Opinion

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Real world biodiversity–ecosystem functioning: a seafloor perspective

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The effective application of biodiversity–ecosystem function (BEF) research to societal needs amid the Anthropocene represents the next grand challenge for ecology. Biodiversity knowledge that is most meaningful to society must reconcile insights derived from theory with detailed experiments and broad-scale trends. This perspective requires science that addresses high species richness, redundancy, and natural variability, which simplified 'model systems' cannot mimic. Here, we illustrate solutions of biodiversity knowledge to management and societal problems that combine BEF with scaling experiments, analysis of BEF along environmental gradients, and mapping technologies. We primarily draw examples from biophysical interactions in seafloor environments, which cover 70% of the Earth and add significantly to global ecosystem functions and services.

The utility of biodiversity–ecosystem function studies amid biodiversity loss

Current rates of biodiversity (see Glossary) loss might soon rival the greatest mass extinctions on Earth [1], raising alarm over potential major loss of ecosystem functions and services [2]. Land-use change associated with agricultural intensification and habitat loss, pollution, invasive species, and climate change contributes to species loss on land. Similar problems occur in our oceans, but here humans still have a significant role as hunters where fishing changes food webs, abundances of nontarget species, and habitats, resulting in multiple cascading effects [3]. Functional marine extinctions driven by local extirpations cause major declines in top predators, loss of seafloor function, and habitat alteration, despite few documented global species extinctions [4–6].

Against this backdrop of change, ecologists increasingly emphasize the role of biodiversity in the delivery of ecosystem services. Marine ecosystems support approximately half of global primary productivity [7] and a range of ecosystem services operating from local to global scales [8,9]. Thus, as with their terrestrial counterparts [10], biodiversity change and loss in the ocean could foreshadow significant consequences for crucial functions and services that we are only beginning to appreciate.

BEF studies could help demonstrate how ecosystems work and respond to change. Furthermore, BEF research has succeeded in documenting that biodiversity matters. Indeed, small-scale laboratory and field experiments that often manipulate species composition demonstrate a range of relationships between function and species richness; many are positive, especially in complex ecosystems and over longer timescales of study [11,12].

Glossary

Anthropocene: the most recent geologic time period, in which anthropogenic activities have had a dominant impact on Earth systems.
Biodiversity–ecosystem function (BEF) research: studies on BEF relationships.
Biodiversity: the extent of genetic, taxonomic, and ecological diversity over all spatial and temporal scales.
Carbon sequestration: the process of capture and long-term storage of atmospheric carbon.
Continental shelf: the extended perimeter of the continents and associated coastal plain.
Denitrification: the microbial reduction of NO_3^- to N_2O, and of N_2O to N_2.
Ecosystem engineers: organisms or structures produced by organisms that alter substrate, flow regime, geochemical setting, food supply, or predation pressure for associated organisms.
Ecosystem function: changes in energy and matter over time and space through biological activity.
Ecosystem service: the benefits that humans obtain from ecosystems.
Emergent properties: a property that arises at one level of organization as a consequence of interactions among entities at a lower level of organization; it is a property unique to the higher level of organization and usually not predictable from knowledge of properties at lower levels.
Functional group: organisms with similar trophic, morphological, physiological, behavioral, biochemical, or environmental responses.
Functional extinction: a decline in a population to the point that it no longer has a significant role in ecosystem function.
Hypoxia: reduced oxygen content in water that is detrimental to aerobic organisms.
Mineralization: the process of degrading organic material.
Multifunctionality: the potential for individual organisms to contribute to more than one ecosystem function.
Niche partitioning: the process by which natural selection drives competing species into different patterns of resource use or different niches.
Patch: a spatial aggregation of some resources.
Polynya: ice-free sea surrounded by sea ice.
Trait: any morphological, physiological, or phenological feature measurable at the individual level.
Upwelling: wind-driven and/or topographic-induced motion of dense, cooler, and usually nutrient-rich water toward the ocean surface.

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Keywords: biodiversity; ecosystem function; scaling; gradients; multifunctionality; sediments; marine; sediments; invertebrates.

