Integrating Different Organizational Levels in Benthic Biodiversity – Ecosystem Functioning (BEF) Studies

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1. Introduction

Biodiversity of vertebrate species in all regions of the world has diminished nearly 30% between 1970 and 2005, and 14% when considering only marine species (Humphrey et al., 2008). About 40% of the world's oceans are severely affected by anthropogenic impacts (Humphrey et al., 2008). Among the main reasons for the drastic marine biodiversity decline are habitat loss or fragmentation due to unsustainable urbanization of the coasts (Schlacher et al., 2007), overexploitation of species, especially overfishing (Pauly et al., 1998), pollution resulting from agricultural and urban run-off (Glibert et al., 2006; Paez-Osuna et al., 1999), chronic oil pollution near oil platforms and terminals (Brown & McLachlan, 2002), as well as the invasion of exotic species (Grosholz, 2002). The all-encompassing climate change presents additional environmental challenges. Ecological processes are put at stake due to the loss of species and changes in community patterns, because they depend on the integrity and continuity of communities and ecosystems. These processes guarantee ecological services such as nutrient cycling, stabilization of sediments, and water purification insuring the well-being of plants, animals and humans. Therefore, much scientific effort has turned towards the relationship between biodiversity and ecosystems functioning (BEF) in order to better understand the consequences of the ongoing biodiversity loss.

Most BEF studies consist of experiments, which investigate the relationship between some measure of diversity and some measure of ecosystem functioning. *Diversity* encompasses all levels of biological organization from genes to ecosystems; however, most BEF studies emphasize the consequences of species richness. *Ecosystem functioning* includes all ecological processes such as element cycling, resource use, biomass production, trophic and other

relationships among the organisms, as well as any form of resistance or resilience of the community and the system. The ways in which ecosystem functioning is measured experimentally vary greatly among studies. Among others, nutrient flux (Emmerson et al., 2001), primary and secondary production (Duffy et al., 2003), as well as food web dynamics (Duffy et al., 2007), but also resistance to and resilience from disturbance (e.g., Hughes & Stachowicz, 2004) and invasion success (Stachowicz et al., 1999) have been assessed.

In this chapter, we aim at giving a succinct overview of the seminal BEF studies and presenting a new experimental approach in this field of research. In the following sections, we present various experimental systems and organisms with special emphasis on benthic communities. For this purpose we scanned the reviews by Covich et al. (2004), Duffy et al. (2007), Hooper et al. (2005), Loreau et al. (2001), Stachowicz et al. (2007), and Worm et al. (2006,) and selected more than 30 of the most cited studies. To extend the survey to the present, we selected relevant studies from those citing the above-mentioned reviews. We focus on the different experimental approaches, highlight advantages and shortcomings of the applied methodologies or systems, and we briefly summarize the most important results. As will be shown, benthic BEF studies have hitherto investigated the effects of species and genetic diversity separately. Against this background, we present a new experimental model system of a benthic food web, which allows investigating the effects of species and genetic diversity in combination.

2. The pioneering BEF study systems

2.1 Terrestrial plants

The pioneering BEF studies were conducted on terrestrial plant systems (e.g., Tilman & Downing, 1994; Tilman, 2006). They established plots of different plant species richness and measured resilience and resistance from a major draught in terms of primary productivity (i.e., plant biomass; Tilman & Downing, 1994). Others applied similar methods and repeated the same experiment at a number of sites differing in climate and major environmental factors in order to search for general (global) patterns (Hector et al., 1999). These studies were among the first to provide clear experimental evidence about the positive relationships between taxonomic and functional diversity and productivity, substantiating the need for biodiversity conservation. However, they also demonstrated the difficulties with the experimental setups, such as the problem of scales (space and time), or the "sampling effect", i.e., the probability that the assemblage of the highest diversity is the most likely to contain the most productive species (Benedetti-Cecchi, 2004). Further, although these studies included different "functional groups" by including functionally different plants (i.e., nitrogen-fixing legumes, grasses and herbs), they only considered the basic trophic level of primary producers.

