

## **Marine biodiversity and ecosystem function relationships: the potential for practical monitoring applications**

James Asa Strong<sup>1\*</sup>, Eider Andonegi<sup>2</sup>, Kemal Can Bizsel<sup>3</sup>, Roberto Danovaro<sup>4</sup>, Mike Elliott<sup>1</sup>, Anita Franco<sup>1</sup>, Esther Garces<sup>5</sup>, Sally Little<sup>1</sup>, Krysia Mazik<sup>1</sup>, Snejana Moncheva<sup>6</sup>, Nadia Papadopoulou<sup>7</sup>, Joana Patrício<sup>8</sup>, Ana M. Queirós<sup>9</sup>, Chris Smith<sup>7</sup>, Kremena Stefanova<sup>6</sup> and Oihana Solaun<sup>2</sup>.

<sup>1</sup> The Institute of Estuarine and Coastal Studies, University of Hull, Hull, HU6 7RX, UK.

<sup>2</sup> AZTI - Tecnalia, Astondo Bidea, Edificio 609, Parque Tecnológico de Bizkaia, 48160 Elexalde Derio, Vizcaya, Spain.

<sup>3</sup> Institute of Marine Sciences and Technology Baku, Blvd. No 100, P.K. 478, Inciralti-Izmir, Turkey.

<sup>4</sup> CONISMA, Polytechnic University of Marche, Piazza Roma, 22, 60121 Ancona, Italy.

<sup>5</sup> Institut de Ciències del Mar, CSIC, Spain. Passeig Marítim de la Barceloneta, 37-49. E-08003 Barcelona, Spain.

<sup>6</sup> Institute of Oceanology-BAS, First May Street 40, P.O.Box 152, Varna 9000, Bulgaria.

<sup>7</sup> Hellenic Centre of Marine Research, Athens Sounio Ave. P.C. 19013, Anavyssos Attiki, Greece.

<sup>8</sup> European Commission, Joint Research Centre, E. Fermi 2749, 21027 Ispra (VA), Italy.

<sup>9</sup> Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, UK.

\*Corresponding author: [j.strong@hull.ac.uk, +44 1482 433685]

Running header: Potential of marine BEF relationships in monitoring

## **Abstract**

There is an increasing demand for environmental assessments of the marine environment to include ecosystem function. However, existing schemes are predominantly based on taxonomic (i.e. structural) measures of biodiversity. Biodiversity and Ecosystem Function (BEF) relationships are suggested to provide a mechanism for converting taxonomic information into surrogates of ecosystem function. This review assesses the evidence for marine BEF relationships and their potential to be used in practical monitoring applications (i.e. operationalized).

Five key requirements were identified for the practical application of BEF relationships: 1) a complete understanding of strength, direction and prevalence of marine BEF relationships, 2) an understanding of which biological components are influential within specific BEF relationships, 3) the biodiversity of the selected biological components can be measured easily, 4) detail which ecological mechanisms are the most important for generating marine BEF relationships, e.g. identity effects or complementarity, and 5) establish what proportion of the overall functional variance is explained by biodiversity, and hence BEF relationships.

Many positive and some negative BEF relationships were found within the literature, although many reproduced poorly the natural species richness, trophic structures or multiple functions of real ecosystems. Null relationships were also reported. The consistency of the positive and negative relationships was often low that compromised the ability to generalize BEF relationships and confident application of BEF within marine monitoring. Equally, some biological components and functions have received little or no investigation.

Expert judgement was used to attribute biological components using spatial extent, presence and functional rate criteria. This approach highlighted the main contributing biological components to the ecosystem functions, and that many of the particularly influential components were found to have received the least amount of research attention.

The need for biodiversity to be measurable (requirement 3) is possible for most biological components although difficult within the functionally important microbes.

Identity effects underpinned most marine BEF relationships (requirement 4). As such, processes that translated structural biodiversity measures into functional diversity were found to generate better BEF relationships.

The analysis of the contribution made by biodiversity, over abiotic influences, to the total expression of a particular ecosystem function was rarely measured or considered (requirement 5). Hence it is not possible to determine the overall importance of BEF relationships within the total ecosystem functioning observed. In the few studies where abiotic factors had been considered, it was clear that these modified BEF relationships and have their own direct influence on functional rate.

Based on the five requirements, the information required for immediate ‘operationalization’ of BEF relationships within marine functional monitoring is lacking. However, the concept of BEF inclusion within practical monitoring applications shows promise for providing surrogate indicators of functioning.

### **Keywords**

Biodiversity and ecosystem function relationships, marine, practical applications, operationalization, monitoring

## ***1. Introduction***

The physical, chemical and biological processes that transform and translocate energy or materials in an ecosystem are termed ecosystem functions (Naeem, 1998; Paterson *et al.*, 2012). Ecosystem functioning generally describes the combined effects of individual functions, with the overall rate of functioning being governed by the interplay of abiotic (physical and chemical) and/or biotic factors (Reiss *et al.*, 2009). Furthermore, these ecosystem functions represent a significant component of ecosystem health (Tett *et al.*, 2013) and provide ecosystem services that benefit society (Paterson *et al.*, 2012). It is now widely hypothesised that ecosystem function is compromised by a global trend of biodiversity loss, linked to human activities and climate change (Loreau, et al. 2001; Covich et al. 2004). This is widely referred to as the Biodiversity Ecosystem Function relationship (BEF).

The need to ensure the sustainable functioning of aquatic ecosystems is acknowledged by many marine policy obligations, either explicitly (e.g. the European Marine Strategy Framework Directive, MSFD, 2008/56/EU), or indirectly (by addressing structural aspects which can be related to functioning; e.g., EU Water Framework Directive WFD, Habitats Directive). The MSFD aims to achieve Good Environmental Status (GENS) of European seas by 2020. The MSFD definition of GENS includes the requirement that ‘the structure, functions and processes of the constituent marine ecosystems allow those ecosystems to function fully and to maintain their resilience to human-induced environmental change ‘The GENS assessment can be interpreted as requiring 1) functioning to be considered at all levels of biological organization (cell, individual, population, community and ecosystem) and 2) the potential to relate these functions to GENS indicators and overall ecosystem health (Tett *et al.*, 2013). Consequently, this review aims to fulfil the clear need of addressing functioning in ecosystem monitoring by assessing the evidence for biodiversity and ecosystem function relationships and their potential to support this objective.

Structurally-based biodiversity assessments, such as species richness and abundance (Gray and Elliott 2009), are extensively used to monitor components of the marine ecosystem (Birk et al., 2012). These structural indicators are routinely used because they are well established, cost-effective and provide structural surrogates (proxies) for ecosystem condition and functional state (Gray and Elliott, 2009).

However, development of Biodiversity and Ecosystem Functioning (BEF) relationship theory potentially provides a more direct, proven and tangible link between structural measures of biodiversity, specific ecosystem functions and ultimately ecosystem functioning assessments. Using these relationships in practical monitoring applications ('operationalizing' BEF) provides a route by which biological diversity information can be translated potentially into surrogates of ecosystem functionality that ultimately help fulfil monitoring obligations and policy goals. Although direct measurements of specific ecosystem functions are often more straight-forward and cost-effective, the use of biodiversity information and BEF relationships has the following benefits: 1) one biological dataset can provide surrogates of multiple ecosystem functions; 2) combines the analysis of structural and functional status; 3) predictions of function can be generated, based on known sensitivity of individual species, within realistic patterns of biodiversity loss, and 4) a transparent approach where functional evaluations are based on biodiversity, thereby incorporating the biological apparatus of functional delivery within these assessment.

This review aims to explore the prevalence and nature of marine BEF relationships and the potential of these relationships to be used in operational monitoring of marine environmental health. The key objectives are to 1) discuss what information is required for the consistent and confident application of BEF relationships within ecosystem functioning monitoring; 2) review the available information on how marine biodiversity relates with specific ecosystem functions and examine both strength, consistency, direction and important application principles such as mechanism of delivery (complementarity and identity effects); 3) identify the biological components that are most relevant in their contribution to specific ecosystem functions, taking into account also their relevance to current, key management and policy frameworks; 4) assess the limitations and future work required to fully operationalize BEF relationships, and 5) provide a framework for the incorporation of BEF relationships within marine monitoring. Hence we give: 1) the key requirements for the practical application, 2) a review of the BEF evidence in relation to these requirements and 3) an overall assessment of the potential of BEF relationships to be used in practical applications of ecosystem monitoring and a framework by which this could be achieved.

## **1.1. Biodiversity and Ecosystem Functioning relationships**

Biodiversity and Ecosystem Functioning research has recently proliferated in response to scientific and public awareness of the widespread and unprecedented human-induced biodiversity turnover ( $\beta$  diversity scale) and loss in many biological components (i.e. biodiversity is routinely deconstructed into measurable, manageable and meaningful biological components or features: broad groupings, based on either taxonomic or ecological similarity, could include for example microbes, benthic invertebrates, phytoplankton, and fish) resulting in the global emergence of communities with novel species configurations (Pimm *et al.*, 1995; Bulling *et al.*, 2010; Dornelas *et al.*, 2014; Pandolfi *et al.*, 2014). Such changes have potential implications for the provision of ecosystem services and societal benefits (Chapin *et al.* 1997, Covich *et al.* 2004; Solan *et al.*, 2004; Worm *et al.*, 2006; Atkins *et al.*, 2011; Cardinale *et al.*, 2012; Hooper *et al.*, 2012; UK National Ecosystem Assessment, 2014).

Biodiversity and Ecosystem Functioning research is increasingly centred on whether altered species diversity affects functions (Loreau, *et al.* 2001; Covich *et al.* 2004). The underlying BEF theory postulates that changes in biodiversity will result in altered ecosystem functions or, more particularly, that higher and more efficient functioning rates comes from highly diverse areas. This is presumed to be because diverse communities are more likely to contain a greater range of functional traits and environmental sensitivities (Chapin *et al.* 1997). High diversity therefore entails opportunities for more efficient resource use as well as providing stability to ecosystem processes in variable environments and in the face of disturbance (Chapin *et al.* 1997). Alternatively, systems with species-poor communities are theoretically likely to be functionally poorer, less resistant (capacity to resist change) and resilient (capacity to recover from change) to disturbance than systems with species-rich communities (Covich *et al.* 2004; Stachowicz *et al.* 2007). However, this has been questioned for naturally stressed areas such as estuaries in which a lower diversity but high physico-chemical variability appears to confer greater resilience and resistance (Elliott and Quintino, 2007).

Before analyzing the evidence on BEF relationships in the marine environment and its potential for practical application within monitoring programmes, it is important to clarify the main concepts

regarding the BEF theory. Precision of the definition and measurement of BEF relationships and their elements is especially important to understand the potential and limitations for the general operationalization within monitoring programmes. A brief summary of BEF concepts and mechanisms is only given here to allow a better understanding of the results presented in this paper; further detailed information can be found in Scherer-Lorenzen (2005) and Reiss *et al.* (2009).

Biodiversity and ecosystem function relationships, if present, can take many forms (Figure 1). These arise from linear positive or negative relationships (proportional gain or loss) or exponential (high and low redundancy models) (Naeem and Wright, 2003). Positive, linear BEF relationships suggest that additional units of biodiversity (this can be taxonomic units such as species richness or functional diversity) have an equal and additive contribution to an ecosystem function (Naeem and Wright, 2003). This would be indicative of situations where complementarity (transgressive over-yielding) was occurring, i.e. individual species perform better in diverse communities when compared to monoculture due to facilitation and niche partitioning in shared resource use. When several biodiversity units are capable of providing the same function, and therefore the same change in ecosystem function, logarithmic relationships are likely. The species range beyond the asymptote are often considered to be redundant (Naeem and Wright, 2003). Complementarity provides what might be considered the truest form of BEF relationships. However, in situations where particular species have a disproportionate functional role, they can also generate positive BEF relationships and are termed identity effects (this form of non-transgressive over-yielding can also be called sampling or selection effects). Where identity effects (see glossary) are prevalent, stepped or riveted relationships might be apparent. Functional diversity measures (such as Biological Traits Analysis that uses a series of life history, morphological and behavioural characteristics of species present in assemblages to indicate aspects of their ecological functioning e.g. Bremner, 2008), rather than taxonomic methods, are suggested as way of partially compensating for both redundancy and identity effects.

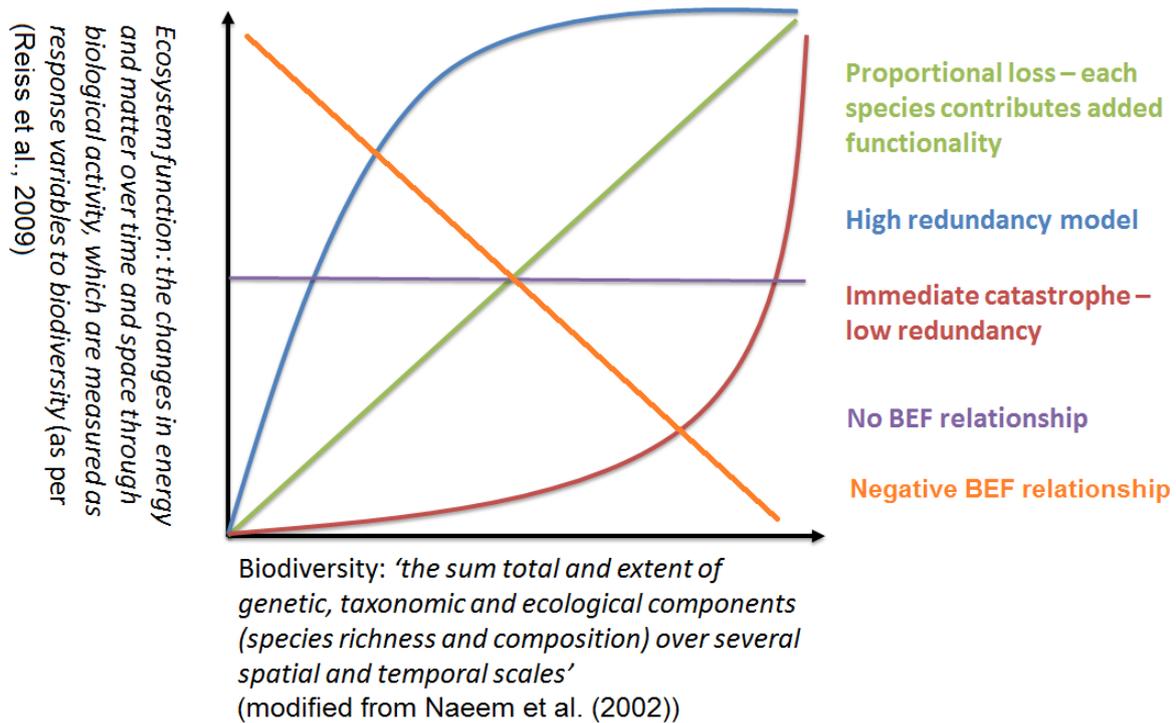


Figure 1. Potential 'Biodiversity and Ecosystem Function' relationships.

Despite equivocal evidence, there is a general consensus that marine biodiversity and ecosystem function relationships do exist, and positive and negative effects of biodiversity have been observed in several marine ecosystem functions (Worm *et al.*, 2006; Stachowicz *et al.*, 2007; Cardinale *et al.*, 2012; Gamfeldt *et al.*, in press). Assessing the existence, strength and shape of this relationship provides a basis for the indirect estimation of key ecosystem functions using structural measures of biodiversity. This implies the potential to use BEF relationships in practical applications (often termed operationalization) and generate predictions of specific ecosystem functions from existing biodiversity information.

## ***2. Practical application of BEF relationships within GEnS monitoring and management***

Although the overall form of many BEF relationships has been documented (Stachowicz *et al.*, 2007; Naeem *et al.*, 2009; Cardinale *et al.*, 2012; Gamfeldt *et al.*, in press) this alone does not provide sufficient information to immediately use these relationships for practical applications (operationalize).

Five key issues, as considered below, aim to define whether BEF relationships can form an integrated component in consistent, pragmatic and indicative marine monitoring. This requires us to investigate the following issues: 1) the existence of BEF relationships, 2) which biological components contribute to which ecosystem functions and therefore involved in specific BEF relationships, 3) whether the biodiversity and function of the selected biological components be measured easily, 4) detail which mechanisms generates BEF relationships, e.g. identity effects, and 5) establish what proportion of the overall variance of a given function is explained by biodiversity, and hence BEF relationships.

