contribution of burrowing fauna to the mediation of biogeochemical processes. Hence, in this

388 case, the need for synthesis of empirical data with the aim of model development (box 6,

389 fig.1) helped to highlight a shortcoming in our understanding of bioturbation as a multi-

390 faceted process (c.f. Kristensen, Penha-Lopes et al. 2012).This information is now being used

391 to improve bioturbation trait descriptions in the model (boxes 7 to 9). An evaluation strategy

392 has been formulated, and new model structure implementations will be validated against the

393 data (boxes 10 and 11). The explicit representation of biodiversity in the BEF relationship

394 will be implemented in the subsequent model structure development. In its present form, the

395 representation of bioturbation is still better represented by box 9c, and is currently being

396 evaluated against seasonal response in infaunal biomass and benthic-pelagic nutrient fluxes

397 (box 11).

398

399 *2.1.2 Pelagic case-study*

400 Diatoms play a crucial role in marine ecosystems and biogeochemical cycles (Sarthou,

401 Timmermans et al. 2005; Armbrust 2009). They exhibit remarkable diversity in many traits

402 including size. In the English Channel-North Sea region alone, field sampling programs

403 indicate that diatom species span nearly seven orders of magnitude in cell volume (Rousseau,

404 Leynaert et al. 2002; Widdicombe, Eloire et al. 2010). Significantly, this variability has a

405 seasonal component: the community mean cell volume (log-transformed, biovolume-

406 weighted) in this region reaches a minimum in late spring (6,000 μm^3 at the Western Channel

407 Observatory, 10,000 μm^3 in the Belgian Coastal Zone) and a maximum in autumn (70,000

408 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):

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

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

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

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

555

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

Conflicts of interest

561 None stated.

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