2.2 Microbial communities

In order to investigate experimentally the relationship between diversity and ecosystem functioning at multiple trophic levels, BEF studies on aquatic microbial communities followed. These studies allowed new insights into functional diversity, because they considered species diversity within several trophic levels from producers to predators (McGrady-Steed et al., 1997; Naeem & Li, 1997; Petchey et al., 1999). Replicated aquatic microbial microcosms were established with varying numbers of species per functional group (McGrady-Steed et al., 1997; Naeem & Li, 1997; Petchey et al., 1999). Each microcosm

contained autotrophs (algae), decomposers (bacteria) as well as first- and second-order consumers (protists) either of varying numbers of randomly assembled species (1, 2 or 3 species) from a species pool (Naeem & Li, 1997), or of aquatic microbial communities representing a biodiversity gradient as it might occur in nature after species loss across all trophic levels (31 species in the "complete", i.e. most diverse assemblage; McGrady-Steed et al., 1997). Although this approach risks confounding species richness with species composition, additional experimental and statistical controls were applied to separate these factors. The simulated "natural" communities consisted of 4 (McGrady-Steed et al., 1997) or 5 (Petchey et al., 1999) trophic levels: producers (e.g., diatoms), herbivores (e.g. *Brachionus*), bacterivores (e.g. *Rotaria*), predators (e.g. *Heliozoa*), and a bacterial assemblage with 4 to 16 species per functional group (McGrady-Steed et al. 1997; Petchey et al., 1999). The lowest diversity group consisted of fewer species per trophic level or functional groups, simulating diversity loss across trophic levels. As proxies of ecosystem functioning, CO_2 concentration (i.e. ecosystem respiration; McGrady- Steed et al., 1997), algae and bacterial biomass (Naeem & Li, 1997) were measured. In line with these studies, Bell et al. (2005) manipulated microcosms with an original pool of 72 species. They argued that manipulating low numbers of species can show which processes are possible, but that manipulating high numbers of species gives an idea about which processes may become important in nature (Bell et al., 2005). Their study system consisted of semi-permanent rain pools from the base of European beech trees. In another approach, algal (producer) and bacterial (decomposer) species diversity were manipulated simultaneously, and algal biomass was measured as a proxy of primary production (Naeem et al., 2000). Algae were chosen randomly from a pool of eight, and bacteria were chosen from a pool of 12 species.

In all the above-mentioned studies, biodiversity had a positive stabilizing effect: ecosystem respiration became more predictable (McGrady-Steed et al., 1997), community biomass as well as density measures were more consistent (Naeem & Li, 1997), and bacterial respiration increased with species richness (Bell et al., 2005). A higher predictability and lower variability of measures of ecosystem functioning underpin the idea that species diversity enhances ecosystem stability, whereas the stimulatory effect on respiration *per se* demonstrates a positive relationship between diversity and ecosystem process rates. On the other hand, extinction risk in warming environments remained unaffected by biodiversity, but instead depended on the trophic position (Petchey et al., 1999). However, diverse communities were more likely to contain temperature-tolerant species and therefore retained more species than depauperate ones (Petchey et al., 1999). Further, the simultaneous manipulation of two trophic levels showed that neither algal nor bacterial species richness alone could explain the significant differences among microcosms, but that the algal biomass was a joint function of both algal and bacterial diversity implying important interactions among functional groups (Naeem et al., 2000).

Studies on microbial communities are very useful as they can be carried out at very high species richness levels (Bell et al., 2005). Moreover, microbial communities are omnipresent, and play fundamental roles in virtually all ecosystems. Besides, experiments allow changing diversity across trophic levels. This is an important issue since species loss is not random; it rather depends on the trophic position, with top predators being especially prone to extinction (Petchey et al., 1999). However, all microbial organisms of those studies are unicellular, and it remains unclear to what extent the results can be extrapolated to communities comprising metazoans. A meta-analysis linking metazoan species diversity

with various proxies for ecosystem functioning across a range of deep-sea regions suggests that species diversity profoundly affects marine benthic ecosystem functioning (Danovaro et al., 2008). Therefore, mesocosm studies with benthic communities and systems provide useful options to take BEF studies to the next level.