0169-5347/
 http://dx.doi.org/10.1016/j.tree.2014.05.002

Past BEF research has addressed many biodiversity characteristics (e.g., species, habitats, or ecosystems), functions (e.g., productivity, decomposition, food web linkages, or habitat formation), and their interconnection [13]. However, recent studies primarily focus on species richness in simplified systems, which act as representative 'models' for more complex natural systems, despite pleas to the contrary [14]. If we hope to advise management and conservation more effectively on the ramifications of biodiversity loss, then we must quickly bridge the chasm between simplified, small-scale experiments and complex, large-scale processes. Specifically, field experiments and sampling strategies must be designed with this bridge in mind. Terrestrial ecologists have had some success linking knowledge derived from small-scale, simplified experiments to large-scale agriculture, but in diverse systems, both terrestrial and marine, we still struggle to develop the insights and specific applications that managers need. Drawing examples primarily from marine ecosystems, we propose strategies to bridge small-scale experimental studies with the broad-scale needs of society and managers in linking biodiversity and ecosystem functions, and developing strategies to ensure their sustainability.

The need for a new approach

Current BEF manipulative experiments alone cannot directly scale to most real-world problems. Indeed, the scales at which we conduct experimental research to understand the mechanisms that underpin BEF relations mismatch the scales at which biodiversity changes occur (i.e., landscapes and ecosystems). In practice, controlled mechanistic laboratory experiments quickly become intractable. For example, experimental comparisons of all species combinations among the ten macrofaunal species in a typical sediment core from the Baltic Sea generate 511 orthogonal species contrasts. Furthermore, among the more than 22 species in a core in New Zealand sandflats or in the Newfoundland continental shelf, 4 million combinations can be generated. Redundancy and niche partitioning in diverse land and sea ecosystems suggest these ecosystems will respond differently compared with low-diversity 'model systems'. Although the tractability of low-diversity contrasts is appealing, this approach might not sufficiently model the system unless drawn from low-diversity natural systems. Moreover, experimental treatments often mimic average conditions that cannot capture natural ecological change because extreme events often drive reproduction, growth, and disturbance regimes to create years to decades-long legacies in ecosystem function that manipulative experiments can rarely address because of their typically short durations [15]. Variation in spatial structure and temporal change defines the framework in which ecosystem function performance and BEF relations develop. Mechanistic studies should not simply exclude variation, but instead recognize it as an important functional component. These issues complicate inference of causality and demand new strategies to identify how BEF research contributes to understanding of life on Earth.

As in many areas of ecology, theory in biodiversity research has severely outpaced empirical work, challenging our ability to validate our perception of real ecosystems. The inherent heterogeneity of natural ecosystems, which occurs at all levels of biological organization, largely defines biodiversity and contributes to ecosystem functionality. Therefore, it is imperative to account for BEF across the full range of environmental and biological drivers that add complexity and context dependency to BEF relations [16]. For example, food-web linkages are critical to understanding some BEF relations [17], but trophic interactions alone do not define ecosystem interaction networks in many systems where important functions include habitat creation (e.g., trees, kelps, or burrows) and environmental processes (e.g., biogeochemical cycling; Figure 1). By not including environmental context, BEF relations cannot accurately depict complex ecosystems, and most BEF research lacks the appropriate predictive and prescriptive applications needed to bridge this gap.

Alteration of biodiversity often coincides with changes in abundance and biomass, and, thus, the trait composition of communities that directs ecosystem function [18]. For example, habitat-structuring species (e.g., trees on land, earthworms in soil, coral reefs along tropical coastlines, or large invertebrates in seafloor sediments worldwide) define spatial pattern and habitat variation in ecosystems and, ultimately, define the strength and direction of processes that influence ecosystem function [19]. BEF relations at the landscape scale depend on the interplay between the spatial arrangement of species and patchiness in their resources as well as the life-history, feeding, reproduction, and mobility of species, and feedback loops between biota, hydrodynamics, and biogeochemistry. The interplay of patterns and processes suggests strong context dependence that demands resolution [20].