### **2.1. Operational requirement 1: do BEF relationships exist in marine ecosystems?**

Although there is broad acceptance of marine BEF relationships, there is also recognition of their variability and context dependency (Bulling *et al.* 2010; Cardinale *et al.*, 2012). Practical monitoring applications, i.e. operationalization, of the BEF concept however, requires the existence of a clear, consistent and unambiguous relationship between habitats, biological components and ecosystem functions. Furthermore, simply knowing the presence and direction of a BEF relationship is not sufficient for its operational use. The shape of the functional response between a biodiversity indicator and a specific ecosystem function (linear, logarithmic, exponential, power, etc.) also needs to be determined so that predictions can be made across the range of natural gradients of biodiversity. Although different types of BEF relationships have been demonstrated in the literature, especially positive relationships, there is no reason why negative BEF relationships cannot be used in monitoring methodologies. However, the incorporation of positive BEF relationships within a practical ecosystem monitoring application is particularly desirable as improvements in the system structure (biodiversity) would also lead to an improvement in its functioning, thereby generating synergistic enhancements in both conservation and ecological objectives.

In the same way that biodiversity needs to be defined and separated into manageable units, total ecosystem functioning also needs to be subdivided into meaningful components that can be described and measured. High level and holistic measures of ecosystem functioning that account for multifunctionality are rare, with the majority of the literature focusing on the relevance of biodiversity in the context of specific functions (Mouillot *et al.*, 2011). Accordingly, evidence for BEF relationships

in marine temperate systems is grouped under five broad processes (groupings of ecosystem functions) of 1) biomass production, 2) organic matter transformation, 3) ecosystem metabolism, 4) nutrient cycling and 5) physical engineering (Figure 2). This grouping is generally agrees with that used by Giller *et al.* (2004), representing key functions that control and distribute resources in marine ecosystems (nutrients, energy, physical space/habitat), through interactions such as production, consumption and transformation. Within these five categories, the reviewed evidence is collated by discrete biological components including microbes, phytoplankton, zooplankton, macroalgae, angiosperms, benthic invertebrates, fish and cephalopods, seabirds, reptiles and marine mammals.

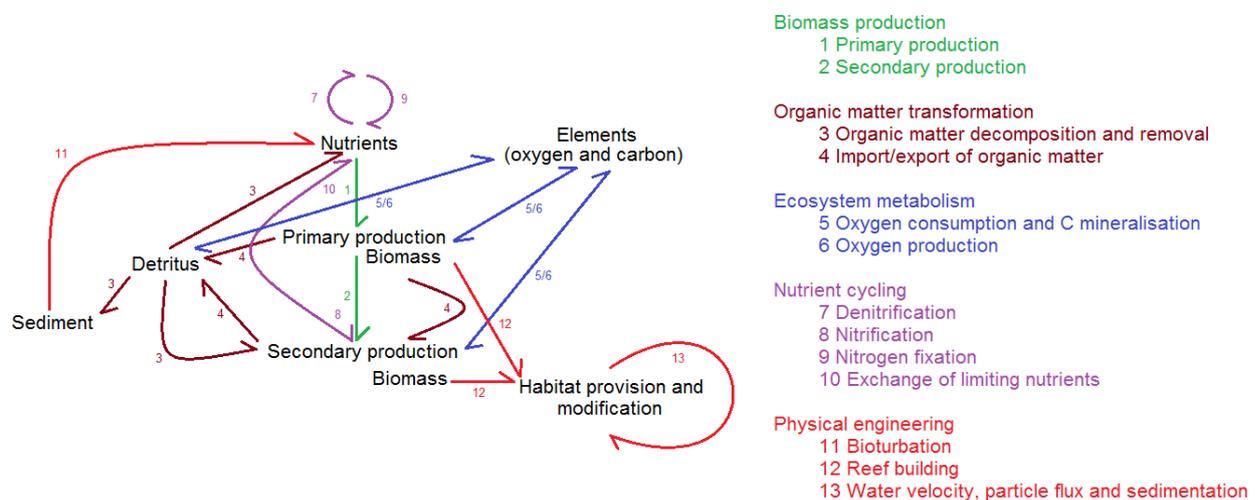


Figure 2. Relationships between ecosystem functions used within the review.

Different biological components can contribute to the same ecosystem function (e.g. phytoplankton, macroalgae and angiosperms all contribute to primary production) although several attributes of a biological component may modify and scale its functional contribution (Table 1). These include: 1) its spatial extent/occurrence within multiple habitats; 2) presence (biomass/abundance), and 3) functional rate. These factors were considered to rank the relative contribution of the different biological components to each ecosystem function (Table 1), as informed by the BEF literature review. Due to the high variability in the measurement units characterizing these attributes within the reviewed studies, and given the need of obtaining comparable data across the different components, functions, studies, etc., a rigorous quantitative assessment method could not be applied, and a scoring system was used

based on semi-quantitative criteria, with a certain degree of expert judgment also involved (Table 2). In particular, the spatial extent of a biological component was scored based on its degree of occurrence at both the habitat and regional scales (Table 2), under the assumption that, although different components can be locally important, those that are more widespread and resident in multiple habitats are more likely to contribute to an ecosystem function at the regional level, in line with the scale of assessment required for regional marine monitoring.

Presence was scored based on the relative biomass typically characterizing a biological component, as assessed by combining the evaluation of its abundance, body size and trophic level. Based on food web reviews, the productivity of a trophic level is typically between 5 – 20% of the level below it (Trites, 2001). Total biomass declines with increasing trophic level whilst average body size increases. This leads to consistent ratios within food webs and the well-recognized pyramidal form of trophic webs. The steepness of these pyramids is related to the transfer efficiency between trophic levels. It therefore seems appropriate to scale the presence of the biological components according to trophic position, i.e. biological components at high higher trophic levels may be less important for certain ecosystem functions than those at lower levels (Table 1 and Table 2).

The assessment of functional rate by each biological component, using body size as a proxy (assuming increasing rates with decreasing body size (Kleiber, 1947)) is important given the potential availability of resources required as function substrates, i.e. potential levels of limitation (Table 2). For example, considering the contribution of phytoplankton, macroalgae and angiosperms to primary production, presence and rate scaling were assessed based on the information on biomass and growth rate. As indicated above, the relative presence of ocean phytoplankton in terms of biomass is very low (Field *et al.*, 1998), but the high growth rate and wide spatial extent makes the phytoplankton a critical and significant contributor to primary production in marine ecosystems. In contrast, although angiosperms and macroalgae have high growth rates and standing biomass, they are confined to a limited number of habitats and regions, thereby decreasing their regional contribution to primary production, hence their lower score compared to phytoplankton (Table 1).

Finally, ecosystem functions that are disproportionately influenced by aspects of spatial extent, presence or rate have been adjusted using expert judgment. For example, functionality provided by physical engineering may be more related to presence (biomass/abundance), whereas biogeochemical processes may be more dependent on processing rates (e.g. of nutrient cycling, organic matter decomposition).

#### 2.1.1. Ecosystem process: biomass production

The rate at which biomass is generated, both by autotrophic and heterotrophic organisms, is a key process supporting the functioning of a viable ecosystem. Primary production, via photosynthesis and chemosynthesis, provides the biomass to support secondary production, thereby allowing energy and nutrient transfer across trophic levels (Figure 2). Secondary production is widely accepted as a critical ecosystem process and is regularly used as a functional metric. Phytoplankton, chemosynthetic microbes, macroalgae and angiosperms are the main primary producers in temperate marine ecosystems (Table 1), supporting heterotrophic microbes, zooplankton, nekton and benthic invertebrates via trophic links. In addition, both primary and secondary production generate by-products that support other ecosystem functions (e.g. ecosystem metabolism, nutrient cycling).

Table 1. Ecosystem functions associated with differing marine biological components (functions modified from Giller *et al.* 2004). Expert judgment was used to allocate low (1) to high (5) values for spatial extent/prevalence (first value), presence, i.e. standing biomass/abundance (second value) and functional rate (third value). Values have been multiplied together to generate a summary value of the potential functional output.

Ecosystem process	Ecosystem function	Biological component						
		Microbes	Phytoplankton	Zooplankton	Macroalgae	Angiosperms	Benthic invertebrates	Higher trophic levels <sup>1</sup>
Biomass production	Primary productivity	5*1.5*3.5=26.25	4*2.5*5.5=55		2*5*3.5=35	1*5*3.5=17.5		
	Secondary productivity	5.5*2.5*3.5=48.125		4.5*3*4.5=60.75			3.5*3*3.5=36.75	4.5*2*1.5=13.5
Organic matter transformation	Organic matter decomposition and removal	5*2.5*4.5=56.25		4*3*4.5=54			3*3*3.5=31.5	4*2*1.5=12
	Import/export of organic matter		4*2.5*5.5=55	4*3*4.5=54	2*5*3.5=35	1*5*3.5=17.5	3*3*3.5=31.5	4*2*1.5=12
Ecosystem metabolism	Carbon mineralization	5*3*4.5=67.5		4*3.5*4.5=63			3*3.5*3.5=36.75	4*2.5*1.5=15
	Oxygen consumption	5*2.5*4.5=56.25		4*3*4.5=54			3*3*3.5=31.5	4*2*1.5=12
	Oxygen production		4*3*5.5=66		2*5.5*3.5=38.5	1*5.5*3.5=19.25		
Elemental cycling	Denitrification	2*2.5*4.5=22.5						
	Nitrification	5*2.5*4.5=56.25						
	Nitrogen fixation	4*2.5*4.5=45						
	Exchange of limiting nutrients	5*3*4.5=67.5	4*3*5.5=66	4*3.5*4.5=63	2*5.5*3.5=38.5	1*5.5*3.5=19.25	3*3.5*3.5=36.75	4*2.5*1.5=15
Physical structuring	Bioturbation						3*3*3.5=31.5	
	Habitat provision				2*5.5*3=33	1*5.5*3=16.5	3*3.5*3=31.5	
	Water velocity and particle flux modification				2.5*5.5*3=41.25	1.5*5.5*3=24.75	3.5*3.5*3=36.75	

<sup>1</sup> Fish, cephalopods, seabirds, reptiles and marine mammals.

Table 2. Criteria used to estimate the spatial extent, presence and functional rate of biological components examined by ecosystem function.

Score	Spatial Extent		Presence				Rate	
	Regions	Habitats	Body size	Abundance	Primary production	Secondary production	Body size	Limitation
1	Few regions	Some habitats	Micro	Low	+ 0.5	- 0.5	Mega	Low/high
2	Some regions	Some habitats	Micro	High	+ 0.5	- 0.5	Macro	High
3	Some regions	Many habitats	Macro	Low	+ 0.5	- 0.5	Macro/Micro	Low
4	Many regions	Some habitats	Macro	High	+ 0.5	- 0.5	Micro	High
5	Many regions	Many habitats	Mega	-	+ 0.5	- 0.5	Micro	Low

### 2.1.1.1. Ecosystem function: primary production

The primary route of carbon fixation is photosynthesis, although the required context of functional importance necessitates the separation of the biological components of biodiversity. Phytoplankton photosynthetically fixes up to 50,000 Tg of carbon per year, contributing to nearly half of global primary production (Longhurst *et al.*, 1995) (on average  $140 \text{ g C m}^{-2} \text{ yr}^{-1}$  Falkowski *et al.*, 1998).

In addition, photosynthetic carbon fixation by macroalgal kelps such as the giant kelp *Macrocystis pyrifera*, ranges from  $0.46$  to  $3.50 \text{ kg C m}^{-2} \text{ yr}^{-1}$ , with furoid species contributing around  $0.30$  to  $1.30 \text{ kg C m}^{-2} \text{ yr}^{-1}$  (Lüning 1990; Barrón *et al.*, 2003). Seagrass meadows are also highly productive habitats contributing an estimated mean net community productivity of  $1.19 \text{ kg C m}^{-2} \text{ yr}^{-1}$  (Duarte *et al.*, 2010). Suzuki (1997) suggests that the total global area of marine macroalgae and angiosperms is approx.  $600,000 \text{ km}^2$  producing approx.  $0.460 \text{ Tg C yr}^{-1}$ . Muraoka (2004) suggests that this is equal to 23% of the total of oceanic carbon dioxide uptake estimation by Siegenthaler and Sarmiento (1993). Microbes can also synthesize inorganic carbon using reduced chemical compounds as energy sources, contributing to about 52% of carbon fixation globally via microbial nitrification processes (estimated addition of organic matter approx.  $7700 \text{ Tg C y}^{-1}$ ; Middelburg, 2011). This suggests that chemosynthetic processes can be quantitatively more important than previously thought (Molari *et al.* 2013). Despite this, there have been no investigations of microbial BEF associated with chemosynthetic primary production.

Although oceanic autotrophs account for approximately 46 % of the biospheric net primary production, they only account for about 0.2% of the global primary producer biomass (Field *et al.*, 1998), and so standing biomass does not reflect production (Cebrian, 2002). However, many BEF-related studies have identified positive relationships between phytoplankton species richness (taken as an indicator of biodiversity) and primary production (Balvanera *et al.* 2006; Cardinale *et al.* 2006; Cardinale *et al.* 2007; Hector *et al.* 2007; Ptacnik *et al.* 2008; Goebel *et al.*, 2014). Experimental studies have revealed positive, asymptotically saturating relationships between ecosystem-wide phytoplankton diversity and productivity (Goebel *et al.*, 2014). Within the positive BEF relationships identified, both identity effects

and complementarity can produce positive diversity-productivity relationships (Loreau and Hector 2001; Cardinale *et al.*, 2006).

Both negative (Kraufvelin *et al.*, 2010; Bracken and Williams, 2013) and positive BEF relationships have been reported within macroalgal assemblages in the context of photosynthetic carbon fixation (Bruno *et al.*, 2005; Arenas *et al.*, 2009; Boyer *et al.*, 2009; Griffin *et al.*, 2009). Although not using an experiment designed to specifically test the relationship between diversity and productivity, Kraufvelin *et al.* (2010) observed declining primary production within increasing macroalgal species richness in temperate rocky shores (SE Norway) driven by strong identity effects associated with the resident fucoids. A similar relationship was observed by Bracken and Williams (2013) for seaweed assemblages in a northern California (USA) rocky shore, where photosynthetic efficiency was used as an indicator of primary production. Unlike many other studies, experimental species richness gradients species richness gradients were obtained through random allocation (typical of most studies) and non-random methods (mimicking naturally occurring assemblages). While increases in species richness did not lead to changes in function when species were randomly combined, a negative relationship with photosynthetic efficiency was detected when using realistic (non-randomly selected) assemblages (although no relationship was found with maximum photosynthetic rate). Alternatively, Griffin *et al.* (2009) found that functional diversity of rock pool macroalgae (a measure of the range of species functional traits in the system; Tilman, 2001), rather than species richness, correlated positively with primary productivity. However, the consistency of such BEF relationships may be weakened in natural trophic structures, as typical BEF experiments do not include consumers. Indeed, Reynolds and Bruno (2012) incorporated herbivores in their macroalgal treatments and showed that the positive relationship observed between macroalgal diversity and primary production disappeared in the presence of consumers. Doubt thus remains about the predictability of potentially positive BEF relationships between macroalgae and carbon fixation in real ecosystems.

Regardless of whether species richness (Bruno *et al.*, 2005, Lanari and Coutinho, 2014) or functional diversity (Griffin *et al.*, 2009) is used, species identity appears to be an important driver in determining the rate of primary production in macroalgae (with the exception of Boyer *et al.*, 2009), even when

negative BEF relationships are considered (Kraufvelin *et al.*, 2010). Davies *et al.* (2011) found that individual species biomass explained observed changes in primary production in macroalgae assemblages, and that this could be related proportionally to the effect of changes in single species biomass. This effect was also observed in similar experiments with saltmarsh plants and indicates that biomass may in some circumstances underlie identity effects in primary producer BEF relationships, thereby complicating the importance of biodiversity *per se* for the sustenance of primary production in such systems.

Angiosperm studies provide the only substantial evidence for the role of genetic diversity within BEF relationships for productivity. Positive BEF relationships were apparent between seagrass genetic diversity (*Zostera marina*) (Williams, 2001; Hughes and Stachowicz, 2004; Ehlers *et al.*, 2008; Hughes and Stachowicz, 2009; Hughes *et al.*, 2010) and primary productivity, and also between angiosperm species richness (seagrass and transitional angiosperms in the Baltic) and primary productivity (Gustafsson and Boström, 2011). Genetic diversity was found to be particularly important for sustaining primary production during stressful conditions or following perturbations (Williams, 2001; Hughes and Stachowicz, 2004; Ehlers *et al.*, 2008; Hughes and Stachowicz, 2009). Reusch *et al.* (2005) found that genetically diverse treatments also supported more epiphytic fauna, suggesting the influence of genetic diversity can propagate through to changes in secondary productivity. However, Hughes *et al.* (2010) found that BEF relationships were heavily influenced by grazer species identity. Overall, it is apparent that this relationship cannot be generalized and the context (i.e. the wider system of which angiosperms are part, including grazers) is a determinant factors affecting BEF relationships.