3. BEF experiments on benthic communities

Benthos includes all organisms that live in or on water-covered substratum. These can be coastal and intertidal areas as well as limnic systems, including different types of substrates such as seagrass meadows, rocks, sand or mud. Sandy beaches, mudflats and other ecosystems found in intertidal zones act as buffer zones between the terrestrial and marine biomes, hosting a high diversity of species, which play a significant role in the global storage and cycling of nutrients (Covich et al., 2004; Snelgrove et al., 1997). In addition, some coastal ecosystems such as seagrass meadows provide a rich source of primary productivity, as well as habitats for numerous fishes and invertebrates (Hughes & Stachowicz, 2004), and are among the most 'valuable' ecosystems on earth (Constanza et al., 1997).

Most of the benthic fauna are small organisms indiscernible to the naked eye, but they play a fundamental ecological role. For example free-living marine nematodes decompose organic matter, and facilitate the recycling of nutrients (Heip et al., 1985). Benthic diatoms not only constitute an essential part of the fundament of the benthic food chain, but in intertidal sediments their excretions stabilize the substratum by effectively binding sediment particles together (Stal, 2010). The communities of these buffer zones are severely affected by anthropogenic impacts from both the terrestrial and the marine side. The combination of those impacts with increasing surface water temperature and long exposure to high air temperature during spring tides may exceed the tolerance of some intertidal organisms. Because of the serious consequences this may have for the biological and the physical integrity of the ecosystem, but also because of their accessibility, relatively easy handling, and because of the typically high local diversity, benthic communities have become important for BEF studies.

3.1 Effects of genotypic diversity on benthic ecosystem functioning

There are very few studies about the effects of genotypic diversity on benthic ecosystem functioning. The most common approach has concentrated on plants or algae that reproduce clonally. In these experiments, genetic diversity refers to genotypic richness and usually monocultures of single genotypes are compared to mixtures of different genotypes (Bell, 1991; Hughes & Stachowicz, 2004; Reusch et al., 2005). In this context, the cosmopolitan eelgrass *Zostera marina* has received special attention. In extensive field experiments, the different genotypes were planted singly and in combination in a random block design after removing pre-existing eelgrass (Hughes & Stachowicz, 2004; Reusch et al., 2005). Experiments conducted on this system revealed a positive relationship between genotypic diversity and ecosystem functioning. *Zostera marina* of higher genotypic diversity recovered more rapidly from natural disturbances such as grazing geese or algal blooms (Hughes & Stachowicz, 2004, 2011). Genotypic diversity was also crucial to recovery (resilience) from experimentally implemented disturbance (i.e., biomass removal; Hughes & Stachowicz, 2011). Also biomass production, plant density and faunal abundance were enhanced (Reusch et al., 2005), especially in winter, when eelgrass experienced stress from

abiotic and biotic factors (Hughes & Stachowicz, 2009). Similar results were obtained when genotypes of the green alga *Chlamydomonas reinhardtii* were set up in culture tubes in monocultures and all possible pair wise combinations: the mixtures were consistently more productive and less variable in their productivity under simulation of different environmental conditions (Bell, 1991).

To our knowledge, there are very few experimental studies on benthic animals investigating the role of genetic diversity on ecosystem function, two of which assessed the effects on intertidal invertebrates. Within-species diversity was manipulated in the barnacle *Balanus improvisus* by altering the number of parental broods (Gamfeldt et al., 2005). In a similar way, the number of maternal families was controlled in the amphipod *Gammarus duebeni* from intertidal rock pools (Gamfeldt & Kallstrom, 2007). Both experiments found positive effects of increased genetic diversity: larval settlement of *B. improvisus* increased and the more diverse amphipod assemblages exhibited more predictable (but not higher on average) survival when exposed to multiple stressors (Gamfeldt & Kallstrom, 2007). Apart from that, studies relating genetic diversity to some (though particular) measure of ecosystem functioning have mainly focused on tolerance to toxic substances, indicating that genetically diverse populations resist to or recover better from contamination (Pease et al., 2010; Phillips & Hickey, 2010).