Multifunctional ecosystems sustain and generate ecosystem services

In all ecosystems, a tangled web of processes [21,22] deliver multiple functions that contribute to the delivery of ecosystem services (Figure 1). On land, vascular plants and soil organisms that are critical for terrestrial production also affect carbon sequestration and cycling above and below ground [23]. In the oceans, continental shelves occupy only 7% of the seafloor, but they mineralize 52% of global organic matter [24], regenerating nutrients that are critical for ocean productivity. Indeed, highly productive coastal systems tightly couple water column and seafloor carbon and nutrient cycling. Large plants (mangroves and seagrasses) and macrophytes (seaweeds) sequester carbon into coastal sediments, whereas plant material transported off the continental shelf can be sequestered in the deep ocean [25]. The deep ocean provides the major long-term sink for carbon assimilated and exported by sinking phytoplankton. On the seafloor, as in soils [10], animals such as nematodes [26] and burrowing invertebrates [18] modify the habitat for microbes, significantly altering carbon flux, storage, and recycling of nutrients over multiple timescales [18]. Even if we focus on a specific ecosystem function, such as carbon sequestration, we must recognize the multifaceted nature of BEF relations (Figure 1). Some functions are tightly coupled (e.g., carbon remineralization or nutrient efflux), whereas others are not (e.g., habitat provisioning and nutrient cycling in seagrasses and

