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## THEME SECTION

# Marine biodiversity and ecosystem function: empirical approaches and future research needs

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## Introduction

**M. Solan<sup>1,\*</sup>, D. G. Raffaelli<sup>2</sup>, D. M. Paterson<sup>3</sup>, P. C. L. White<sup>2</sup>, G. J. Pierce<sup>1</sup>**<sup>1</sup>Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, UK<sup>2</sup>Environment Department, University of York, Heslington, York YO10 5DD, UK<sup>3</sup>University of St. Andrews, Gatty Marine Laboratory, Sediment Ecology Research Group, St. Andrews, Fife KY16 8LB, UK

Marine systems are among the world's most productive and diverse ecosystems, but they are also subject to intense human pressures; approximately 40% of the world's population lives within 100 km of the coast (Cohen et al. 1997) and a significant proportion of these inhabitants depend on the ocean for food, economic prosperity and well-being. As in many terres-

trial systems, a multitude of direct and indirect human influences have significantly altered the composition and diversity of marine communities at almost every trophic level (e.g. Pauly et al. 1998). This has led to concern over the functional consequences of biodiversity loss, which are especially relevant given the high levels of extinction already witnessed and the anti-

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anticipated future influence of anthropogenic forcing (Sala et al. 2000). In response to such anxiety, an unprecedented increase in research over the last decade or so has explicitly examined the proposition that a reduction in biodiversity will cause a decrease in the provision of ecosystem-level processes (reviewed in Hooper et al. 2005). The establishment of this line of inquiry is credited to the proceedings of a seminal conference that sought to formalize, for the first time, the association between biodiversity and ecosystem function (Schulze & Mooney 1993). Understanding the mechanisms that underpin this presumed causal relationship has since become one of the primary research goals in ecology (Hooper et al. 2005).

Following the emergence of a novel paradigm, the road towards a new consensus is supported by a parallel progression of observational, experimental and theoretical evidence. These are the primary axes along which fundamental ecological principles are derived and, providing that the conclusions drawn from these alternative approaches merge, are the means by which inferences about cause–effect relationships can be validated. In the biodiversity–ecosystem function arena (hereafter BEF) the mainstay of research to date has almost exclusively been weighted towards ecological experimentation in terrestrial plant systems, although there have been a small number of notable contributions on the marine environment (e.g. compare citations in Hooper et al. 2005 with Covich et al. 2004). Curiously, correlational evidence or anecdotal observations in support of BEF relationships (Emmerson & Huxham 2002) are seldom cited on their own, or alongside new findings, and are generally viewed with skepticism, despite overwhelming support for the notion that biological diversity regulates ecosystem processes (Schläpfer et al. 1999). Yet the use of experimental systems is not without issue, nor do they provide a scientific panacea in the context of BEF related research. Experimental data generated from simple synthetic model communities in highly controlled systems (mesocosms) have been routinely criticized on many levels (for summary, see Mooney 2002).

Whether or not the same mechanistic processes identified from synthetic laboratory experiments are equally valid and transferable to the real world (terrestrial and/or marine) remains an open question. Historical and cultural differences between specialists within ecology (Raffaelli et al. 2005) have meant that the marine community has often lagged behind their terrestrial counterparts; the BEF process has been no exception. Aquatic ecologists were less enthusiastic and initially failed to see the significance of BEF research, despite direct appeals for participation (Emmerson & Huxham 2002) and the publication of methodologies that demonstrate how marine ecology

could contribute to the BEF dialogue (Raffaelli et al. 2003). One of the most significant barriers to inter-specialist cohesion within the BEF community related to the treatment of biodiversity as an explanatory variable, rather than as the response variable, as had been common practice (e.g. Flint & Kalke 2005). This conceptual stalemate emerged because contemporary perspectives within the BEF framework challenged older and more familiar conventional marine ideology (Raffaelli et al. 2005). Although these differences have largely been reconciled, the gap in research effort between marine and terrestrial ecology remains an issue, particularly as BEF research could greatly benefit from insights yet to be gleaned from marine systems (Raffaelli et al. 2003). This is particularly true since the manipulation of terrestrial systems with their long-lived and static primary producers is more logistically difficult than experimentation in marine systems where small, mobile and abundant organisms can be selected and established in culture as the basis of experimentation (Defew et al. 2002, Paterson 2005).

As in many instances within the scientific process, controversy and debate can stimulate enlightenment and progress. It is in this spirit that we assembled the current 'Theme Section', where we have attempted to bring together a broad range of marine ecologists and encouraged them to express their opinions, substantiated or otherwise, alongside more traditional scientific prose within a BEF framework. We include contributions that represent a wide range of trophic levels, habitats and scales as well as a broad range of conceptual approaches. Our aim is to stimulate discussion both within and between the traditional domains of terrestrial and marine ecology within the BEF framework.

The Theme Section starts with Duffy & Stachowicz (2006) who present selected examples of how genetic, species, and functional group diversity may affect pelagic ocean ecosystem processes. They argue that several mechanisms known to underpin observed diversity effects in marine benthic and terrestrial systems are likely to operate in pelagic systems. Next, Forster et al. (2006) examine the relationship between the diversity of intertidal benthic diatom biofilms and estimated net primary production. In so doing, they highlight the difficulties of using biomass as a surrogate for primary productivity in marine systems. Ruesink et al. (2006) use a case study to examine the impact that introduced species have on primary and secondary production in an estuary. They conclude that gains in species—as much as species losses—can markedly influence ecosystem processes and that associated changes in ecosystem functioning are often directly attributable to a few high-impact species. The effect of such species also forms the basis of the contribution by Waldbusser & Marinelli (2006). Reporting on

results obtained from a series of field experiments in an intertidal muddy-sand flat, they show that specific behavior and interactions between organisms appear to affect sediment function.