The few studies relating genetic (genotypic) diversity to ecosystem functioning show that genetic diversity can be important for the stability and productivity of coastal ecosystems. Generally, increased genetic diversity enhances the continuity and reliability of ecosystems. The advantage of clonally reproducing organisms such as plants or algae is that they provide the relatively easy and thus straightforward possibility of setting up experimental groups of contrasting genotypic diversity. However, this method is not applicable to sexually reproducing organisms. For those, it is necessary to produce different levels of genetic diversity by controlled mating prior to the experiment. For example Gamfeldt & Kallstrom (2007) sampled natural populations of *G. duebeni* and then separated pairs of mating individuals to form different "families". With these families, they then formed inbred strains (lowest genetic diversity level) and strains of two to four different families (increasing diversity). This procedure provides reliable levels of contrasting genetic diversities, but it is time consuming and requires considerable effort and material. Nevertheless, it is probably the only reliable method of obtaining contrasting diversity levels for sexually reproducing organisms if natural inbred (representing low diversity) and outbred populations (high diversity) are unavailable. This is probably the main reason, why studies investigating the role of genetic diversity on the system functioning are still scarce.

3.2 Effects of species diversity on benthic ecosystem functioning
3.2.1 Macrophyte vegetations

Seagrass *Zostera marina*, pondweed or cordgrass *Spartina* ecosystems have been used widely to investigate the effect of species richness, species composition as well as food chain length and trophic cascades on ecosystem processes. For example all possible species combinations of four functionally and morphologically different submerged aquatic macrophytes (pondweed) were planted in artificial wading pools (Engelhardt & Ritchie, 2001). Although local wetlands are usually dominated by single vascular species, there was a clear effect of increased plant diversity leading to higher plant and algal biomass as well as lower loss of phosphorus (Engelhardt & Ritchie, 2001).

In several outdoor experiments, species diversity of different trophic levels was manipulated and the role of grazer diversity on plant biomass as well as grazer secondary production was investigated (Duffy et al., 2001). Grazers play an important role in the health of seagrass ecosystems because they feed preferentially on epiphytic algae and thus prevent eelgrass from becoming overgrown by epiphytes. In the experiment, the three grazer crustacean species (two isopods and one amphipod), which dominate the seagrass epifauna in the study area, were assembled in all possible species combinations (1 to 3 species and a grazer-free control), assessing the accumulation of epiphytic algae and eelgrass biomass as well as grazer secondary production. Results showed that all three grazer species differed substantially in their impact on ecosystem processes. For all processes measured, species composition was more important for eelgrass and grazer biomass accumulation than species richness. The study emphasized that species of one functional group need not necessarily be functionally redundant. In a follow-up experiment, six common grazer species (one gastropod, three amphipods and two isopods) were combined to further investigate the role of species diversity and species composition in relation to eelgrass ecosystem functioning (Duffy et al., 2003). Again, species were assembled in random combinations (one, three and six-species treatments) in outdoor mesocosms. The water supply was filtered, but allowed microscopic propagules of algae and sessile invertebrates to recruit. In addition to eelgrass, algal and grazer biomass, also measured was organic carbon in the sediment. Contrary to the previous study, increased biodiversity enhanced secondary production. Yet, increasing grazer diversity reduced total community diversity and allowed a sessile, grazing-resistant invertebrate to become dominant, presumably due to intraguild competition among grazer species.

In the previous experiment, interaction effects of species diversity and species composition were measured as deviations from expected additive effects based on single-species effects. In another attempt to separate the two effects, a mesocosm experiment was conducted where species richness and species composition were manipulated independently across multiple trophic levels including macrophytes, benthic grazers and carnivorous predators (Downing & Leibold, 2002). One, three or five species per functional group were assembled and within each level of richness, seven unique species compositions were nested and replicated. This being an extensive and statistically robust method, the results showed that species diversity as well as species composition had important effects on ecosystem functioning. Ecosystem productivity was highest at the highest diversity level, which implies that species within a functional group are not redundant, a result similar to that of Duffy et al. (2001). Not all measures of ecosystem functioning reacted similarly to species diversity or composition: phytoplankton biomass increased while zooplankton biomass decreased with total species richness. Moreover, there was a strong effect of species altering ecosystem processes indirectly by altering abundances of other species, implying that trophic interactions are highly important for the functioning of communities and ecosystems.