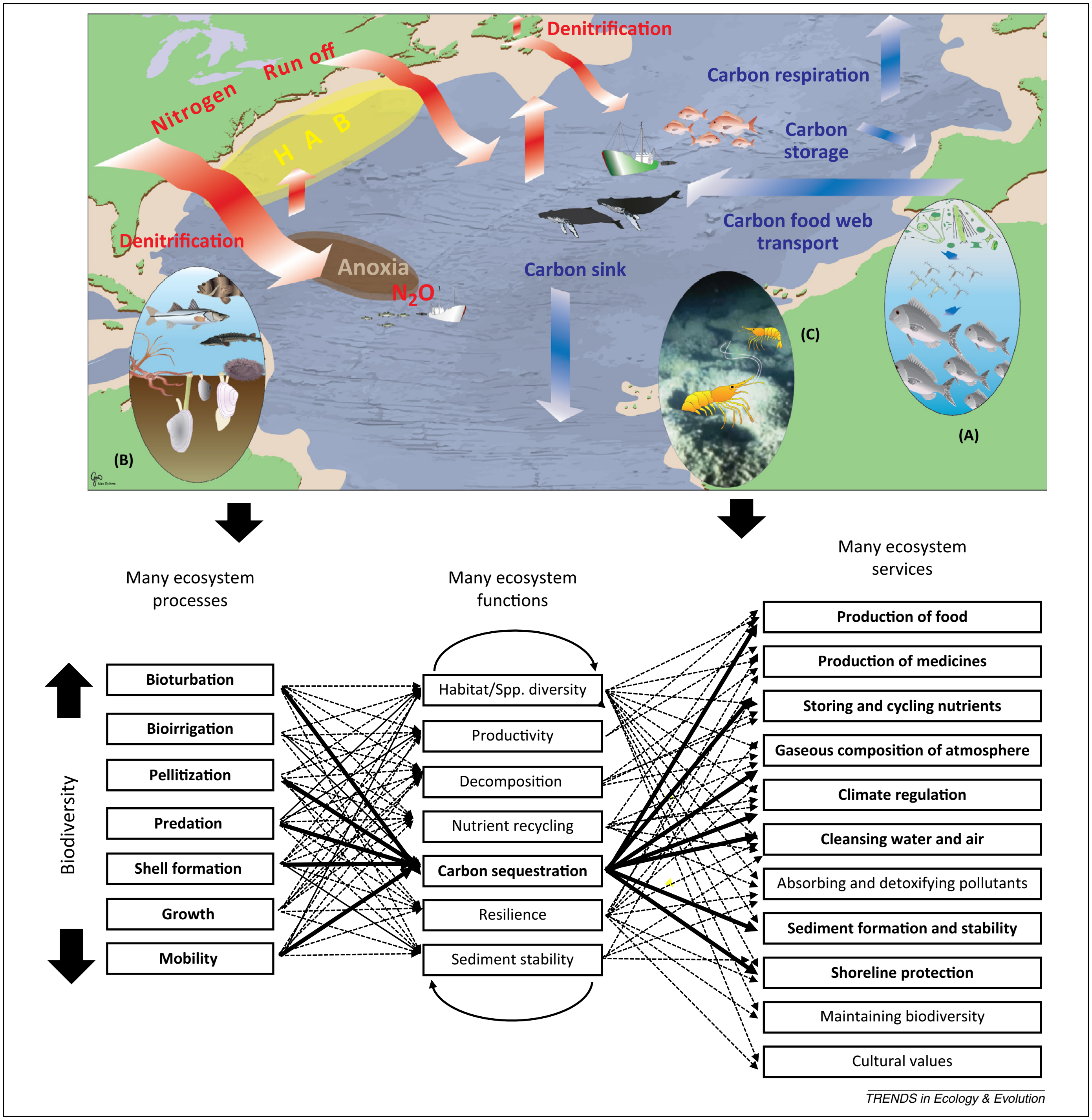

Figure 1. The role of marine species in multiple ecosystem functions and services. Carbon and nitrogen cycling closely link species to multiple functions and services. Top panel: Nitrogen runoff from land and internal recycling results in high rates of primary production and, thus, carbon fixation, fuelling the food web and increasing respiration **(A)**. Denitrification, particularly in coastal sediments, returns nitrogen to the atmosphere and healthy seafloor ecosystems recycle organic matter, regenerate ammonia and nitrate, and oxygenate sediments **(B)**. Food web carbon transfer and physical processes transport organic material offshore and to the seafloor, where it may be broken down or permanently buried **(C)**. Excess nitrogen input that cannot be denitrified leads to eutrophication, and hypoxia, anoxia, harmful algal blooms (HAB) and mortality on the seafloor. Lower panel (expanded from [9]): these and other processes show multiple links between biodiversity, ecosystem function, and the delivery of ecosystem services. Interlinkages among ecosystem processes (the precursors to functions), functions, and services complicate understanding of seafloor ecosystems. Unbroken arrows denote linkages specific to carbon sequestration. Broken lines denote other linkages.

mangroves). When functions are intimately coupled in nature, their effects in isolation become ecologically meaningless; in these cases, emergent properties are part of the solution rather than the problem.

Laboratory experiments and simple field manipulations rarely mimic emergent properties generated by multifunctionality [27]. Furthermore, these emergent properties complicate meta-analysis of small-scale experiments and might render generalities meaningless. Mechanistic understanding of a few species over short space and timescales provides important insight and guidance, but we must understand what those linkages represent in the broader ecosystem to gain insights into more complex ecosystems.

Seafloor sediments as exemplary ecosystems integrating multiple scales of biodiversity

Seafloor sediments cover much of the surface of the Earth and rival most of the ecosystems of the Earth in their contribution to global ecosystem services [8,28]. By emphasizing their unique history of scientific exploration, we use seafloor systems as examples for rapid advancement and suggest key parallels with how soil ecologists view BEF [29].

Most studies of seafloor ecosystems have integrated habitat, biota, biogeochemical, and hydrodynamic processes within multitrophic communities, thereby allowing BEF linkages to be made [30–32]. Community-level studies transcend trophic levels and link multiple processes to ecosystem function. Indeed, many seafloor studies addressed links between biota and carbon sequestration, nutrient regeneration, productivity, habitat diversity and complexity, and decomposition, long before scientific acceptance of the ecosystem function and service concept.

Seafloor studies that recognize geochemical and physical influences on seafloor biodiversity pave the way for studies on multifunctionality and species interactions. Moreover, globally pervasive seafloor ecosystems span environmental, biogeographic, and disturbance gradients, which are ideal for designing scaled-up studies that interpolate between experimental sites to define regional-scale BEF relations. New opportunities in real-world research could utilize breakthroughs in field genomics, environmental sensors, and observing platforms (cabled observatories, autonomous underwater vehicles, or ocean gliders) to address how different forms of biodiversity (individuals, patches, communities, and landscapes) contribute to ecosystem functions. Importantly, such approaches might offer surprises that could generate new insight into BEF [33–36].