#### 2.1.1.2. Ecosystem function: secondary production

Within microbial assemblages, about half of the carbon fixed into marine organic matter is consumed by heterotrophic prokaryotes (both direct consumption of primary production and undirected detritus sources). Typically only approx. 20% of the detrital organic pools used to sustain heterotrophic metabolism is converted into prokaryotic biomass, whereas most is respired (del Giorgio and Cole, 1998). Prokaryotic biomass thus transfers some energy and material to the higher trophic levels of the marine food webs (Di Poi *et al.*, 2013) and its metabolism largely contributes to carbon mineralization

and respiration rates of benthic ecosystems (Arndt *et al.*, 2013). Investigations of the links between prokaryotic diversity and functioning in marine ecosystems are, however, rare. Available studies indicate a positive relationship between prokaryote diversity and prokaryote carbon conversion efficiency and metabolism (Danovaro and Pusceddu 2007; Langenheder *et al.*, 2010), i.e. a higher prokaryotic diversity can promote higher levels of secondary production.

Their global distribution, abundance and dominance, makes ciliates among protozoa, and the copepods and euphausiids among metazoa, perhaps the most significant primary consumers. Despite their importance for secondary production (Irigoien *et al.*, 2004; Johnson *et al.*, 2011), nutrient cycling and the translocation of organic matter, there have been no studies examining its BEF relationships. This may be due to difficulties in working with species with small body sizes, occupying intermediate trophic levels and detecting small changes in functional output. Although there are some freshwater and tropical studies, there is little to extrapolate these findings to temperate, marine situations.

Capture and conversion of pelagic and benthic primary production into benthic secondary production is one of the most important functions undertaken by benthic invertebrates (Fowler and Knauer 1986). Benthic biomass is in turn consumed by mobile epifaunal species and fish, thereby supporting other trophic levels and pelagic habitats (Townsend and Cammen, 1988). Evidence for clear and consistent relationships between macrofaunal biodiversity and secondary production is lacking, as both positive (O’Gorman *et al.*, 2008; Harvey *et al.*, 2013) and no (Valdivia *et al.*, 2009) relationships have been reported for this component. However such relationships are likely to be of less relevance in relation to the importance of macrofaunal biomass and identity in predicting secondary production, given the well-established paradigm that secondary productivity decreases with increasing macrofaunal size (production to biomass (P:B) ratio increases with a decrease in size, shorter longevity and age of an organism; Jennings *et al.*, 2002; Gray and Elliott, 2009). As the historical separation between macrofauna and meiofauna in the literature is artificially stipulated by separation at 500 and 63  $\mu\text{m}$  sieves respectively, and that both components include different life stages of the same organisms, this attribute is also likely to apply to meiofauna (Higgins and Thiel, 1988). Thus, it seems that secondary

production may more easily be predicted by macrofauna and meiofauna abundance and biomass, and that biodiversity may thus be a less useful predictor for monitoring purposes.

The meiofaunal biomass turnover rate is on average 5 times higher than that of macrofauna and, despite having a lower biomass (Giere, 2009), this component frequently exceeds the production of macrofaunal assemblages. The potential significance of meiofauna in the functioning of benthic sedimentary environments has been examined within relatively low diversity, free-living nematode communities, whose biodiversity (measured through a set of different indices, including, for example, species richness, Shannon diversity, functional diversity as number of trophic traits) is generally related positively with rates of biomass production and heterotrophic prokaryotic carbon production (Danovaro *et al.* 2008a; Danovaro *et al.* 2008b, Pusceddu *et al.* 2014). The shape of this positive relationship (linear to exponential functions) varied when habitats from different water depths were considered (Danovaro *et al.* 2008b). Experimental responses of natural nematode assemblages to thermal stress led Gingold *et al.* (2013) to hypothesize that either (saturating) rivet-like or idiosyncratic relationships are equally probable between nematode species richness and secondary production. Due to the constraints of the manipulative meiofauna experiments, only correlations between free-living nematodes biodiversity and ecosystem functioning have been investigated (Danovaro *et al.* 2008b, Leduc *et al.* 2013, Pusceddu *et al.* 2014). Although nematodes can dominate some meiofaunal communities (e.g. estuaries examined by Alves *et al.* (2009), in other habitats they may only account for only a modest contribution to community composition, suggesting that the potential for meiofaunal BEF relationships to exist within these habitats remains largely to be investigated.

O’Gorman *et al.* (2008) found that as the diversity of predatory mobile epifaunal fish species increased (with density controlled between treatments), there was an associated increasing trend in secondary production for all intermediate trophic components examined (although only significant for 4 out of the 16 taxonomic components). The greater interference among predators might have been responsible for the higher secondary production recorded in treatments with higher predator diversity, although there is a possible effect of behavioural changes in feeding activity during confinement within the benthic experimental cages. Using functional diversity, Harvey *et al.* (2013) found clear monotonic

relationships with two functional variables (consumption of macroalgae and of periphyton) which are presumed to generate proportional increases in secondary production in a rocky shore community. Despite very strong identity effects within the functional groups, functional richness did play a substantial role in explained some of the variance in ecosystem functionality during removal treatments.

Seagrass habitats provide an additional source of BEF investigations within epiphytic consumer assemblages. Although some studies have failed to find positive BEF relationships between grazer diversity and grazer secondary production (Duffy *et al.*, 2001, 2005, but only in the absence of higher trophic level consumers; Canuel *et al.*, 2007), others have detected them (Duffy *et al.*, 2003, 2005, in the presence of higher trophic level consumers; France and Duffy, 2006). A negative relationship was observed by Duffy *et al.* (2001) within mesocosm experiments (lacking trophic levels above the grazers) and it was associated with a low grazers species range (three rather than six species in Duffy *et al.* (2003) and four species in Duffy *et al.* (2005)), indicating that grazer diversity effects on secondary production may only be apparent at wider ranges of grazer richness (Duffy *et al.*, 2003). The contrasting findings between treatments by Duffy *et al.* (2005) were influenced by the presence of higher trophic levels. Functioning did increase with richness when higher trophic predators were present. Duffy *et al.* (2005) suggest that richness is linked to the enhanced epifaunal grazing pressure on resources and the dampening of community fluctuation from predation pressure. France and Duffy (2006) developed this theme by experimentally modifying grazer diversity, dispersal and spatial scale within a meta-community structure. Richness within meta-community units and, to a less extent, the dispersal potential affected the net productivity at multiple levels within experimental units and large meta-communities. Most BEF relationships observed, both positive and negative, were underpinned by strong species identity effects that sometimes obscured the influence of species richness alone. It was suggested that the identity effects were mediated through a combination of qualitative and quantitative differences in grazing methods and different population growth rates between species (Duffy *et al.*, 2001). Similarly, Canuel *et al.* (2007) found that identity effects dominated epifaunal grazer functions that convert primary productivity, from seagrass and associated epiphytic algae, into organic matter

within the sediment, with grazer richness and food chain length having little or no influence (the latter finding being in contrast to that of Duffy *et al.*, 2005).

Fish and cephalopods are both opportunistic predators taking zooplankton, macroalgae and other fishes and cephalopod species, and are themselves prey for other organisms (Cury *et al.*, 2003), hence they play a pivotal role in marine food webs by linking lower and upper trophic levels. Cephalopods (particularly squid) have exceptionally high feeding rates (Clarke, 1996; Wells and Clarke 1996; Hunsicker and Essington, 2008) and also sustain many marine predators, such as bony fish, elasmobranchs, marine birds and mammals, especially whales (e.g. Clarke, 1996; Smale, 1996). Their importance as prey is enhanced by their very high individual growth rates, which, together with other life cycle characteristics (exclusively carnivorous diet, semelparity, short lifespan) leads to high biomass turnover rates or productivity (Boyle, 2002). Despite this, there has been no investigation of BEF relationships between fish or cephalopod diversity and temperate marine secondary production, a fact most likely due to the higher mobility and longer life cycles of these organisms e.g. compared to benthic invertebrates, leading to greater difficulties in undertaking manipulation experiments for testing of BEF relationships. Equally, BEF does not appear to have been studied in seabirds and marine mammals.

#### 2.1.2. Ecosystem process: organic matter removal and transformation

The transformation of non-living organic matter encompasses the essential ecosystem functions that distribute and remove organic matter from the ecosystem (Figure 1). The consumption of organic matter is associated with an additional input of secondary production as well as with the mobilization of nutrients in the system, both resources being made available for re-use in primary production processes, via the microbial loop. Benthic invertebrate bioturbation can also bury matter thereby removing it from the ecosystem (Figure 2). Almost all biological components move organic matter between habitats (e.g. faecal production by zooplankton is particularly important for the vertical transport of organic matter from the photic zone).

Organic material produced in the pelagic zone (e.g. as waste products of biological processes) is a resource which is transferred and made available to the benthic system through settlement, with

zooplankton faecal pellets being believed to be the main biological vehicle for benthic-pelagic coupling. Aggregates may disintegrate physically (Milligan and Hill, 1998), as well as being solubilized and remineralized by micro-organisms (Smith *et al.*, 1992) and zooplankton (Kjørboe, 2000) whilst settling. A significant amount of dissolved organic matter (DOM) can also be released through inefficient feeding, excretion and defaecation, which suggests that herbivory might be an important source of bacterial substrate (Lampert, 1978; Gude, 1988). Despite the role of zooplankton in facilitating the flux of organic matter to the seabed, there are no relevant BEF studies investigating the effect of zooplankton diversity of such process. Larger animals also contribute to the horizontal and vertical transfer of organic matter between ecosystems, in the form of living biomass (Stowasser *et al.*, 2005; Hastie *et al.*, 2009). Fish and cephalopods are highly mobile animals and often undertake long feeding and spawning migrations. Combined with their role as intermediate predators in marine food webs, this leads to significant translocation of organic matter that can affect ecosystem functioning and community structure on a seasonal and regional basis (Hastie *et al.*, 2009). However, as with other ecosystem functions, experimentation difficulties with large and mobile species may have contributed to the lack of BEF evidence for these higher trophic components.

Both marine seagrass and macroalgal communities are significant sources of organic carbon to the ecosystem, as more than 85% of temperate seagrass and macroalgal communities studied by Barrón *et al.* (2012) supported a net dissolved organic carbon release. Furthermore, there are substantial amounts of macrophyte-generated detritus exported to remote habitats where it provides a substantial organic input (Harrold *et al.*, 1998; Maslo and Lockwood 2014). Harrold *et al.* (1998) observed that significant amounts of macroalgal biomass were being transported from the inshore habitats of production into deep-water canyon systems.

Macrofaunal species are capable of substantial filtration/gathering of organic matter and sizeable biodeposit production (Widdows *et al.*, 1998; Arntz *et al.*, 1999), especially in densely populated epifaunal communities such as bivalve beds (Giles and Pilditch, 2006). Once consumed, material is either assimilated into biomass or rejected in the form of faeces and pseudo-faeces (Wotton and Malmqvist 2001). These biodeposits and the benthic invertebrate biomass are available for consumption

by other species, hence providing organic transfer between habitats and trophic levels (Snelgrove 1999). The subsequent flux of bioavailable nitrogen compounds from metabolized biodeposits can be considerable, leading to rapid recycling of nutrients, thereby enhancing rates of primary production and phytoplankton biomass locally (references in Newell, 2004).

With regard to BEF relationships between macrofaunal diversity and organic matter-related ecosystem functions, Godbold *et al.* (2009) documented a positive BEF relationship between species richness of benthic echinoderms and the use of phytodetrital food sources. Equally, the merging of productivity, decomposition and infiltration (water-drainage characteristics of the salt marsh) into one metric, termed multifunctionality, by Hensel and Silliman (2013) increased as taxonomically diverse marsh-consuming species were progressively combined within treatments. It was suggested that redundancy within the system was low as each function was controlled by no more than two consumers, and that it is likely that the apparent redundancy is reduced when more ecosystem functions are examined simultaneously. As with almost all of the studies examined, both Godbold *et al.* (2009) and Hensel and Silliman (2013) stated that functional differences between the species (i.e. identity effects – see glossary) were responsible for the positive relationships between diversity and functionality.

Prokaryotic microbes are mostly responsible for organic decomposition (Cho and Azam, 1988; Arnosti, 2011), especially archaeal assemblages degrading detrital proteins (Lloyd *et al.*, 2013) and recycling organic matter (Takano *et al.*, 2010). As with other microbial ecosystem functions, there are few studies and hence less evidence for the presence of BEF relationships within microbial assemblages. Danovaro and Pusceddu (2007), using prokaryotic diversity (through molecular fingerprinting analysis), observed several positive relationships including one with organic matter decomposition rates. The diversity of free-living nematodes and other meiofaunal species was also found to generally relate positively with rates of organic matter degradation (Danovaro *et al.*, 2008; Pusceddu *et al.*, 2014; but in contrast see Leduc *et al.*, 2013 for null relationships).

### 2.1.3. Ecosystem process: ecosystem metabolism

In addition to nutrients and energy needed to support ecosystem functioning, other elements are involved in the metabolic processes behind the production, consumption and decomposition of organic

matter (Figure 2). They can be both essential resources and waste products of ecosystem functions such as carbon mineralization (using respiratory waste products from all biological components; Table 1), oxygen consumption (metabolic precursor for all biological components) and oxygen production (net excess of photosynthetic waste product from primary producers).

The relationship between carbon assimilation during primary production and oxygen production is expressed by the photosynthetic quotient. This ratio typically lies between 1:1.1 and 1:1.4 (Laws, 1991; Williams and Robertson, 1991), although deviations from these values can be observed depending on the particular primary producer (e.g. macroalgae examined by Rosenberg *et al.*, 1995). Hence net oxygen production is approximately equal to the amount of carbon captured during primary production suggesting that some of the BEF relationships related to primary production might help to understand these metabolic functions. However, abiotic factors may substantially control some ecosystem metabolic functions (e.g. the atmospheric control of dissolved oxygen content in open ocean water), suggesting that BEF relationships probably have little influence; this may explain the absence of dedicated studies for these ecosystem functions.

The dissolved oxygen generated during macroalgal and seagrass photosynthesis exceeds overall consumption and constitutes a major contributor for water column oxygenation (Boudouresque *et al.* 2012). These sources can be particularly important in coastal areas where water bodies range from full oxygen saturation to hypoxia. Seagrass root systems also permeate oxygen into the surrounding sediments, exerting important controls on the depth of the redox transition in coastal areas (Queirós *et al.*, 2011). Based on the relationship provided by the photosynthetic quotient and the BEF evidence with primary production (Williams, 2001; Hughes and Stachowicz, 2004; Ehlers *et al.*, 2008; Hughes *et al.*, 2009; Hughes and Stachowicz, 2009), it is likely seagrass genetic diversity may well also relate to oxygen production. This however is currently untested. There are some freshwater studies examining oxygen production along gradients of macroalgal diversity (e.g. Power and Cardinale, 2009), but there have been no marine studies that have specifically dealt with BEF relationships with this ecosystem function.

Ammonia excretion, phosphate excretion and, in particular, oxygen uptake by marine zooplankton are body-mass dependent and under the influence of habitat temperature, e.g. 84 to 96% of the observed variation in metabolic rate of epipelagic marine zooplankton (Ikeda, 1985). Metabolic needs for maintenance are a function of body weight raised by a power function of 0.75 (Kleiber, 1947), hence energy requirements, oxygen consumption and carbon dioxide production decrease proportionally as body size increases. This may suggest again that BEF relationships may not be as important as biomass and/or species identity within certain functions.

Janson *et al.* (2012) examined a benthic invertebrate assemblage together with sediment and faunal oxygen uptake rates in a temperate estuarine system. Faunal oxygen uptake correlated positively with the species number of some, but not all, functional groups. Equally, abundance and biomass also correlated with faunal oxygen uptake, suggesting other biotic factors were just as important in modifying oxygen uptake, and hence carbon mineralization functions, as diversity. However, the dominant influence over the total oxygen uptake was abiotic factors such as grain size, organic matter content and temperature; this suggests that biotic influences on this ecosystem function are proportionally smaller than abiotic factors.