In a review of seagrass systems, Duffy (2006) suggests that future BEF investigations within seagrass and other aquatic ecosystems would benefit from broadening the concept of biodiversity to encompass the hierarchy of genetic through landscape diversity. Using a few explicit experimental tests of BEF relationships and by inferring from other lines of evidence, he argues that future studies would benefit from focusing on links between diversity and trophic interactions, and on links between regional diversity, local diversity, and ecosystem processes. Next, Stachowicz & Byrnes (2006) apply observational data to study the consequences of species loss for invasion, in order to assess the generality across scales and relative importance of experimental results. They remind us that the BEF process has mostly been framed in the context of what will happen to ecosystem functioning as species richness declines and that there are virtually no data that address the reverse position, despite the fact that it is clear that invasive species can affect ecosystem structure and function.

Ieno et al. (2006) return to the issue of dominant species effects and uncertainties in experimental design. Solutions used to distinguish such effects in terrestrial systems are not always directly transferable to analogous marine experiments, because cumulative processes are routinely used as surrogates for ecosystem function. They present a post hoc experimental validation procedure to distinguish biodiversity effects from effects related to species identity and density when the relative contribution of each species in a mixture cannot be determined. The issues of experimental design are also considered by Naeem (2006), who recognizes that marine ecologists must deal with the large scales of marine systems and the logistical difficulties of attempting to conduct the kinds of complex, combinatory experiments that have been done in terrestrial ecology. By way of solution, he presents an alternative approach that obviates the need for complex experiments and goes beyond the limited scales of current BEF studies. Raffaelli (2006) continues with the issue of scale and trophic complexity and argues that it is possible, through the parallel development of alternate non-experimental approaches, to carry out BEF experiments at the spatial and temporal scales appropriate to those issues that affect society's needs. Finally, Bulling et al. (2006) examine the strengths and limitations of model systems and assess how useful these systems might be in addressing spatial scales, multiple trophic levels, variation and environmental stochasticity.

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#### LITERATURE CITED

- Bulling MT, White PCL, Raffaelli D, Pierce GJ (2006) Using model systems to address the biodiversity–ecosystem functioning process. *Mar Ecol Prog Ser* 311:295–309 (in this Theme Section)
- Cohen JE, Small C, Mellinger A, Gallup J, Sachs J (1997) Estimates of coastal populations. *Science* 278:1209
- Covich AP, Austen M, Bärlocher F, Chauvet E and 7 others (2004) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54(8): 767–775
- Defew EC, Paterson DM, Hagerthey SE (2002) The use of natural microphytobenthic assemblages as laboratory model systems. *Mar Ecol Prog Ser* 237:15–25
- Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. *Mar Ecol Prog Ser* 311:233–250 (in this Theme Section)
- Duffy JE, Stachowicz JJ (2006) Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. *Mar Ecol Prog Ser* 311:179–189 (in this Theme Section)
- Emmerson M, Huxham M (2002) How can marine ecology contribute to the biodiversity–ecosystem functioning debate? In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, p 139–146
- Flint RW, Kalke RD (2005) Reinventing the wheel in ecology research? *Science* 307:1875
- Forster RM, Créach V, Sabbe K, Vyverman W, Stal LJ (2006) Biodiversity–ecosystem function relationship in microphytobenthic diatoms of the Westerschelde estuary. *Mar Ecol Prog Ser* 311:191–201 (in this Theme Section)
- Hooper DU, Chapin FS, Ewel JJ, Hector A and 11 others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75(1):3–35
- Ieno EN, Solan M, Batty P, Pierce GJ (2006) How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Mar Ecol Prog Ser* 311:263–271 (in this Theme Section)
- Mooney HA (2002) The debate on the role of biodiversity in ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, p 12–17
- Naeem S (2006) Expanding scales in biodiversity-based research: challenges and solutions for marine systems. *Mar Ecol Prog Ser* 311:273–283 (in this Theme Section)
- Paterson DM (2005) Biodiversity and functionality of aquatic ecosystems. In: Barthott W, Porembski S, Linsenmair KE (eds) Biodiversity: structure and function. Encyclopedia of life support systems (EOLSS). EOLSS developed under the auspices of UNESCO. Publishers, Oxford ([www.eolss.net](http://www.eolss.net))
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860–863
- Raffaelli D (2006) Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Mar Ecol Prog Ser* 311:285–294 (in this Theme Section)
- Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2003) Biodiversity and ecosystem functioning in shallow coastal

- waters: an experimental approach. *J Sea Res* 49(2): 133–141
- Raffaelli D, Solan M, Webb TJ (2005) Do marine and terrestrial ecologists do it differently? *Mar Ecol Prog Ser* 304: 283–289
- Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisehart LM (2006) Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. *Mar Ecol Prog Ser* 311:203–215 (in this Theme Section)
- Sala OE, Chapin FS III, Armesto JJ, Berlow E and 15 others (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Schläpfer F, Schmid B, Seidl I (1999) Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos* 84(2):346–352
- Schulze ED, Mooney HA (1993) *Biodiversity and ecosystem function*. Springer-Verlag, Berlin
- Stachowicz JJ, Byrnes JE (2006) Species diversity, invasion success and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Mar Ecol Prog Ser* 311:251–262 (in this Theme Section)
- Waldbusser GG, Marinelli RL (2006) Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. *Mar Ecol Prog Ser* 311: 217–231 (in this Theme Section)