The challenge of scaling up

Zooming out in spatial scale for any ecosystem requires integrating different aspects of complexity (see Box 1 for a seafloor ecosystem). Species richness scales nonlinearly with geographic area, implying that there is a need to consider the spatial integration of BEF relations, even within habitat type [37]. Delivering ecosystem functions often involves animals reshuffling and irrigating sediments, as well as altering energy and matter flux between the water column and seafloor [32]. In turn, these processes create habitat,

Box 1. From problems to solutions in BEF studies

Defining the functional form and interdependence of BEF relations will prove more useful to society if it incorporates three linked challenges: (i) tractability of species combinations; (ii) scaling from small experiments to ecosystems; and (iii) addressing multifunctionality. Moving across scales in ecological and socioecological organization requires the integration of multiple theories and empirical studies, with key processes shifting in importance across these transitions. Figure I illustrates the challenges whereas the bullet points below identify solutions.

- Species contrasts: target studies on vulnerable species and use natural-history information to identify functional groups and traits, key species, and community descriptors. In addition to species diversity per se, consider organism size and density [69] in assessing diversity elements, such as dominance, redundancy, and rarity.
- Scaling problems: prioritize experiments that vary plot size or exploit gradients [53,59] to resolve scaling bias [57]. Consider how and why processes vary with environmental settings. Use variance as information, not noise. To understand causality in complex systems, consider cross-scale interactions and define interaction networks. Conduct insightful multilocation experiments that allow for meta-analyses to be performed on balanced but diverse data sets. Use comparative and multiple approaches that encompass differences in trophic relations, connectivity, and biogeochemistry to develop a hilltop to seafloor context for BEF relations.
- Multifunctionality: use natural or human-induced gradients to provide insight into the form and interdependence of BEF relations and their relationship to ecosystem service delivery. Develop theory that connects processes across scales and links to multiple functions. Develop methods to translate ecosystem functions to services and beyond to management. Societal relevance transcends spatial scales but weighs most on larger, more visible scales. Mismatches between legislative frameworks and benefits restrict the implementation of the ecosystem approach in coastal environments.