Although macroscopic faunal components are important, benthic prokaryotic assemblages in the thin oxic layer of the seabed account for more than half of the total organic carbon mineralization (Jørgensen and Revsbech, 1989; Arndt *et al.*, 2013), with respiration rates ranging from 1 to 10  $\mu\text{mol O}_2 \text{ cm}^{-3} \text{ d}^{-1}$  (Rasmussen and Jørgensen, 1992). Although biodiversity and ecosystem functioning studies have often examined various aspects of ecosystem production, the specific functions relating to oxygen consumption and carbon mineralization have been rarely studied. Leduc *et al.* (2013) observed no relationships between species and functional nematode diversity with the sediment community oxygen consumption in naturally highly diverse meiofaunal communities along the upper slope off New Zealand. This was in contrast to the positive relationships detected by Danovaro *et al.* (2008b) and Pusceddu *et al.* (2014) within higher diversity meiofaunal assemblages, suggesting a breakdown of the exponential BEF relationship at high levels of diversity, which may be due to increased competition or greater functional redundancy (Leduc *et al.*, 2013).

#### 2.1.4. Ecosystem process: nutrient cycling

The C:N:P stoichiometry of phytoplankton ultimately controls the water column nutrient ratios, which are subsequently modified by microbial reactions such as the microbial degradation of settling material, nitrification, anaerobic ammonium oxidation ('anammox')/denitrification and nitrogen fixation (Figure 1). These microbial processes can significantly influence the overall budget of nitrogen availability and can generate significant differences between oceanic regions (Gruber and Sarmiento, 1997). The physical processes, such as the bioturbation of sediments by benthic invertebrates (Table 1), can also increase the flux of nutrients released from sediment-based, microbial processes (Gray and Elliott, 2009).

##### *2.1.4.1. Ecosystem function: denitrification, nitrification and nitrogen fixation*

As denitrification is inhibited in the presence of oxygen, this process only occurs within anoxic water and sediment conditions (Tiedje, 1988). By contrast, nitrogen fixation occurs in all of the oceanic basins (Gruber and Sarmiento, 1997), with a major contribution from the marine diazotrophic cyanobacterium *Trichodesmium* spp. (Carpenter, 1983) and secondarily from diatom genera *Rhizosolenia* and *Hemiaulus* (containing the endosymbiotic nitrogen fixing cyanobacteria *Richelia intracellularis*) (Arrigo, 2005 and references therein), accounting overall for an estimated increase in the current global supply of nitrogen by 28 Tg N yr<sup>-1</sup> (Gruber and Sarmiento, 1997). Seagrass meadows are also zones of intense nitrogen fixation which can significantly contribute to the overall primary production (Welsh 2000). Despite the importance of denitrification, nitrification and nitrogen fixation in determining the availability of nitrogenous products to other ecosystem processes, these functions have yet to be examined in relation to biodiversity gradients. This paucity probably reflects the difficulty in defining microbial biodiversity and measuring functional output within experimental manipulations.

##### *2.1.4.2. Exchange of limiting nutrients*

The availability of limiting compounds is also heavily modified by primary producer uptake and vice versa. In addition to the use of inorganic sources, various phytoplankton species can use dissolved organic nitrogen directly to meet their N needs and heterotrophic uptake of dissolved organic carbon has been observed in a number of dinoflagellates (Lewitus and Caron, 1991) and chrysophytes (Wheeler

*et al.*, 1977, Kristiansen, 1990). Bacterioplankton (Liu *et al.*, 2010; Tappin *et al.*, 2012) and phytoplankton (Mulholland and Lee, 2009) can directly utilize oligopeptides by both external hydrolysis and direct assimilation depending on molecular size. Ptacnik *et al.* (2008) and Goebel *et al.* (2014) found positive BEF relationships in the phytoplankton. Using more than 3000 natural phytoplankton samples, Ptacnik *et al.* (2008) found that the amount of algal carbon per unit total phosphorus was positively related to genus richness suggesting a positive relationship between phytoplankton diversity and resource use efficiency of the phytoplankton communities in freshwater environments and the Baltic Sea. Goebel *et al.* (2014) also observed positive, asymptotically saturating relationships between ecosystem-wide phytoplankton diversity and nutrient uptake. Complementarity, and specifically facilitation, interactions between coexisting phytoplankton types were found to underlie much of the positive relationship - the composition of traits in assemblages determining the magnitude of complementarity and identity effects.

Macroalgal species assimilate both nitrate and ammonium from the water column (Naldi and Wheeler, 1999). Annual macroalgae act as carbon and nutrient (mainly nitrogen and phosphorus) sinks during bloom periods and subsequently become sources during die off periods through leaf shedding, grazing and mechanical breakage of leaves. Perennials, particularly those capable of forming dense stands such as kelp forests, also represent significant elemental pools. Seagrasses are capable of assimilating nitrogenous sources from both roots and leaves, although the uptake from the sediment, via the roots, is the major source (e.g. *Zostera marina*; Short and McRoy, 1984). Both positive and negative BEF relationships have been documented within macroalgal assemblages. Bracken and Stachowicz (2006) observed a positive relationship between species richness and nitrogen assimilation, but only when both ammonium and nitrate uptake rates were examined simultaneously, indicating increased resource partitioning and hence complementarity within intertidal macroalgal assemblages. By contrast, a decrease in nutrient uptake with increasing seaweed species richness was detected by Bracken and Williams (2013) on rocky shores. This negative relationship was only apparent when they used realistic, non-randomly assigned, species richness for treatments. This suggests that random species allocation to treatments, typical of many BEF experiments, may significantly change the expression of BEF

relationships, potentially confounding many BEF findings. Positive relationships were also highlighted between seagrass (*Zostera marina*) genetic diversity and nutrient cycling (Hughes *et al.* 2009; Hughes and Stachowicz, 2004). As shown with other functions, genetic diversity was particularly important following disturbance as pore water ammonium concentrations also decreased with increased genetic diversity after disturbance (Hughes and Stachowicz, 2004).

Although sediment microbial activity is recognized as the main source of nutrients to the overlying water column, ammonium excretion from benthic invertebrates can be a significant contribution to this recycling function (Wotton and Malmqvist 2001; Jordan *et al.*, 2009). The flux of nutrients, liberated by microbial processes within the sediment, can be significantly enhanced by macrofaunal bioturbation processes (Birchenough *et al.*, 2012). Bioturbation can enhance nutrient cycling by as much as 35% (Gutiérrez, 2011), and nutrients derived in this way can contribute up to 80% of those required by pelagic primary producers (Dale and Prego, 2002). With the exception of one study (Bolam *et al.*, 2002), positive relationships between benthic invertebrate species richness and nutrient sediment flux were present in several studies including Emmerson and Raffaelli (2000) (ammonium flux), Waldbusser *et al.* (2004) (inverse phosphate flux), Ieno *et al.* (2006) (ammonium and phosphate), Bulling *et al.* (2010) (ammonia only but not with phosphate) and Karlson *et al.* (2010) (nutrient incorporation within the sediment through biodeposit production). In all of these studies, except for Karlson *et al.* (2010), identity effects underpinned the observed BEF relationships, hence highlighting the overwhelming importance of the role of individual species in affecting nutrient fluxes rather than species richness *per se*. Although failing to detect either a positive or negative BEF relationship, Bolam *et al.* (2002) also suggested identity effects were present and, expressed through functional diversity, are important in maintaining nutrient fluxes. By contrast, Karlson *et al.* (2010) concluded that the positive, over-yielding relationship between benthic macrofaunal deposit feeders and phytodetrital processing observed was mainly explained by niche partitioning and/or facilitation (complementarity) rather than identity effects.

The importance of the role of individual species (hence identity effects) within infaunal BEF relationships was also highlighted by Biles *et al.* (2003) who examined both species and functional richness against ammonium release from sediments. In fact, while there was not a relationship between

nutrient flux and species richness, the use of functional richness (trait diversity) produced a stronger, positive association with the studied ecosystem function, thus highlighting the potential value of traits analysis to provide biodiversity measures for BEF assessment and operationalization while compensating for identity effects (Biles *et al.*, 2003; Hensel and Silliman, 2013). However, Emmerson *et al.* (2001) showed that the effect of either benthic species richness or functional diversity on ammonia release in intertidal areas varied spatially, with highly idiosyncratic relationships occurring in different sites. Similarly Queiros *et al.* (2011) highlighted the influence of habitat complexity and sediment type on the relative role of infaunal species as drivers of function. Hence, geographic location (and associated abiotic environmental features) and species identity can significantly affect the expression of BEF relationships, especially when underpinned by identity effects, therefore they need to be taken into account while attempting to operationalize BEF relationships for monitoring purposes.

There are few studies examining BEF relationships in fish, cephalopod, seabird, reptile and mammal assemblages. This is probably due to the difficulty of experimental manipulations with these animals in controlled conditions, their occupation of higher trophic levels and possibly their probable small contribution to these functions (Table 1). In studies other than temperate marine habitats, McIntyre *et al.* (2007) (tropical freshwater lake system) and Allgeier *et al.* (2014) (tropical habitat) both found that declining fish diversity reduced nutrient recycling processes. These relationships were dominated by identity effects with relatively few species dominating nutrient recycling (McIntyre *et al.*, 2007; Allgeier *et al.*, 2014).

#### 2.1.5. Ecosystem process: physical environmental modification

The occurrence of many species provides habitat for others, such as dense vegetated habitats generated by macroalgal and angiosperm beds (Table 1). Species adding complexity to seabed habitats tend to accentuate BEF relationships by promoting additional diversity, which in turn can lead to elevated functioning (Rilov *et al.*, 2012; Kochmann *et al.*, 2008). Ecosystem engineer species may also have a disproportionate effect on the physical environment, which can improve conditions for other species or significantly change other functional rates (Figure 2).

#### 2.1.5.1. Ecosystem function: reef building, water velocity and particle flux/sedimentation modification

Epifaunal benthic invertebrates can be found in extremely high densities and generate biogenic structures that can influence the physical environment and provide important habitat for other species (Rigolet *et al.*, 2014). The rugosity (complexity) and elevation of some of these structures is sufficient to reduce flow rates and resuspension and increase accretion (Wildish and Kristmanson, 1984). Macroalgae, such as the fucoids (order Fucales) intertidally and kelps (order Laminariales) subtidally, are the main foundation species on most temperate hard substrata habitats (Jones *et al.*, 1994). Both of these macrophyte groups modify environmental parameters, for example, by providing moist intertidal microclimates during emersion (Jenkins *et al.*, 1999); modification of boundary conditions, sedimentation and shoreline stabilization (Hull, 1987; Boudouresque *et al.* 2012, Infantes *et al.* 2012, Jackson *et al.* 2013) and also providing a physical structure for colonization (Epifanio *et al.*, 2003; Rabaut *et al.*, 2007).

With regard to BEF relationships within the context of provision of physical habitat, Williams (2001) found a positive association between intra-specific genetic diversity within *Z. marina* and leaf shoot density. Although Hughes and Stachowicz (2004) failed to find the same relationship under normal growth conditions, following a period of intense grazing by wildfowl, they did find that more leaf shoots, and hence greater habitat provision, remained in plots with higher genetic diversity, suggesting greater resistance in these treatments. The greater remaining biomass may also lead to a greater output of other functional products. There are no studies that have examined benthic invertebrate diversity and habitat provision.

#### 2.1.5.2. Ecosystem function: biomodification of the sediment matrix

Biomodification of the sediment matrix through bioturbation, bioirrigation, biodeposition and biostabilisation (Gray and Elliott, 2009) are fundamental infaunal processes with implications for a range of ecosystem functions. These activities exert significant influence over benthic sedimentary geochemical environments through impacts on oxygen, pH and redox gradients (Lohrer *et al.*, 2004; Stahl *et al.*, 2006; Pischedda *et al.*, 2007; Queiros *et al.*, 2011; Birchenough *et al.*, 2012), contaminant sequestration and release (Teal *et al.*, 2009) and sediment granulometry (Montserrat *et al.*, 2009),

biomodification processes affect bacterial activity and composition (Mermillod-Blondin, 2011; Gilbertson *et al.*, 2012), carbon (Kristensen, 2001) and nitrogen cycling (Gilbert *et al.*, 1998; Emmerson and Raffaelli, 2000). As with the nutrient fluxes discussed above, there are positive relationships between species richness and sediment oxygenation/sediment mixing, as indicated by the depth of the redox potential discontinuity layer (Waldbusser *et al.*, 2004; Godbold and Solan, 2009). Waldbusser *et al.* (2004) also observed that the variability of the oxygen flux was reduced in the multispecies treatment, indicating that richness may also stabilize certain ecosystem functions. Both Waldbusser *et al.* (2004) and Godbold and Solan (2009) suggest that the positive influence of species richness on ecosystem function was again a product of identity effects mediated through functional traits, and that higher levels of biodiversity reduce the relative influence of abiotic factors (Godbold and Solan, 2009).

#### 2.1.6. Conclusions for operational requirement 1

The evidence for BEF relationships within different functions and for all biological components has been summarized in Table 3. Biodiversity and ecosystem function relationships, stemming from both taxonomic and functional diversity measures, were demonstrated in the literature for several functions and biological components. The vast majority of the reported relationships were positive. However, not all components or functions were involved, with notable knowledge gaps that might inhibit the development of mechanisms that could convert biodiversity measures to holistic and realistic surrogates of ecosystem function: this may ultimately prevent the application of BEF relationships for practical monitoring roles.

Table 3. Biodiversity and ecosystem function relationship evidence summary table for the biological components of microbes, phytoplankton, zooplankton, macroalgae, angiosperms, benthic invertebrates, fish and cephalopods.

Ecosystem process	Ecosystem function	Biological component with BEF relationship evidence	Biodiversity mechanism underpinning BEF relationship	Additional observations
Biomass production	Primary productivity	Phytoplankton <sup>1</sup>	Identity + complementarity	Measuring biodiversity problematic
		Macroalgae <sup>2</sup>	Identity > complementarity	Both species and functional richness
		Angiosperms – genetic diversity <sup>3</sup>	Not known	Particularly important during disturbance/stress
		Angiosperms – species diversity <sup>4</sup>	Identity (species only)	Tropical and Baltic studies only <sup>4</sup>
	Secondary productivity	Microbes <sup>5</sup>	Not known	Measuring biodiversity problematic
		Benthic invertebrates <sup>6</sup>	Identity > complementarity	Meiofaunal evidence sparse
Organic matter transformation	Organic matter decomposition and removal	Microbes <sup>7</sup>	Not known	One study only
		Meiofauna <sup>8</sup>	Not known	Conflicting evidence
		Benthic macro-invertebrates <sup>9</sup>	Identity	One study only
	Import/export of organic matter	No evidence		
Ecosystem metabolism	Oxygen consumption and carbon mineralization	No evidence		The dominant influence of abiotic factors for some of these ecosystem functions may suggest that BEF relationships have little influence and may explain the absence of dedicated studies for these ecosystem functions.
	Oxygen production	No evidence		
Nutrient cycling	Denitrification	No evidence		
	Nitrification	No evidence		
	Nitrogen fixation	No evidence		

	Exchange of limiting nutrients	Phytoplankton <sup>10</sup>	Complementarity (facilitation)	Limited evidence base
		Macroalgae <sup>11</sup>	Complementarity	Additional trophic levels modified the BEF relationship <sup>12</sup>
		Angiosperms <sup>13</sup>	-	Genetic diversity
		Benthic invertebrates <sup>14</sup>	Identity > complementarity	Both species and functional richness <sup>19</sup>
		Fish <sup>15</sup>	Identity	Evidence from a freshwater and tropical system <sup>15</sup>
Physical environment modification	Bioturbation	Benthic invertebrates <sup>14 &amp; 16</sup>	Identity	Reduced variability with richness also documented <sup>17</sup>
	Reef building	Angiosperms – genetic diversity <sup>18</sup>	Not known	Conflicting evidence from normal and disturbed conditions
	Water velocity, particle flux and sedimentation	No evidence		

## References

- 1 Balvenera *et al.*, 2006; Cardinale *et al.*, 2006; Hector *et al.*, 2007
- 2 Bruno *et al.*, 2005; Arenas *et al.*, 2009; O’Lanari and Coutinho, 2014
- 3 Hughes *et al.*, 2009; Williams, 2001
- 4 Terrados *et al.*, 1998; Duarte *et al.*, 2000; Gustaffsson and Böstrom, 2011
- 5 Danovaro and Pusceddu 2007; Langenheder *et al.*, 2010
- 6 Duffy *et al.*, 2003; Duffy *et al.*, 2005; France and Duffy, 2006 ; Gorman *et al.*, 2008; Harvey *et al.*, 2013; Hensel and Silliman, 2013
- 7 Danovaro and Pusceddu, 2007
- 8 Danovaro *et al.*, 2008; Pusceddu *et al.*, 2014
- 9 Solan *et al.*, 2004; Godbold *et al.*, 2009; Queirós *et al.*, 2011; Hensel and Silliman, 2013 10 Ptacnik *et al.*, 2008
- 11 Grifin *et al.*, 2009; Bracken and Stachowicz, 2006
- 12 Reynolds and Bruno, 2012
- 13 Hughes *et al.*, 2009
- 14 Emmerson and Raffaelli, 2000; Waldbusser *et al.*, 2004; Ieno *et al.*, 2006; Bulling *et al.*, 2010; Karlson *et al.*, 2010

15 McIntyre *et al.*, 2007 (freshwater lake system); Allgeier *et al.*, 2014 (tropical system)

16 Waldbusser *et al.*, 2004; Godbold and Solan, 2009

17 Waldbusser *et al.*, 2004

18 Williams, 2001

19 Biles *et al.*, 2003

The lack of evidence for positive BEF relationships could partly be due to a lack of studies investigating specific functions (e.g., oxygen production/consumption and carbon mineralization) or specific components (e.g., zooplankton, fish, cephalopods, seabirds and mammals in secondary production). In some cases, the evidence supporting positive BEF relationships was sparse or inconsistent (e.g., large variability in the response of the relationships between meiofaunal biodiversity and secondary production), with limited representativity of the geographic area (e.g., positive relationship between angiosperm species diversity and primary production was available for tropical and Baltic areas only) or the marine habitat (e.g., nutrient recycling and fish diversity in freshwater). Methodological influences were due to: 1) the small number of species typically used in BEF experiments (see Stachowicz et al. 2007); 2) the definition and number of ecosystem functions used (few studies are multi-functional); 3) the use of random or realistic biodiversity gradients; 4) the type of experiments (laboratory, mesocosm or field trials); 5) experimental duration; 6) spatial replication, 7) an absence of the simultaneous testing of abiotic factors, and 8) the number of trophic levels included (see below). These all contributed to occasionally over-powering contextual dependency, further complicating the determination of over-arching BEF relationships.