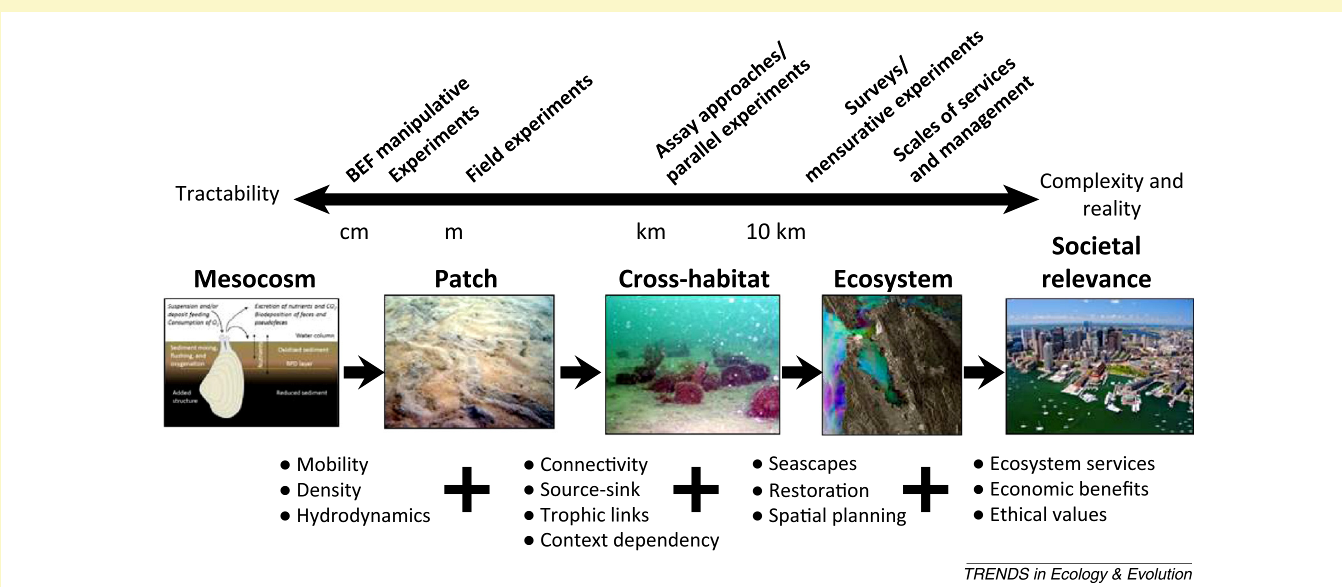

Figure I. BEF challenges.

regenerate nutrients, and increase productivity. Many interactions between individual organisms and biogeochemical processes occur on submeter-length scales [38,39], but the rates of processes can vary with habitat, even in deep-sea sediments that are no longer considered homogeneous [40]. As on land, biodiversity loss on the seafloor is far from random; large, slow-growing, and vulnerable species usually become functionally extinct first. These extinctions shift community dominance patterns, although detecting such changes requires sampling sufficient to characterize community composition and eventually assess its functional consequences.

Some functions that are not apparent at the scale of individuals emerge at the scale of patches (1–100s m) [41]. For example, patch size and density influence hydrodynamics near the seafloor, which can alter exchange of particulate matter, nutrients, and gases [42]. Species from adjacent habitats often exploit the edges of patches, where settlement, sedimentation patterns, and predatory–prey dynamics can be more variable than at the patch core [43]. For example, eelgrass use by juvenile cod has expedited the protection of the eelgrass habitat in Canada because eelgrass patch size strongly influences its utility for that function [44]. This example illustrates that management considers functions such as habitat provisioning rather than single (often charismatic or exploited) species alone, but this continuing evolution in thinking will take time and better knowledge. Current management actions have focused on some key environments (e.g., mangroves or estuaries [31]) that deliver functions such as nutrient regeneration hotspots, but the focus has been primarily on habitat rather than nutrient-related functions per se. Nonetheless, key agreements, such as the Convention on Biological Diversity or the Convention on Fishing and Conservation of the Living Resources of the High Seas, recognize the role of biodiversity in delivery of ecosystem functions and services, and anticipate that scientific evidence will effectively demonstrate such links.

As in terrestrial systems [45], integrating functions across habitats reveals connectedness and trophic dynamics that drive many important BEF relations (Box 1). The mosaic of habitat patches can create important transition zones and halo effects around resources [46,47]. These landscapes can provide corridors for organism movement, allowing trade-offs between predatory and competitive interactions [48]. Functional trait-based approaches can help in understanding BEF, particularly in species-rich systems [49]. Nevertheless habitat type can strongly modify the functional consequences of morphological and behavioral traits [50]; trait expression and biodiversity–environment relations can change along environmental gradients. Disturbance gradients cause shifts in species behaviors and interactions, affecting BEF outcomes [51]. In fact, natural and anthropogenic disturbance gradients can help evaluate how changes in biodiversity affect ecosystem function (Table 1), and clarify how the environment drives context dependency [52,53]. These seafloor examples demonstrate opportunities to address challenging gaps in BEF from mesocosm (cm–m) to ecosystem (10s of km) scales (Box 1). The biodiversity crisis adds urgency to bridging these gaps to understand how changes in biodiversity will influence ecosystem function and deliver benefits that support life and economies [54].

Spatial and temporal heterogeneity [40] provides an opportunity for embedded manipulative experiments and measurements along environmental gradients, with great potential to increase inference across scales [35,36]. Importantly, observation and measurement in natural ecosystems are needed to understand BEF relations. For example, large, less abundant or mobile ecosystem engineers or predators can dramatically influence function, but they are not easily scalable to laboratory experiments [55] and, thus, tend to be ignored. Gradients that encompass known biodiversity or ecosystem function hotspots, such as productive estuaries, polar polynyas, or deep-sea canyons, offer particularly compelling contrasts for experimental designs. In addition, newly disturbed versus more pristine systems (e.g., seabed newly exposed to fishing by retreating ice or marine protected areas) or contrasts that utilize complexities of nature (e.g., localized nutrient upwelling or runoff) provide excellent scenarios for scaling laboratory experiments (Figure 1). Alternatively, we could map patterns in response variables (e.g., functions) or surrogates (e.g., trait analysis) and nest point measurements or experiments to facilitate scaling up [56,57]. Long-term data sets also offer some solutions for extrapolating across scales to link the measurement of functions at short temporal scales to long-term changes in ecosystems.