In several cases, trophic interactions added complexity and ambiguity to BEF relationships, preventing clear generalizations between studies. As well as BEF relationships changing the availability of functional products within an ecosystem, biodiversity itself can directly influence trophic dynamics. As food web size increases (measured by the number of species) the number of feeding links per species (linkage density) also increases (Christensen and Pauly, 1993). This increases the abundance of prey available to predators in species rich food webs and may also have implications for redundancy within the system. Therefore, food webs with higher biodiversity may both increase in overall available resource and have a higher connectivity between trophic levels allowing for more routes for the movement of these resources. For example, Finke and Denno (2004), Hillebrand and Cardinale (2004), Spivak *et al.* (2007), O’Gorman *et al.* (2008), Edwards *et al.* (2010), Reynolds and Bruno (2012) and Hensel and Silliman (2013) all found that changes in species richness at differing trophic levels also induced structural and functional changes in adjoining levels. Changes in both the resource distribution

within a food web (via BEF boosted functions) and the structural changes associated with diversity changes alone might induce or modify ‘trophic cascades’, thereby complicating the expression of biodiversity induced changes to ecosystem functioning. In contrast, Borer *et al.* 2005 and O’Connor and Bruno (2009) did not observe trophic changes with species richness. The meta-analysis of terrestrial and marine studies by Borer *et al.* 2005 indicated that predator and herbivore taxonomy and physiology were more influential in stimulating cascades than richness (i.e. identity effects). The complexity of both trophic dynamics and BEF relationships make it particularly difficult to predict overall ecosystem functioning with increasing biodiversity in one or multiple biological components/trophic levels (Snelgrove *et al.*, 2014). On balance, there are many studies to support the BEF premise that biodiversity does influence ecosystem function. Negative relationships were rarely evident or reported when compared with positive relationships.

## **2.2. Operational requirement 2: what biological components are required to represent biodiversity within a BEF relationship?**

Biodiversity is routinely represented and deconstructed into measurable, manageable and meaningful components. Biodiversity assessments often focus on specific components (e.g., benthic infauna, angiosperms, and fish) which are assumed to be representative or proxies for the biodiversity of the ecosystem as a whole. Measuring a component of the system is usually easier and more cost effective than measuring the overall system biodiversity, considering also that the expertise of the researchers undertaking the assessment is often limited to one or few biological components. Translating BEF relationships into workable monitoring applications requires that the biodiversity components selected are also relevant to the given BEF relationship. It is therefore necessary to identify which biological components are required to represent biodiversity within a given BEF relationship of interest. For example, the use of angiosperms alone for estimating total regional primary production will be inadequate unless phytoplankton and macroalgae can also be combined, as they can significantly contribute to this function. It is therefore necessary to establish: 1) what biological components are needed to be selected to represent biodiversity for assessing a particular ecosystem function, and 2) what is their relative importance in influencing and contributing to the overall functional output.

By providing a framework for contextualizing individual biological components within multi-component systems, Table 1 aids in the selection of the required biological components and practical application of BEF relationships into monitoring programmes. This is a simplistic attempt to examine functional output by biological component that does not include the interactions between biological components and functions (e.g., the availability, routes or processes that the products of a certain function are subsequently used within). It indicates that value may stem from indicating which biological components should be prioritized in biodiversity measurement for use in operationalized BEF monitoring (assuming a BEF exists for a specific component within the context of a specific function). In addition, these results, in combination together with the gaps in BEF evidence highlighted above for certain biological components and functions, indicate research priorities to allow the appropriate assessment of ecosystem functioning at the regional level. For example there is a lack of studies examining the microbe, phytoplankton and zooplankton assemblages, which, according to Table 1, may have a primary contribution to several ecosystem functions.

#### 2.2.1. Conclusions for operational requirement 2

The scoring of the biological components indicates that the large BEF evidence gaps align with several of the more functionally important components. For example, microbial processes generating primary and secondary production, phytoplankton translocation of organic matter, zooplankton secondary production and the physical engineers of habitats by benthic invertebrates. Hence for many of the main ecosystem functions, there is insufficient evidence for enough contributing biological components to adequately represent 'biodiversity' in many BEF relationships. The approach in Table 1 needs further development to provide a confident 'look-up' tool for practical applications using BEF relationships.

#### **2.3. Operational requirement 3: can the biodiversity of the selected biological components be measured easily?**

Having selected the appropriate biological components for a given BEF relationship of interest, monitoring methodologies require that biodiversity of those components can be assessed and expressed in compatible units. Measures of biodiversity used in most reviewed studies appear straightforward at the macroscopic scale (e.g. macrofaunal species richness) and have tangible relationships with several

ecosystem functions. However, defining and measuring biodiversity in consistent and meaningful units for the microscopic biological components, such as the microbial assemblages, and at the genetic scale, poses significant challenges. For example, most of the prokaryotes cannot be identified by cultivation-based approaches but require molecular analyses (16S rRNA genes). Recently, the transition from Sanger sequencing to the next generation of high throughput sequencing technologies has opened new horizons in exploring the biodiversity of prokaryotic assemblages (Giovannoni and Stingl 2005; Sogin *et al.*, 2006; Roesch *et al.*, 2007; Caporaso *et al.*, 2010). Next generation sequencing technologies applied to 16S rRNA genes have not only increased the current databases, but also allows the identification of rare bacterial taxa for which ecological significance is even more uncertain than that of the dominant taxa (Sogin *et al.*, 2006; Gobet *et al.*, 2012).

Overall, applications incorporating BEF relationships require that the biodiversity measures of the biological components selected are consistent, cost-effective to monitor and calculate, and mechanisms to control the estimate bias associated with sampling limitations are in place. It is clear that the working monitoring tools, based on BEF relationships, will potentially span several biological components and that this must ultimately be represented as comparable and easily obtained measures of biodiversity. The difficulty in defining biodiversity units within functionally important components, such as microbes, not only prevents the development of practical BEF-based applications, but also compromises the development of the underlying evidence base. Furthermore, insufficient knowledge is available on the other measures tiers of biodiversity, such as genetic or guilds, to establish the most appropriate measure of biodiversity for the combined components.

#### **2.5. Operational requirement 4: how does biodiversity generate ecosystem function relationships?**

Depending on the underlying BEF relationship mechanism, standard units used to describe structural elements of biodiversity may not have the most direct relationship with specific functions and therefore may require expression as alternative measures of biodiversity. For example, BEF relationships underpinned by identity effects are often irregular (similar to riveted BEF models) when maintained in structural biodiversity units. In this situation, taxonomic units may benefit from translation into functional diversity using traits-based analysis, such as Biological Traits Analysis (e.g. Bremner, 2008),

into more standardized units that have a more uniform and linear relationship with ecosystem functioning. For BEF relationships emerging from complementarity, direct (taxonomic) measures of biodiversity, such as species richness, may be sufficient to express the influence of biodiversity. Therefore, operational use of BEF relationships requires: 1) that the mechanism of delivery for each BEF/biological component combination is known, and 2) that the units used to express biodiversity best represent the mechanisms that underpin positive BEF relationships.

Unlike many of the terrestrial studies where complementarity is prevalent (Cardinale *et al.*, 2007), positive marine BEF relationships examined in the marine environment (this study and others, e.g. Stachiwicz *et al.*, 2007; Cardinale *et al.*, 2012; Gamfeldt *et al.*, in press) are mostly driven by identity effects (Table 3). In many studies, the increased functional rates observed were mostly ascribed to the presence of particular species (and their associated functional abilities or traits), rather than to an increase in species diversity (e.g. richness) *per se*. As a result, functional diversity has been used on several occasions within BEF research (e.g. through Biological Traits Analysis, BTA) (Emmerson and Raffaelli, 2000; Emmerson *et al.*, 2001; Bolam *et al.*, 2002; Godbold and Solan 2009; Harvey *et al.*, 2013). When compared with species richness, the expression of biodiversity as functional diversity has often provided a better relationship with ecosystem functionality (Griffin *et al.*, 2009). However, despite this, identity effects were still apparent in some of these studies (Norling *et al.*, 2007; Griffin *et al.*, 2009), suggesting that trait-based analysis is insufficient to fully capture the underlying properties that generate identity effects. Roles are often repeated across species within assemblages, suggesting that different species differ in either their performance or influence. For example, Törnroos *et al.* (2014) found that 66% of all of the possible traits measured in marine benthic macrofaunal species (in Northern Europe) were still expressed despite a reduction in species richness from 151 to 6 taxa, indicating that most traits (hence functional roles) are shared and categorical descriptions of species role are replicated within natural assemblages. This suggests that identity effects are not just an expression of the species functional role, as assessed with BTA, but also ‘role performance’ and/or ‘role influence’ are relevant in determining the species contribution to the overall functioning of the system. The rate, efficiency or influence of a particular role is not coded within BTA, and this is understandable considering how the

performance of any species can change depending on numerous factors including age, abundance, habitat, community composition and environmental conditions (Queiros *et al.*, 2011).

Despite the difficulty of attributing species with both categorical functional roles (e.g. BTA) and quantitative information of role performance or influence, these approaches demonstrate a greater capability to detect and compensate for identity effects in BEF relationships, thus allowing ecosystem function to be estimated from species information. Furthermore, species providing disproportionate contributions to overall functionality can be identified from structural community data rather than from functional response experimentation. Knowing when and which species are functionally important allows for focused species-based monitoring and management. Furthermore, if the information on role, performance/influence and pressure sensitivity of species can be combined, it should also be possible to model, and therefore predict, the vulnerability of functionally important species and the expected loss of ecosystem functionality along a realistic gradient of species loss.

#### **2.4. Operational requirement 5: what proportion of the overall variance of a given function is explained by biodiversity?**

Although a BEF relationship may be present for a particular function, there is also a need to determine the contribution made by biodiversity to the total expression of a particular ecosystem function. It is possible to detect a BEF relationship (operational requirement 1) yet have it only explain a very small proportion of the functional variance because other factors, such as abiotic variables, actually dominate the functional rates (Figure 3). For BEF-based monitoring, the contribution of biodiversity to functioning must be sufficiently large to be detected above the influence of abiotic factors, or the relative biotic and abiotic variability needs to be understood.

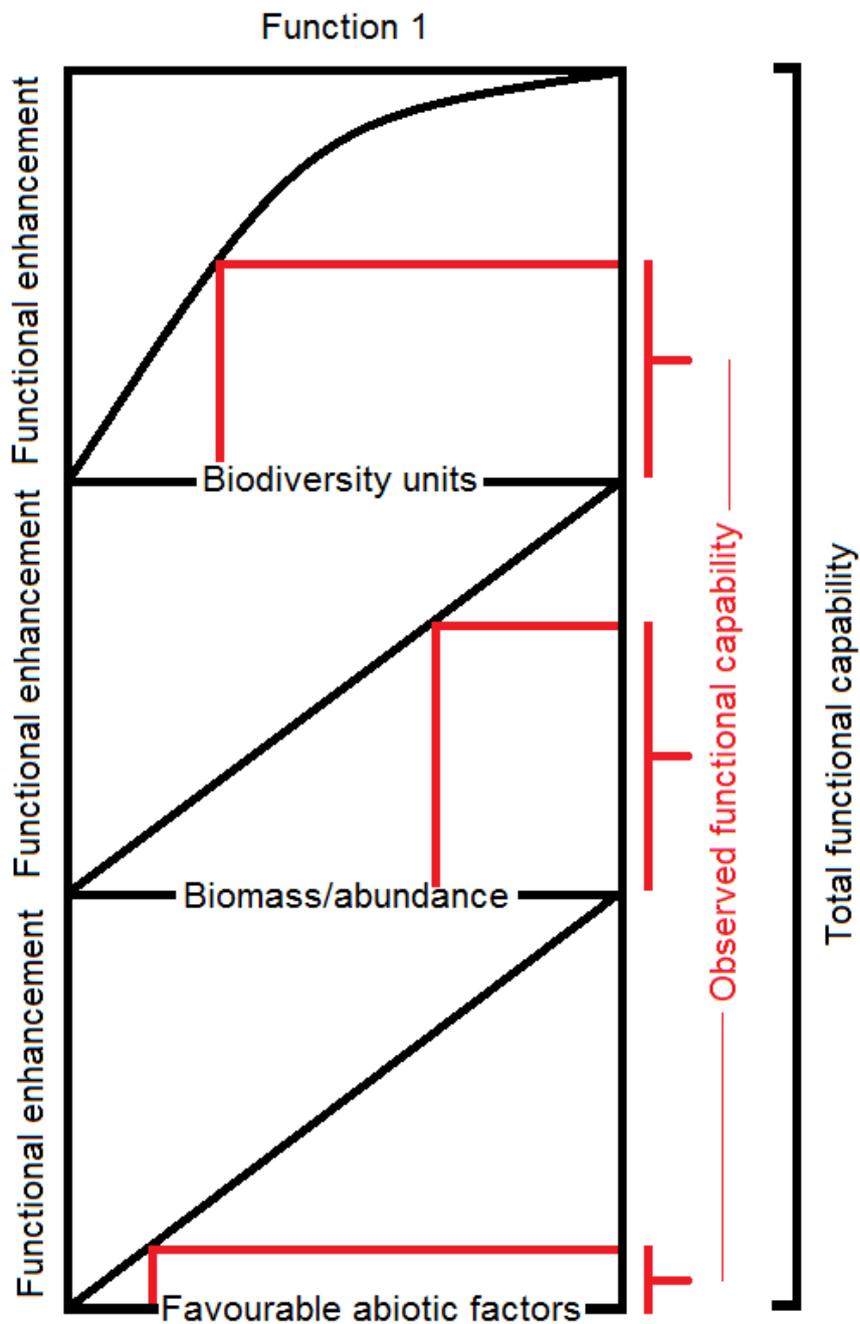


Figure 3. Representation of overall capacity for a single ecosystem function as a composite of three equally important contributing factors. Hypothetical contribution of each factor show in red.

This review shows that studies rarely measure or consider the magnitude of the biodiversity influence on ecosystem functions compared to other abiotic or biotic factors (Figure 3). Hence it is not possible to determine the overall importance of operationalized BEF measures within the total ecosystem functioning observed. Where abiotic factors have been also considered, it was clear that these may modify the BEF relationship and have their own direct influence on functional rate (Biles *et al.*, 2003;

Godbold and Solan, 2009; Bulling *et al.*, 2010; Queiros *et al.*, 2011). As such, the effects of biodiversity may be of secondary importance when compared to the influence of other abiotic and biotic drivers of ecosystem function (Goldbold, 2012) and may also be substantially transformed under changing abiotic regimes (Gamfeldt *et al.*, in press). The practical application using BEF relationships require that the contribution of all of the factors (both biotic and abiotic) to ecosystem functioning are quantified and any interactions between factors are known and can be compensated for.