Table 1. Steps forward that provide solutions to make BEF science matter and impact governance

BEF Challenges	Solutions and Contributions	Limitations
Effectively addressing...		
• many combinations of species	Select species based on theory, natural history	Low-diversity environments
• number and intensity of stressors	Work along natural gradients in space, time	Constrained by unique situations
• number of interactions of functions	Context, field experience, work with users	Range of individual expertise
• variation across habitats/ecosystems	Selection of habitat and relevant environments	
Developing frameworks that address...		
• temporal relevance	Work along natural gradients in time	Episodic events, luck
• complex dynamics	Integrative studies	Finite resources
• relevance to management needs	Dialogue, common language, adaptive science	Momentum, resources
Making output relevant to...		
• ecosystem service thinking	Interdisciplinary training, work with social scientists	Language, transdisciplinary thinking
• the global biodiversity crisis	Match scales of information to society's needs	Global problems, local science
• society	Effective communication for policy, public	Global science, local management
• broader management	Participatory processes	
• modeling and scenarios	Address scaling, multifunctionality, translation	
Science that moves governance	Solution-focused, policy-relevant science, training	Science and management timelines

The challenge of multifunctionality

To extend the seafloor example to a new more real-world approach, we propose a framework to overcome the challenges identified above (Box 1). By combining field measurements along diversity gradients, manipulative field experiments, and modeling, significant new insights will be gained not only for oceans, but also for terrestrial and freshwater systems (Box 1).

Environmental gradients, such as those generated by hypoxic events on the seafloor, are increasingly problematic worldwide [58]. Working along a gradient from low, medium, to fully oxygenated bottom waters, comparison of single or multiple functions such as carbon breakdown and sequestration [59], nutrient regeneration [38], and sediment oxygenation [40,60] can be linked to biodiversity in ways that facilitate mapping BEF over large scales. For example, high spatial resolution sampling along a hypoxic oxygen gradient off Pakistan revealed dramatic, threshold changes in bioturbation and community structure [61]. Reduced oxygen often decreases diversity and abundances of seafloor invertebrates; however, oxygen concentrations alone were not strong predictors of these bioturbation patterns, suggesting that multiple factors drive these dramatic changes in processes and rates that underpin many seafloor ecosystem functions. Oxygen availability can constrain colonization sequences, with potential impacts on dynamics and subsequent functions [62]; such differences could create fortuitous opportunities to understand how different species combinations affect subsequent function. Similarly, field experiments spanning oxygen levels, modifying natural biodiversity, and measuring multiple ecosystem functions *in situ* can help partition the relative role of the environment and biodiversity in driving multiple ecosystem functions [51] and key traits important in maintaining functions such as nutrient fluxes.

Experimentally disturbing the seafloor on different spatial scales provides insight into recovery processes that help in understanding the effects of disturbance gradients such as bottom trawling, seabed mining, coastal hypoxia, or contrasting regions adjacent to protected areas. Practical and ethical considerations limit the scale of experimental disturbance, but even small changes in the spatial scale of disturbance (cm^2–10s of m^2) can change how colonists and the environment interact [63], how species interact [64], and the ensuing temporal dynamics [65].

Moving beyond the scales at which manipulative experiments are feasible, we can integrate gradient studies (see above) with manipulative and descriptive approaches [66]. Now, we must consider the collective impact of individual disturbance events across the seafloor landscape. These events create a mosaic of patches in different states of recovery that define the potential for cumulative impacts associated with specific types of disturbance. Disturbance impacts on poor dispersing, vulnerable, or long-lived species can fragment habitats and magnify cumulative and chronic effects of even small-scale distubance events [67]. In this context, manipulative experiments at multiple locations, nested within variable habitats, ecological connectedness, and environmental conditions can elucidate potential cumulative impacts on biodiversity and ecosystem function [68].