The influence of biodiversity on ecosystem functioning is further complicated as different functions will interact in an ecosystem, hence an increase in the functional output within one ecosystem function may change the availability of resources or substrate for use in other ecosystem functions. At the same time, this 'spill-over' enhancement effect can be modified by resource availability, with scarce or limited resources likely generating the greatest spill-over augmentation. For example, an increase in nitrogen fixation will also enhance primary and secondary production locally, the potential enhancement or 'spill-over' in this case being determined by the amount of nitrogen fixed and the existing availability of nitrogen locally. In contrast, dissolved oxygen for respiration may already be sufficiently available from the atmospheric input that further biological inputs induce little or no functioning benefit, e.g. as in eutrophication. It is also possible that the excessive supply of functional product resources may in fact become detrimental to some adjoining trophic levels. For example, the metabolic production of ammonium may benefit autotrophs but potentially be toxic to heterotrophs. Furthermore, some functional products may be in a form that is unavailable for subsequent reprocessing. Phytoplankton biomass is rapidly consumed by the zooplankton, however, the biomass produced in seagrass beds is often high in refractory carbon and rarely consumed by secondary producers directly (Kennedy and Björk, 2009).

The interactions outline above increase the difficulties in obtaining accurate predictions about the value of BEF-induced functional spill-over to other biological components/trophic levels. With regard to practical application of BEF relationships and meaningful reporting, these interactions may complicate or overwhelm the response of individual ecosystem functions to biodiversity. However, considerations

of resource demand and functional spill-over does provide a framework for putting BEF relationships within separate ecosystem functions and biological components into a multicomponent perspective.

### ***3. Conclusions***

Five important considerations were identified for the practical application of BEF relationships in monitoring (i.e. operationalization), however the information required for immediate use is currently lacking and therefore prevents wide-spread implementation of BEF-based functional monitoring. This review reported many positive and some negative relationships within many biological components, habitat and ecosystem functions. Null relationships were also reported. The consistency of the positive and negative relationships was often low which complicates universal acceptance and confident use of BEF relationships within monitoring application. Equally, some biological components and functions have received little or no investigation. There was a notable shortage of studies examining BEF relationships within microbial, phytoplankton, zooplankton, fish, cephalopod, seabird and marine mammal components, which is most likely explained by methodological constraints. The benthic flora and fauna have received the greatest amount of BEF research effort and as such, there is more scope for trialling operationalized BEF-based monitoring within these systems - other habitats will probably remain dependent on direct measures of functional processes for the time being. The other significant information shortage is on the relative contribution of biotic and abiotic effects on functioning for almost all biological components and ecosystem functions. Without this information it is not possible to contextualize the influence of BEF relationships for overall functional expression.

Although there are significant short-comings of the evidence for BEF relationships in many biological components and the interactions between biological components and ecosystem functions, e.g. trophic cascades and functional spill-over. Evidence is also lacking for the value of biodiversity *per se* in ecosystem functional responses, the approach shows promise as a cost-effective (especially when structure measures of biodiversity are already being collected) and sensitive surrogate measure of a substantial element of ecosystem functioning. The use of BEF relationships represents the ability to examine ecosystem functions via the species-based apparatus of functional delivery, for example, the genotypes, individuals, species and assemblages of ecosystems, rather directly measure ecosystem

functions. Furthermore, as long as the appropriate biological components are sampled, functional surrogates derived from biodiversity should be able to provide proxy information on multiple functions simultaneously unlike direct measures on single functions. Once the underlying evidence is in place, a methodology using biodiversity-based estimates of ecosystem function is likely to be cost-effective and complementary to other forms of monitoring (especially as components of biodiversity are routinely sampled for several other purposes). Furthermore, it should also be theoretically possible to combine existing information on the sensitivity of species with BEF relationships so that predictions of biodiversity-induced ecosystem functioning can be generated from realistic scenarios of species loss. This approach might be particularly informative for relationships underpinned by identity effects and hence a reduced number of highly influential species. There is also the potential for the wide-scale identification of species with strong identity effects for use as indicator species and functionally-relevant surrogates of total biodiversity with BEF relationships. This may reduce the need for full enumeration of the contributing biological components or initial translation of biodiversity into functional diversity units, thereby potentially reduce the cost of operationalizing BEF relationships.

Despite the current lack of sufficient evidence to support each of the operational requirements described above, it is still possible to establish a protocol highlighting how BEF relationships might contribute within a realistic ecosystem function monitoring framework (Figure 4). Figure 4 suggests a process by which 1) the initial functionality requirement is divided into constituent functions, 2) biodiversity is sampled, 3) the biodiversity is expressed as comparable and functionally-relevant units, 4) biodiversity is combined with other important contributors of the rate of ecosystem function (i.e. abiotic influences), and 5) estimated ecosystem functions are recombined into overall assessments of ecosystem functionality. Although the currently available information is insufficient for implementing this protocol in practice, it constitutes a conceptual framework that will stimulate and direct future work focusing on developing operational applications for BEF relationships.

Until the significant knowledge gaps described above are filled, BEF-based functional monitoring remains highly attractive yet unachievable. The greater need for the inclusion of functional considerations within wide-spread marine monitoring and assessment, (for example the MSFD),

without a proportional increase in resources to deliver them, will hopefully promote BEF research and its adoption within useful practical applications.

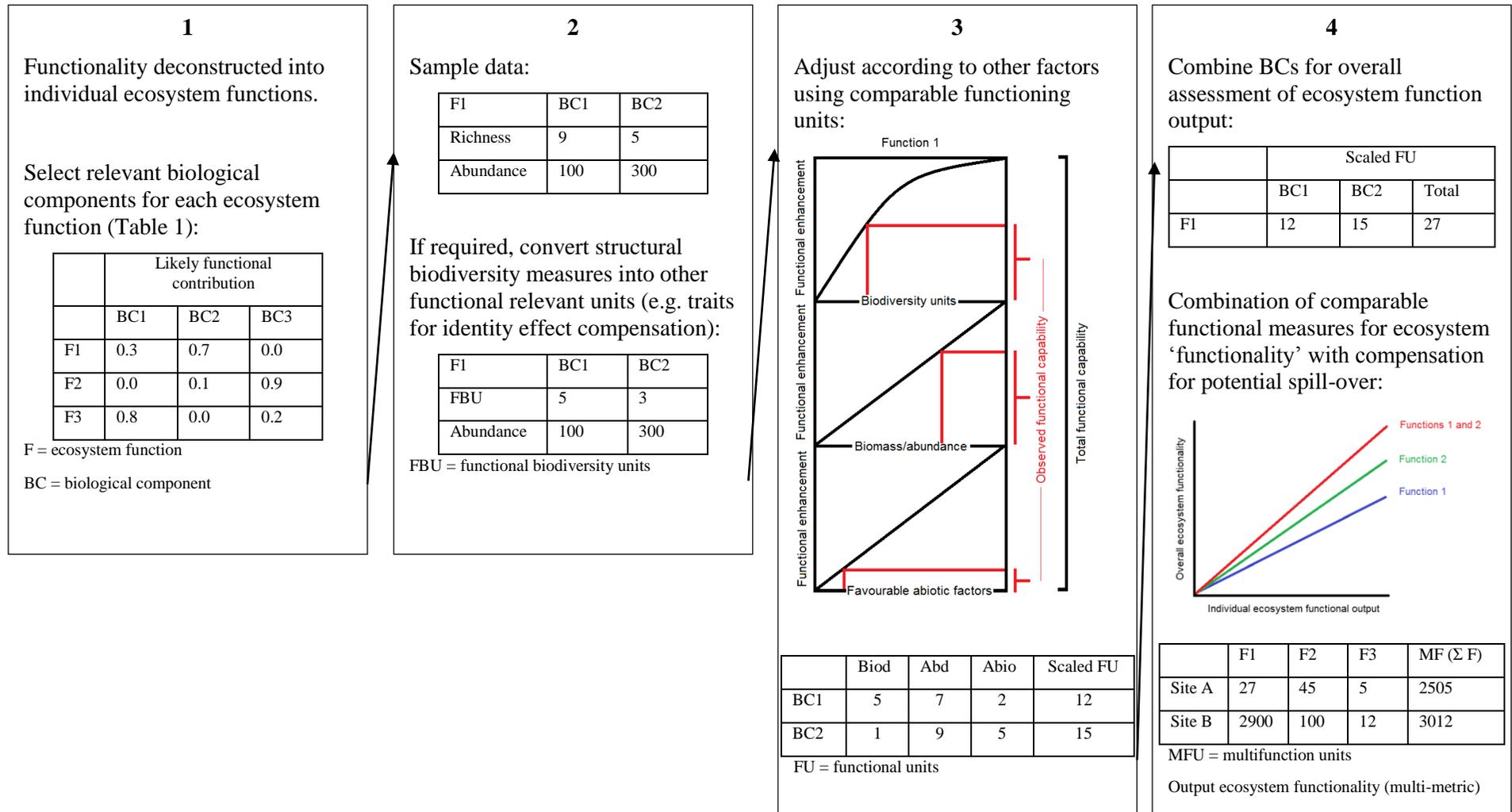


Figure 4. Potential framework for the practical application of BEF relationships within marine ecosystem functionality monitoring.

Future work must strive to detail BEF relationships from more ecosystem functions and especially from under-reported biological components. Many of the biological components that potentially contribute the most to functional delivery have received the least amount of attention, for example, because of the difficulty in measuring and defining biodiversity, which also needs addressing if BEF research and useable working applications are to develop. Further work is also required to understand the influence of biotic and abiotic on ecosystem functions and the interaction between functions (mutual inducement and spill-over), in order to possibly generalize them for operational purposes. Detailed work is required to understand both the functional form of BEF relationships over realistic spatial and temporal gradients of biodiversity as well as the impact of scale. Although they have not been addressed in detail in this review, the shortcomings of Biological Trait Analysis to fully compensate for identity effects need to be better understood and the role performance and/or influence needs to be better represented within these tools for the translation of identity effects.

### **Acknowledgements**

This review has resulted from the DEVOTES (DEVELOPMENT OF innovative TOOLS for understanding marine biodiversity and assessing good Environmental Status) project funded by the European Union Seventh Programme for research, technological development and demonstration, ‘The Ocean of Tomorrow’ Theme (grant agreement no. 308392), [www.devotes-project.eu](http://www.devotes-project.eu).

## ***References***

- 2008/56/EC, D. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). E. Commission.
- Allgeier, J.E., Layman, C.A., Mumby, P.J. and Rosemond, A.D. 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology*, doi: 10.1111/gcb.12566.
- Alves, A. S., Adao, H., Patrício, J., Neto, J. M., Costa, M. J., & Marques, J. C. 2009. Spatial distribution of subtidal meiobenthos along estuarine gradients in two southern European estuaries (Portugal). *Journal of the Marine Biological Association of the United Kingdom*, 89(08), 1529-1540.
- Arenas, F., Rey, F., and Sousa Pinto, I. 2009. Diversity effects beyond species richness: evidence from intertidal macroalgal assemblages. *Marine Ecology Progressive Series*, 381, 99-108.
- Arndt S., Jørgensen B.B., LaRowe D.E., Middelburg J.J., Pancost R.D., Regnier P. 2013 Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews* 123, 53–86
- Arnosti, C. 2011. Microbial extracellular enzymes and the marine carbon cycle. *Annual Review of Marine Science*, 3, 401-425.
- Arntz, W.E., Gili, J.M. and Reise, K. 1999. Unjustifiably ignored: Reflections on the role of benthos in marine ecosystems. Dordrecht, Springer.
- Arrigo K.R. 2005. Marine microorganisms and global nutrient cycles. *Nature*, 437, 349-355.
- Atkins, J. P., Burdon, D., Elliott, M., & Gregory, A. J. 2011. Management of the marine environment: integrating ecosystem services and societal benefits with the DPSIR framework in a systems approach. *Marine Pollution Bulletin*, 62(2), 215-226.

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. and Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecological Letters*, 9, 1146-1156.
- Barrón, C., Apostolaki, E. T., and Duarte, C. M. 2012. Dissolved organic carbon release by marine macrophytes. *Biogeosciences Discussions*, 9(2), 1529-1555.
- Barrón, C., Marbá, N., Duarte, C.M., Pedersen, M.F., Lindblad, C., Kersting, K., Moy, F. and Bokn, T. 2003. High Organic Carbon Export Precludes Eutrophication Responses in Experimental Rocky Shore Communities. *Ecosystems*, 6, 144-153.
- Biles, C. L., Solan, M., Isaksson, I., Paterson, D. M., Emes, C., and Raffaelli, D. G. 2003. Flow modifies the effect of biodiversity on ecosystem functioning: an *in situ* study of estuarine sediments. *Journal of Experimental Marine Biology and Ecology*, 285, 165-177.
- Birchenough, S.N.R., Parker, R.E., McManus, E. and Barry, J. 2012. Combining bioturbation and redox metrics: Potential tools for assessing seabed function. *Ecological Indicators*, 12(1), 8-16.
- Bolam, S.G., Fernandes, T.F. and Huxham, M. 2002. Diversity, biomass, and ecosystem processes in the marine benthos. *Ecological Monographs*, 72(4), 599-615.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D and Halpern, B.S. 2005. What determines the strength of a trophic cascade? *Ecology*, 86(2), 528-537.
- Boudouresque, C.F., Bernard, G., Bonhomme, P., Charbonnel, E., Diviacco, G., Meinesz, A., Pergent, G., Pergent-martini, C., Ruitton, S. and Tunesi, L. 2012. Protection and conservation of *Posidonia oceanica* meadows. RAMOGE and RAC/SPA publ., Tunis 1-202.
- Boyer, K. E., Kertesz, J. S., and Bruno, J. F. 2009. Biodiversity effects on productivity and stability of marine macroalgal communities: the role of environmental context. *Oikos*, 118(7), 1062-1072.
- Boyle, P. 2002. Cephalopod biomass and production: an introduction to the symposium. *Bulletin of Marine Science*, 71, 13-16.

- Bracken, M.E. and Stachowicz, J.J. 2006. Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology*, 87(9), 2397-2403.
- Bracken, M.E. and Williams, S.L. 2013. Realistic changes in seaweed biodiversity affect multiple ecosystem functions on a rocky shore. *Ecology*, 94(9), 1944-1954.
- Bremner, J. 2008. Species traits and ecological functioning in marine conservation and management. *Journal of Marine Biology and Ecology*, 366, 37-47.
- Bremner, J., Rogers, S.I. and Frid, C.L.J. 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series*, 254, 11-25.
- Bruno, J.F., Boyer, K.E., Duffy, J.E., Lee, S.C., and Kertesz, J.S. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecology Letters*, 8(11), 1165-1174.
- Bulling, M.T., Hicks, N., Murray, L., Paterson, D.M., Raffaelli, D., White, P.C., and Solan, M. 2010. Marine biodiversity–ecosystem functions under uncertain environmental futures. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2107-2116.
- Canuel, E.A., Spivak, A.C., Waterson, E.J., and Duffy, J. 2007. Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. *Limnology and oceanography*, 52(2), 590-602.
- Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., Knight, R. 2010. QIIME allows analysis of high-throughput community sequencing data. *Nature methods*, 7(5), 335-336.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. and Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989-992.

- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. and Weis, J.J. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104, 18123-18128.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., MacE, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. and Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature*, 486: 59-67.
- Carpenter, E. J. 1983. Nitrogen fixation by marine Oscillatoria (*Trichodesmium*) in the world's oceans. In: Carpenter, E.J. and Capone, D.G. (eds) *Nitrogen in the Marine Environment*, 65-103. Academic Press, New York.
- Cebrian, J. 2002. Variability and control of carbon consumption, export, and accumulation in marine Communities. *Limnology and Oceanography*, 47(1), 11–22.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala O.E. and Tilman, D. 1997. Biotic Control over the Functioning of Ecosystems. *Science*, 277(5325), 500-504.
- Cho, B. C. and Azam, F. 1988 Major role of bacteria in biogeochemical fluxes in the ocean's interior. *Nature*, 332, 441-443.
- Christensen, V. and Pauly, D. (Eds.). 1993. *Trophic models of aquatic ecosystems* (No. 26). WorldFish.
- Clarke, M.R. 1996. Cephalopods as prey III. Cetaceans. *Philosophical Transactions of the Royal Society of London B*, 351, 1053–1065.
- Covich, A. P., Austen, M. C., Bärlocher, F., Chauvet, E., Cardinale, B. J., Biles, C. L., Inchausti, P., Dangles, O., Solan, M., Gessner, M.O., Statzner, B. and Moss, B. 2004. The Role of Biodiversity in the Functioning of Freshwater and Marine Benthic Ecosystems. *BioScience*, 54(8), 767-775.
- Cury, P., Shannon, L., and Shin, Y. J. 2003. The functioning of marine ecosystems: a fisheries perspective. In Sinclair, M. and Valdimarsson G. (eds.) *Responsible Fisheries in the Marine Ecosystem*, pp. 103. FAO/CAB International, Rome, Italy/Wallingford, UK.