The challenge of translating BEF science to societal needs

The translation from ecosystem process to functions to services highlights the importance of considering how multiple processes interact. Marrying theory and empirical research helps ground truth and translate complex theory into knowledge to inform difficult decision-making. In essence, interactions at one scale of organization produce emergent properties at a higher scale (*cf*. seafloor carbon sequestration; Figure 1). This complex translation requires embracing complexity and recognizing the importance of interactions across scales (fast and slow or small and broad) as well as positive and negative interactions. Integrating diverse techniques can help characterize interaction networks, and identify the strength of causality (e.g., artificial neural networks [69]; structural equation modeling [70]; and convergent cross mapping [71]). New statistical tools can interpolate and map species, environments, and potentially functions and services, as well as their key drivers [72]. Only by nesting ecosystem services into broader social–ecological system interactions can we identify the true value of biodiversity to humanity and identify feedbacks that can lead to change [73] (Table 1).

Proving the value of BEF in addressing societal issues and global crisis requires that we translate knowledge across many scales of socioecological organization (Table 1). BEF research has successfully demonstrated that biodiversity, and specifically species richness, matters to some elements of ecosystem function [74] and managers and policy-makers widely accept that biodiversity matters [e.g., International Union for the Conservation of Nature (IUCN) or United Nations Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services (IPBES)]. BEF research can and must evolve rapidly to produce scientific results that managers can apply to real-world problems. Important contributions await in ecosystem-based management, resilience thinking, and restoration of degraded ecosystems. This venture requires broadening the scope of research to match the scope originally envisioned [13].

Concluding remarks

Our vision focuses on understanding linkages between biodiversity and biogeochemical and biophysical relations, and scaling across space, time, and levels of ecological organization. These fundamental processes support the life-supporting capacity of our planet. However, recognizing and managing the feedbacks between ecological and economic systems will be increasingly important as we transition to a world of human domination with no more wild frontiers, bringing all of its unintended consequences. Particularly in the deep ocean and polar ecosystems, these frontiers might remain wild and comparatively pristine in the near future, but how can we move forward with poor diversity knowledge and vast, unsampled regions? We must begin by prioritizing experimental efforts in frontier environments before they degrade, and applying the same scaling strategies and surrogate approaches outlined above. Given that seafloor sediments and terrestrial soils support many similar functions (e.g., carbon storage or nutrient recycling), the lessons learned and approaches outlined here offer parallel opportunities on land, particularly in light of the degree to which human activities have modified many terrestrial ecosystems.

Over the past decade, many researchers have identified a need to link experimental outputs to management needs, but real action to achieve that objective remains rare. Governance often seeks to maintain ocean functions such as productivity, yet with little understanding of how biodiversity and ocean functions link; knowledge of this type could provide guidance on key management issues such as design of marine protected areas. We must find new ways for this knowledge to sit with society and motivate action, balancing human adaptation to the limits of the adaptive capacity of nature [75].

Acknowledgments

We thank the Walter and Andrée de Nottbeck Foundation (Tvärminne Senior Research Fellowships awarded to P.V.R.S. and S.F.T.) and Tvärminne Zoological Station for their financial and logistical support in writing this manuscript. We also thank the Natural Sciences and Engineering Research Council of Canada Discovery Grant Program and Canadian Healthy Oceans Network (CHONe) for supporting P.V.R.S., the Royal Society of New Zealand Marsden Fund (NIW1102) for supporting S.F.T., and the COCOA project (funded by BONUS, the joint Baltic Sea research and development programme (Art 185), funded jointly from EU's 7th Programme for research, technological development and demonstration and from the Academy of Finland) for supporting A.N. Judi Hewitt, Kari Ellingsen, Joanna Norkko, Anna Villnäs, and three anonymous reviewers provided helpful comments on earlier drafts of this manuscript.

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