- Dale, A. W., and Prego, R. 2002. Physico-biogeochemical controls on benthic-pelagic coupling of nutrient fluxes and recycling in a coastal upwelling system. *Marine Ecology Progress Series*, 235, 15-28.
- Danovaro, R., Corinaldesi, C., Filippini, M., Fischer, U.R., Gessner, M.R., Jaqchet, S., Magagnini, M. and Velimirov, B. 2008a. Viriobenthos in freshwater and marine sediments: a review. *Freshwater Biology*, 53, 1186-1213.
- Danovaro, R., and Pusceddu, A. 2007. Biodiversity and ecosystem functioning in coastal lagoons: does microbial diversity play any role? *Estuarine, Coastal and Shelf Science*, 75(1), 4-12.
- Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M. and Gooday, A.J. 2008b. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Current Biology*, 18, 1-8.
- Davies, T. W., Jenkins, S. R., Kingham, R., Kenworthy, J., Hawkins, S. J. and Hiddink, J. G. 2011. Dominance, biomass and extinction resistance determine the consequences of biodiversity loss for multiple coastal ecosystem processes. *PloS One*, 6.12: e28362.
- del Giorgio, P.A. and Cole, J.J. 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics*, 29, 503–541.
- Di Poi, E., Blason, C., Corinaldesi, C., Danovaro, R., Malisana, E., Fonda-Umani, S. 2013. Structure and interactions within the pelagic microbial food web (from viruses to microplankton) across environmental gradients in the Mediterranean Sea. *Global Biogeochemical Cycles*, 27(4), 1034-1045
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. and Magurran, A.E. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344, 296-299.
- Duarte, C.M., Marbà, N., Gacia, E., Fourqurean, J.W., Beggins, J., Barrón, C., and Apostolaki, E.T. 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4).

- Duffy, E., Richardson, P.J. and Canuel, E.A. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, 6(7), 637-645.
- Duffy, E., Richardson, P.J. and France, K.E. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters*, 8(3), 301-309.
- Duffy, J.E. and Harvilicz, A.M. 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Marine Ecology Progress Series*, 223, 201-211.
- Duffy, J.E. and Stachowicz, J.J. 2006. Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. *Marine Ecology Progressive Series*, 311, 179-189.
- Edwards, K.F., Aquilino, K.M., Best, R.J., Sellheim, K.L. and Stachowicz, J.J. 2010. Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. *Ecology Letters*, 13(2), 194-201.
- Ehlers, A., Worm, B. and Reusch, T.B. 2008. Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine Ecology Progress Series*, 355, 1-7.
- Elliott, M. and Quintino, V. 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin*, 54, 640-645.
- Emerson, C.W. 1991. A method for the measurement of bedload sediment transport and passive faunal transport on intertidal sandflats. *Estuaries*, 14(4), 361-371.
- Emmerson, M.C., and Raffaelli, D.G. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. *Oikos*, 195-203.
- Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M. and Raffaelli, D. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature*, 411(6833), 73-77.

- Epifanio, C.E., Dittel, A.I., Rodriguez, R.A. and Targett, T.E. 2003. The role of macroalgal beds as nursery habitat for juvenile blue crabs, *Callinectes sapidus*. *Journal of Shellfish Research*, 22, 881-886.
- Falkowski P.G., Barber, R.T. and Smetacek, V. 1998. Biogeochemical Controls and Feedbacks on Ocean Primary Production. *Science*, 281: 200-206.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. and Falkowski, P. 1998. Primary production of the Biosphere: Integrating Terrestrial and Oceanic Components. *Science*, 281(5374), 237–240.
- Finke, D.L. and Denno, R.F. 2004. Predator diversity dampens trophic cascades. *Nature*, 429(6990), 407-410.
- Fowler, S.W. and G.A. Knauer. 1986. Role of large particles in the transport of elements and organic-compounds through the oceanic water column. *Progress in Oceanography*, 16(3), 147-194.
- France, K.E., and Duffy, J.E. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, 441(7097), 1139-1143.
- Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N. 2014. Marine biodiversity and ecosystem functioning: what's known and what's next? *PeerJ PrePrints* 2:e249v1 <http://dx.doi.org/10.7287/peerj.preprints.249v1>
- Giere, O. 2009. *Meiobenthology: the microscopic motile fauna of aquatic sediments*. 2nd Edition, Springer, Berlin
- Gilbert, F., Stora, G., and Bonin, P. 1998. Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an in situ experimental approach. *Marine Ecology Progress Series*, 163, 99-107.
- Gilbert, P.M., Anderson, D.M., Gentien, P., Granéli, E. and Sellner, K.G. 2005. The global, complex phenomena of harmful algal blooms. *Oceanography* 18(2): 136-147.
- Gilbertson, W. W., Solan, M., and Prosser, J. I. 2012. Differential effects of microorganism–invertebrate interactions on benthic nitrogen cycling. *FEMS Microbiology Ecology*, 82(1), 11-22.

- Giles, H. and Pilditch, C. A. 2006. Effects of mussel (*Perna canaliculus*) biodeposit decomposition on benthic respiration and nutrient fluxes. *Marine Biology*, 150(2), 261-271.
- Giller, P., Hillebrand, H., Berninger, U.G., Gessner, M.O., Hawkins, S., Inchausti, P., Inglis, C., Leslie, H., Malmqvist, B., Monaghan, M. T., Morin, P. J. and O'Mullan, G. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104(3), 423-436.
- Gingold, R., Moens, T., Rocha-Olivares, A. 2013. Assessing the response of nematode communities to climate change-driven warming: a microcosm experiment. *PLoS One* 8: e66653.
- Giovannoni, S.J., Stingl, U. 2005. Molecular diversity and ecology of microbial plankton. *Nature* 437, 343-348.
- Gobet, A., Boeer, S.I., Huse, S.M., van Beusekom, J.J.E., Quince, C., Sogin, M.L., Boetius, A. and Ramette, A. 2012. Diversity and dynamics of rare and of resident bacterial populations in coastal sands. *ISME Journal*, 6, 542–553.
- Godbold, J.A. 2012. Effects of biodiversity-environment conditions on the interpretation of biodiversity-function relations. *Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration*, 101.
- Godbold, J.A., & Solan, M. 2009. Relative importance of biodiversity and the abiotic environment in mediating an ecosystem process. *Marine Ecology Progressive Series*, 396, 273-282.
- Godbold, J.A., Solan, M. and Killham, K. 2009. Consumer and resource diversity effects on marine macroalgal decomposition. *Oikos*, 118, 77-86.
- Goebel, N.L., Edwards, C.A., Follows, M.J. and Zehr, J.P. 2014. Modeled diversity effects on microbial ecosystem functions of primary production, nutrient uptake, and remineralization. *Ecology*, 95, 153–163.
- Gray, J. S., and Elliott, M. 2009. *Ecology of marine sediments: from science to management*. Oxford University Press.

- Griffin, J.N., Méndez, V., Johnson, A.F., Jenkins, S.R. and Foggo, A. 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos*, 118(1), 37-44.
- Gruber, N., and Sarmiento, J. L. 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochemical Cycles*, 11, 235-266.
- Gude, H. 1988. Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. *Hydrobiologia*, 159, 63-73.
- Gustafsson, C. and Boström, C. 2011. Biodiversity influences ecosystem functioning in aquatic angiosperm communities. *Oikos*, 120, 1037-1046.
- Gutiérrez, J.L., Jones, C.G., Byers, J.E., Arkema, K.K., Berkenbusch, K., Commito, J.A., Duarte, C.M. et al. 2011. Physical ecosystem engineers and the functioning of estuaries and coasts. In: *Functioning of Estuaries and Coastal Ecosystems*' (Eds CHR Heip, CJM Philippart and JJ Middelburg.) Elsevier, Amsterdam.
- Harrold, C., Light, K. and Lisin, S. 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnology and Oceanography*, 43, 669–678.
- Harvey, E., Se' Guin., A., Nozais, C., Archambault, P. and Gravel, D. 2013. Identity effects dominate the impacts of multiple species extinctions on the functioning of complex food webs. *Ecology*, 94(1), 169–179.
- Hastie, L.C., Pierce, G.J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U. and Robin, J.P. 2009. Cephalopods in the north-eastern Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanography and Marine Biology: An Annual Review*, 47, 111-190.
- Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Spehn, E.M., Wacker, L., Weilenmann, M., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Leadley, P.W., Loreau, M., Mulder, C.P.H., Nesshoover, C., Palmborg, C., Read, D.J., Siamantziouras, A.S.D., Terry, A.C. and Troumbis, A.Y. 2007. Biodiversity and

- ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology*, 21, 998-1002.
- Hensel, M.J. and Silliman, B.R. 2013. Consumer diversity across kingdoms supports multiple functions in a coastal ecosystem. *Proceedings of the National Academy of Sciences*, 110(51), 20621-20626.
- Higgins, R.P., and Thiel, H. 1988. Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC London, p 488.
- Hillebrand, H. and Cardinale, B.J. 2004. Consumer effects decline with prey diversity. *Ecology Letters*, 7, 192–201.
- Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, Gonzalez, A., Duffy, J.E., Gamfeldt, L. and O'Connor, M. I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486(7401), 105-108.
- Hughes, A.R. and Stachowicz, J.J. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 101(24), 8998-9002.
- Hughes, A.R. and Stachowicz, J.J. 2009. Ecological impacts of genotypic diversity in the clonal seagrass *Zostera marina*. *Ecology*, 90(5), 1412-1419.
- Hughes, A.R., Best, R.J. and Stachowicz, J.J. 2010. Genotypic diversity and grazer identity interactively influence seagrass and grazer biomass. *Marine Ecology Progress Series*, 403, 43-51.
- Hull, S.C. 1987. Macroalgal mats and species abundance: a field experiment. *Estuarine and Coastal Shelf Science*, 25, 519–532.
- Hunsicker, M.E. and Essington, T.E. 2008. Evaluating the potential for trophodynamic control of fish by the longfin inshore squid (*Loligo pealeii*) in the Northwest Atlantic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2524-2535.

- Ieno, E.N., Solan, M., Batty, P. and Pierce, G.J. 2006. How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series*, 311, 263-271.
- Ikeda T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Marine Biology* 85, 1-11.
- Infantes, E., Orfila, A., Simarro, G., Terrados, J., Luhar, M., and Nepf, H. 2012. Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. *Marine Ecology Progress Series*, 456, 63-72.
- Irigoien, X., Huisman, J. and Harris, R. P. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature*, 429: 863-867.
- Jackson, E.I., Griffiths, C.A. and Durkin, O. 2013. A guide to assessing and managing anthropogenic impact on marine angiosperm habitat- part 1: Literature review. Natural England Commissioned Reports, Number 111. MAIA Marine Protected areas in the Atlantic Arc report.
- Janson, A., Denis, L., Rauch, M and Desroy, N. 2012. Macrobenthic biodiversity and oxygen uptake in estuarine systems: the example of the Seine estuary. *Journal of Soils and Sediments*, 12, 1568-1580.
- Jenkins, S.R., Hawkins, S.J. and Norton, T.A. 1999. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, 188, 81-92.
- Jennings, S., Nicholson, M.D., Dinmore, T.A., Lancaster, J., 2002. The effect of chronic trawling disturbance on the production of infaunal communities. *Marine Ecology Progressive Series*, 243, 251–260.
- Johnson, C.L., Runge, J.A., Curtis, K.A., Durbin, E.G., Hare, J.A., Incze, L.S., Link, J.S., Melvin, G.D., O'Brien, T.D. and Guelpen, L.V. 2011. Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. *PLoS One*, 6: e16491.
- Jones, C.G., Lawton, J.H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69, 373-386.

- Jordan, M.A., Welsh, D.T., Dunn, R.J. and Teasdale, P.R. 2009. Influence of *Trypaea australiensis* population density on benthic metabolism and nitrogen dynamics in sandy estuarine sediment: A mesocosm simulation. *Journal of Sea Research*, 61(3), 144-152.
- Jørgensen, B.B. and Revsbech, N.P. 1989. Oxygen uptake, bacterial distribution, and carbon–nitrogen–sulfur cycling in sediments from the Baltic Sea-North Sea transition. *Ophelia*, 31(1), 29-49.
- Karlson, A.M., Nascimento, F.J., Näslund, J. and Elmgren, R. 2010. Higher diversity of deposit-feeding macrofauna enhances phytodetritus processing. *Ecology*, 91(5), 1414-1423.
- Kennedy, H., and Björk, M. 2009. Seagrasses, in *The Management of Natural Coastal Carbon Sinks in Coastal Ecosystems: Investigating and Realising the Potential*, edited by D. d'A Laffoley and G. Grimsditch, pp. 23–30, IUCN, Gland, Switzerland.
- Kjørboe T. 2000. Colonization of marine snow aggregates by invertebrate zooplankton: Abundance, scaling and possible role. *Limnology and Oceanography*, 45, 479-484.
- Kleiber, M. 1947. Body size and metabolic rate. *Physiological Reviews*, 27, 511–541.
- Kochmann, J., Buschbaum, C., Volkenborn, N., and Reise, K. 2008. Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology*, 364(1), 1-10.
- Kraufvelin, P., Lindholm, A., Pedersen, M. F., Kirkerud, L. A., and Bonsdorff, E. 2010. Biomass, diversity and production of rocky shore macroalgae at two nutrient enrichment and wave action levels. *Marine Biology*, 157(1), 29-47.
- Kristensen, E. 2001. Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments. *Geochemical Transactions*, 2, 92-103.
- Kristiansen, J. 1990. Phylum Chrysophyta. In *Handbook of Protoctista*. Margulis, L., Corliss, J.O., Melkonian, M., and Chapman, D.J. (eds). Boston, MA, USA: Jones and Bartlett, pp. 438–453.
- Lampert, W. 1978. Release of dissolved organic carbon by grazing zooplankton. *Limnology and Oceanography*, 23, 831-834.

- Lanari, M.D.O. and Coutinho, R. 2014. Reciprocal causality between marine macroalgal diversity and productivity in an upwelling area. *Oikos*, 123(5), 630-640.
- Langenheder, S., Bulling, M. T., Solan, M., and Prosser, J. I. 2010. Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PloS One*, 5(5), e10834.
- Laws, E. A. 1991. Photosynthetic quotients, new production and net community production in the open ocean. *Deep Sea Research Part A. Oceanographic Research Papers*, 38(1), 143-167.
- Leduc, D., Rowden, A.A., Pilditch, C.A., Maas, E.W., Probert, P.K. 2013. Is there a link between deep-sea biodiversity and ecosystem function? *Marine Ecology* 34, 334–344.
- Lewitus, A.J. and Caron, D.A. 1991. Physiological responses of phytoflagellates to dissolved organic substrate additions. 1. Dominant role of heterotrophic nutrition in *Poterioochromonas malhamensis* (Chrysophyceae). *Plant Cell Physiology*, 32, 671-680.
- Liu, Z., Kobiela, M., McKee, G., Tang, T., Lee, C., Mulholland, M. and Hatcher, P. 2010. The effect of chemical structure on the hydrolysis of tetrapeptides in seawater: AVFA and SWGA. *Marine Chemistry*, 119, 108-120.
- Lloyd, K. G., Schreiber, L., Petersen, D. G., Kjeldsen, K.U., Lever, M. A., Steen, A. Stepanauskas R., Richter M., Kleindienst S., Lenk S., Schramm A., Jørgensen, B. B. 2013. Predominant archaea in marine sediments degrade detrital proteins. *Nature*, 496, 215-218.
- Lohrer, A.M., Thrush, S.F., Gibbs, M.M. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431, 1092-1095.
- Longhurst, A., Sathyendranath, S., Platt, T. and Caverhill, C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research*, 17(6), 1245-1271.
- Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature*, 413, 548.

- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A. Raffaelli, D., Schmid, B., Tilman, D. and Wardle, D.A. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*, 294 (5543), 804-808.
- Lüning, K. 1990. Seaweeds: Their environment, biogeography, and ecophysiology. C. Yarish and H. Kirkman (Eds). Wiley-Interscience Publication, New York. 527 pp.
- McIntyre, P.B., Jones, L.E., Flecker, A.S. and Vanni, M.J. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences*, 104, 4461-4466.
- McLusky, D. and Elliott, M. 2004. *The Estuarine Ecosystem: Ecology, Threats and Management*, 3rd edn. Oxford University Press, UK. 214 pp.
- Mermillod-Blondin, F. 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. *Journal of the North American Benthological Society*, 30(3), 770-778.
- Middelburg, J.J. 2011 Chemoautotrophy in the ocean. *Geophysical Research Letter*, 38, L24604.
- Miligan, T. and Hill, P. 1998. A laboratory assessment of the relative importance of turbulence, particle composition and concentration in limiting maximal floe size and settling behaviour. *Journal of Sea Research*, 39, 227-241.
- Molari, M., Manini, E. and Dell'Anno, A. 2013. Dark inorganic carbon fixation sustains the functioning of benthic deep-sea ecosystems. *Global Biogeochemical Cycles*, 27, 212–221.
- Montserrat, F., Van Colen, C., Provoost, P., Milla, M., Ponti, M., Van Den Meersche, K., Ysebaert, T. and Herman, P. M. 2009. Sediment segregation by biodiffusing bivalves. *Estuarine, Coastal and Shelf Science*, 83(4), 379-391.
- Mouillot, D., Villéger, S., Scherer-Lorenzen, M. and Mason, N.W. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PloS One*, 6(3), e17476.
- Mulholland, M.R. and Lee, C. 2009. Peptide hydrolysis and the uptake of dipeptides by phytoplankton. *Limnology and Oceanography*, 54(3), 856-868.

- Muraoka, D. 2004. Seaweed Resources as a Source of Carbon Fixation. Bulletin of Fisheries Research Agency, Supplement 1, 59-63.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology, 12(1), 39-45.
- Naeem, S., Bunker, D.E., Hector, A., Loreau, M. and Perrings, C. 2009. Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective.
- Naeem, S. and Wright, J.P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6 (6), 567-579, 2003.
- Loreau, M., Naeem, S. and Inchausti, P. 2002. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press.
- Naeem, S. and Wright, J.P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology letters, 6(6), 567-579.
- Naldi, M., and Wheeler, P. A. 1999. Changes in nitrogen pools in *Ulva fenestrata* (Chlorophyta) and *Gracilaria pacifica* (Rhodophyta) under nitrate and ammonium enrichment. Journal of Phycology, 35(1), 70-77.
- Newell, R. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. Journal of Shellfish Research, 23(1), 51-62.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A. and Bonsdorff, E. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Marine Ecology Progress Series, 332, 11-23.
- O'Connor, M.I. and Bruno, J. F. 2009. Predator richness has no effect in a diverse marine food web. Journal of Animal Ecology, 78(4), 732-740.
- O'Gorman, E.J., Enright, R.A. and Emmerson, M.C. 2008. Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. Oecologia, 158(3), 557-567.
- Pandolfi, J.M. and Lovelock, C.E. 2014. Novelty Trumps Loss in Global Biodiversity. Science 344, 266-267.

- Paterson, D.M., Defew, E.C. and Jabour, J. 2012. Ecosystem function and co-evolution of terminology in marine science and management. Marine biodiversity and ecosystem functioning. M. Solan, R. J. Aspden and D. M. Paterson, Oxford University Press, 1, 1-240.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. and Brooks, T.M. 1995. The Future of Biodiversity. *Science* 269(5222), 347-350.
- Pischedda, L., Poggiale, J. C., Cuny, P. and Gilbert, F. 2008. Imaging oxygen distribution in marine sediments. The importance of bioturbation and sediment heterogeneity. *Acta biotheoretica*, 56(1-2), 123-135.
- Power, L.D., and Cardinale, B.J. 2009. Species richness enhances both algal biomass and rates of oxygen production in aquatic microcosms. *Oikos*, 118(11), 1703-1711.
- Ptacnik, R., Solimini, A.G., Andersen, T., Tamminen, T., Brettum, P., Lepistö, L., Willén, E. and Rekolainen, S. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 5134-5138.
- Pusceddu, A., Gambi, C., Manini, E., Danovaro, R. 2007. Trophic state, ecosystem efficiency and biodiversity of transitional aquatic ecosystems: analysis of environmental quality based on different benthic indicators. *Chemistry and Ecology* 23, 505-515.
- Pusceddu, A., Gambi, C., Corinaldesi, C., Scopa, M., Danovaro, R. 2014. Relationships between meiofaunal biodiversity and prokaryotic heterotrophic production in different tropical habitats and oceanic regions. *PLoS One* 9(3), e91056.
- Queirós, A. M., J. G. Hiddink, G. Johnson, H. N. Cabral, and M. J. Kaiser. 2011. Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions*, 13, 1059-1075.
- Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., & Degraer, S. 2007. A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuarine, coastal and shelf Science*, 75(4), 525-536.

- Rasmussen, H. and Jørgensen, B.B. 1992. Microelectrode studies of seasonal oxygen uptake in a coastal sediment: role of molecular diffusion. *Marine Ecology Progress Series*, 81, 289–303.
- Reiss, J., Bridle, J. R. Montoya, J. M. and Woodward, G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution*, 24(9), 505-514.
- Reusch, T.B., Ehlers, A., Hämmerli, A. and Worm, B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 102(8), 2826-2831.
- Reynolds, P.L. and Bruno, J.F. 2012. Effects of trophic skewing of species richness on ecosystem functioning in a diverse marine community. *PloS One*, 7(5), e36196.
- Rigolet, C., Dubois, S.F. and Thiébaud, E. 2014. Benthic control freaks: Effects of the tubicolous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. *Journal of Sea Research*, 85, 413-427.
- Rilov, G., Mant, R., Lyons, D., Bulleri, F., Benedetti-Cecchi, L., Kotta, J., Queirós, A.M., Chatzinikolaou, E., Crowe, T. and Guy-Haim, T. 2012. How strong is the effect of invasive ecosystem engineers on the distribution patterns of local species, the local and regional biodiversity and ecosystem functions. *Environmental Evidence*, 1(10).
- Roesch, L. F., Fulthorpe, R. R., Riva, A., Casella, G., Hadwin, A. K., Kent, A. D., Daroub, S.H., Camargo, F.A., Farmerie, W.G. and Triplett, E.W. 2007. Pyrosequencing enumerates and contrasts soil microbial diversity. *The ISME Journal*, 1(4), 283-290.
- Rosenberg, G., Littler, D.S., Littler, M.M. and Oliveira, E.C. 1995. Primary production and photosynthetic quotients of seaweeds from Sao Paulo State, Brazil. *Botanica Marina*, 38, 369–377.
- Scherer-Lorenzen, M. 2005. Biodiversity and ecosystem functioning: basic principles, in: Barthlott, W., Linsenmair, K.E., Porembski, S. (Eds.), *Biodiversity: Structure and Function*. Encyclopedia of Life Support Systems (EOLSS). UNESCO, Eolss Publishers, Oxford ,UK.

- Short, F. T., and McRoy, C. P. 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. *Botanica Marina*, 27(12), 547-556.
- Siegenthaler, U. and Sarmiento, J.L. 1993 Atmospheric carbon dioxide and the ocean. *Nature*, 365, 119-125.
- Smale, M.J. 1996. Cephalopods as prey. IV. Fishes. *Philosophical Transactions of the Royal Society London Series B*, 351, 1067–1081.
- Smith, D., Simon, M., Alldredge, A. and Azam, F. 1992. Intensive hydrolytic activity on marine aggregates and implications for rapid particle dissolution. *Nature*, 359, 139-141.
- Snelgrove, P.V.R. 1999. Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats: Ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. *BioScience*, 49(2), 129-138.
- Snelgrove, P.V.R, Thrush, S.F., Wall, D.H., and Norkko, A. 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends in Ecology and Evolution*, 29: 398-405.
- Sogin, M.L., Morrison, H.G., Huber, J.A., Welch, D.M., Huse, S.M., Neal, P.R., Arrieta, J.M. and Herndl, G.J. 2006. Microbial diversity in the deep sea and the underexplored “rare biosphere”. *Proceedings of the National Academy of Sciences*, 103(32), 12115-12120.
- Solan, M., Cardinale, B. J., Downing, A. L., Engelhardt, K. A., Ruesink, J. L., and Srivastava, D. S. 2004. Extinction and ecosystem function in the marine benthos. *Science*, 306(5699), 1177-1180.
- Spivak, A.C., Canuel, E.A., Duffy, J., and Richardson, J. 2007. Top-down and bottom-up controls on sediment organic matter composition in an experimental seagrass ecosystem. *Limnology and Oceanography*, 52(6), 2595-2607.
- Stachowicz, J. J., Bruno, J. F. and Duffy, J. E. 2007. Understanding the Effects of Marine Biodiversity on Communities and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), 739-766.

- Stahl, H., Glud, A., Schröder, C. R., Klimant, I., Tengberg, A., & Glud, R. N. 2006. Time-resolved pH imaging in marine sediments with a luminescent planar optode. *Limnology and Oceanography: Methods*, 4, 336-345.
- Stowasser, G., Bustamante, P., MacLeod, C.D., Wang, J. and Pierce, G.J. 2005. Spawning areas and selected metal concentrations in squid (*Loligo forbesi*) in UK waters, with notes on metal concentrations in other squid species. Report to Geotek Ltd and Hartley Anderson Ltd in the context of the UK Department of Trade and Industry's offshore energy Strategic Environmental Assessment programme. University of Aberdeen, Aberdeen, 24 pp.
- Suzuki Y. (ed.), 1997: Marine biota and global carbon cycling, University of Tokyo press, Tokyo, 208 pp.
- Takano, Y., Chikaraishi, Y., Ogawa, N. O., Nomaki, H., Morono, Y., Inagaki, F., Kitazato, H., Hinrichs, K. U., Ohkouchi, N. (2010) Sedimentary membrane lipids recycled by deep-sea benthic archaea. *Nature Geoscience*, 3, 858-861.
- Tappin, A.D., Loughnane, J.P., Mc Carthy, A.J. and Fitzsimons, M.F. 2012 Removal of atrazine from river waters by indigenous microorganisms. *Environmental Chemistry Letters* 10(1), 89-96
- Teal, L., Parker, R., Fones, G., and Solan, M. 2009. Simultaneous determination of in situ vertical transitions of color, pore-water metals, and visualization of infaunal activity in marine sediments. *Limnology and Oceanography*, 54(5), 1801-1810.
- Tett, P., Gowen, R.J., Painting, S.J., Elliott, M., Forster R., Mills, D. K., Bresnan, E., Capuzzo, E., Fernandes, T.F., Foden, J., Geider, R.J., Gilpin, L. C., Huxham, M., McQuatters-Gollop, A.L., Malcolm, S.J., Saux-Picart, S., Platt, T., Racault, M.F., Sathyendranath, S., van der Molen J. and Wilkinson M. 2013. Framework for understanding marine ecosystem health. *Marine Ecology Progress Series* 494: 1-27.
- Tiedje, J. M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. *Biology of anaerobic microorganisms*, 717, 179-244.

- Tilman, D. 2001. Functional diversity. In: Levin, S. A. (ed.), *Encyclopedia of biodiversity*. Academic Press.
- Törnroos, A., Bonsdorff, E., Bremner, J., Blomqvist, M., Josefson, A. B., Garcia, C., and Warzocha, J. 2014. Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research*. *In press*.
- Townsend, D.W. and Cammen, L.M. 1988. Potential Importance of the Timing of Spring Plankton Blooms to Benthic-Pelagic Coupling and Recruitment of Juvenile Demersal Fishes. *Biological Oceanography* 5(3), 215-228.
- Trites, A.W. 2003. 8 Food Webs in the Ocean: Who Eats Whom and How Much? Responsible fisheries in the marine ecosystem, 125.
- UK National Ecosystem Assessment. 2014. *The UK National Ecosystem Assessment: Synthesis of the Key Findings*. UNEP-WCMC, LWEC, UK.
- Valdivia, N., and Molis, M. 2009. Observational evidence of a negative biodiversity-stability relationship in intertidal epibenthic communities. *Aquatic Biology*, 4, 263-271.
- Waldbusser, G.G., Marinelli, R.L., Whitlatch, R.B. and Visscher, P.T. 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology and Oceanography*, 49(5), 1482–1492
- Wells, M.J. and Clarke, M.R. 1996. Energetics: The costs of living and reproducing for an individual cephalopod. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 351, 1083-1104.
- Welsh, D.T. 2000. Nitrogen fixation in seagrass meadows: Regulation, plant-bacteria interactions and significance to primary productivity. *Ecology Letters*, 3, 58-71.
- Wheeler, P.A., North, B., Littler, M. and Stephens, G. 1977. Uptake of glycine by natural phytoplankton communities. *Limnology and Oceanography*, 22, 900–909.

- Widdows, J., Brinsley, M. and Elliott, M. 1998. Use of in situ flume to quantify particle flux (biodeposition rates and sediment erosion) for an intertidal mudflat in relation to changes in current velocity and benthic macrofauna. Geological Society, London, Special Publications, 139, 85-97.
- Wildish, D.J. and Kristmanson, D.D. 1984. Importance to mussels of the benthic boundary layer. Canadian Journal of Fisheries and Aquatic Sciences, 41(11), 1618-1625.
- Williams, S.L. 2001. Reduced Genetic Diversity in Eelgrass Transplantations Affects both Population Growth and Individual Fitness. Ecological Applications, Vol. 11, No. 5, pp. 1472-1488.
- Williams, P. I., and Robertson, J. E. 1991. Overall planktonic oxygen and carbon dioxide metabolisms: the problem of reconciling observations and calculations of photosynthetic quotients. Journal of Plankton Research, 13(supp1), 153-169.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B., Heike K. Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314, 787-790.
- Wotton, R. S. and Malmqvist, B. 2001. Feces in Aquatic Ecosystems: Feeding animals transform organic matter into fecal pellets, which sink or are transported horizontally by currents; these fluxes relocate organic matter in aquatic ecosystems. BioScience, 51(7), 537-544.

## Glossary of common biodiversity and ecosystem functioning terms

**Biodiversity:** The variability among living organisms from all sources including inter alia, [terrestrial], marine [and other aquatic ecosystems] and the ecological complexes of which they are part; cf. ‘includes diversity within species, between species and of ecosystems’ (Article 2, Convention on Biological Diversity 1992: [www.cbd.int/convention/text/default.shtml](http://www.cbd.int/convention/text/default.shtml)).

**Biological (or biodiversity) components:** groupings of species, separated by distinct functional, taxonomic and/or habitat boundaries. These components are practical subdivisions of biodiversity. Eleven biodiversity components have been used within this review: microbes, phytoplankton, zooplankton, angiosperms, macroalgae, benthic invertebrates, fish, cephalopods, marine mammals, birds and reptiles.

**Biological traits analysis:** an analysis that uses a series of life history, morphological and behavioural characteristics of species present in assemblages to indicate aspects of their ecological functioning (Bremner et al., 2006).

**Complementarity:** see transgressive over-yielding. Species perform better in diverse communities when compared to monoculture due to facilitation and niche partitioning in shared resource use. Contributes to more efficient acquisition of limiting resources and therefore higher productivity.

**Ecosystem functioning:** This relates to rate processes at the ecosystem level, cf. ecosystem structure which is the magnitude of ecosystem components at one time; all levels of biological organisation from the cell to the ecosystem have structural and functional properties whereas ecosystem functioning only relates to the highest level.

**Ecosystem functions:** the physical, chemical and biological processes that transform and translocate energy or materials in an ecosystem are termed ecosystem functions (Naeem, 1998; Paterson et al. 2012).

**Ecosystem process:**

**Identity effects:** a small number of species dominates functionality. Typically reflected by non-transgressive over-yielding (Table 1a and 1b).

**Non-transgressive over-yielding:** a diverse assemblage perform better than a weighted average of the component species (Table 1a and 1b). Commonly related to identity effects.

**Production/Productivity:** biomass production is often expressed as production or productivity, these two terms being often used as synonyms (e.g. McLusky and Elliott, 2004; Scherer-Lorenzen, 2005), and expressing the units of biomass produced per unit area per unit time (e.g. grams of Carbon m<sup>-2</sup> yr<sup>-1</sup>), with the production efficiency (or biomass turnover rate) being measured by the P:B ratio (where P is production and B is mean standing biomass; e.g. in yr<sup>-1</sup> units; McLusky and Elliott, 2004).

**Selection effects/sampling effects:** diversity effects are caused by the greater chance of one or a few dominant, high-biomass species being present in the polyculture. Related to identity effects.

Trait diversity: species defined in terms of their ecological roles. The concept of functional trait diversity is based on the assumption that with increasing trait dissimilarity among species the diversity in resource use strategies increases as well and species overlap along resource axes decreases.

Transgressive over-yielding: diverse assemblages perform better than the best performing species in monoculture (Table 1a and 1b). Also considered a product of complementarity.