Experiments on macrophyte vegetations have successfully shown the effects of species diversity and identity on ecosystem processes. In general (but not always), a positive effect of biodiversity was found on ecosystem processes. However, these experiments were all conducted over a relatively short period of time. In contrast, the effects of seaweed species richness on biomass accumulation were stronger in long-term (3 years) than in short-term (2 months) field experiments (Stachovicz et al., 2008). Although short-term experiments are valuable in estimating the effects of species richness and identity on ecosystem processes,

they are likely to be unable to capture seasonal environmental heterogeneity and population responses. Therefore, they are likely to underestimate the influence of diversity on ecosystem processes in natural ecosystems (Stachowicz et al., 2008).

3.2.2 Benthic invertebrate macrofauna from intertidal soft bottom areas

In a novel experimental approach designed to separate the effects of species richness and species identity, the dominant infaunal macrofaunal species of a mudflat community were collected in two distinct biogeographical areas: three species (one polychaete, an amphipod and a gastropod) in Scotland and five species (three gastropods, one ghost shrimp and one cockle) in South Australia. Null-models based on the response of monocultures (i.e., single species treatments) were constructed and then compared to the experimental results. It was found that individual species contributed idiosyncratically to the measured ecosystem process (ammonia release), and that the effects were biomass (density)-dependent (Emmerson & Raffaelli, 2000).

In a subsequent extended experiment, replicate species pools were sampled from three regions (Scotland, southwest Sweden and south Australia) and placed in mesocosms (Emmerson et al., 2001). The selected species (ranging from one to four species) were dominating the biomass at each of the three sites. Additionally, complete natural communities were sampled at three different sites in Scotland. These contained more species and included the small, delicate species that could not be manipulated directly. Thus two experiments were carried out: one with artificially assembled communities on one hand, and one with natural communities on the other. In the "artificial" assemblages, NH_4-N production became more predictable (i.e., less variable) with increased diversity. In the experiment where natural communities were used, there was a significant positive effect of species richness on nutrient flux; however, the process was driven disproportionately by individual, different species at each site (sampling effect).

The first field experiment on a benthic system was conducted on a mudflat in Scotland. Defaunated sediment was enclosed using cages with different mesh sizes. The cages were then allowed to be colonized by organisms from the surrounding sediments. Through this, groups of low, medium and high species richness as well as low, medium and high biomass of macrofaunal invertebrates were established (Bolam et al., 2002). In each experimental cage the following variables were measured as proxies of ecosystem functioning: phosphate and ammonium fluxes, community respiration, sediment shear strength, water content, water/silt content, organic content, redox potential, nitrate and nitrite. All but one variable remained unaffected by macrofaunal diversity or biomass; only oxygen consumption was positively related to both, but in fact it was driven by the largest species in the study.

Waldbusser et al. (2004) examined the relationship between functional diversity and ecosystem processes by manipulating three functionally diverse polychaete worms from nearshore sediments. They established microcosms of one and three species and kept them for 4 months. They found that species as well as functional diversity had an effect on the measured proxies of ecosystem processes (i.e., oxygen and phosphate fluxes, profiles of oxygen and pH). Although it is difficult to separate species from functional diversity when each species represents a different function, it was clear that single species had disproportionate effects on selected variables and that the three-species assemblage did not result in the additive effect one would have expected from single-species treatments.

In all the above-mentioned studies, a disproportionate effect of single species could be detected. Unlike the community members of macrophyte systems, benthic invertebrates from soft bottom intertidal areas seem to contribute individually to ecosystem functioning with their impact strongly depending on their functional role. Therefore, it can be essential to include such critical species in experiments assessing the effect of species richness on the functioning of the system. Since many experimental approaches include only the dominant species, conclusions drawn may not necessarily hold for the natural system, especially since some key species are not necessarily very abundant. Generally, natural benthic invertebrate assemblages from marine soft bottoms can be sampled easily, and as such provide a good system for BEF studies. Moreover, they can be established in micro- or mesocosms in the laboratory or in the field, and respond rapidly to experimental treatments. However, these organisms can reach very high densities, and especially the members of the meiofaunal component are often difficult to count and identify. Therefore, the choice of working with "artificial" (i.e., fewer species) or "natural" assemblages needs careful planning, which often means facing a trade-off between "natural" and "doable" with the available resources. The decision is most dependent on the scientific question, but also on the possibilities in terms of expertise and time.

3.2.3 Stream invertebrate larvae

Many insects develop as larvae on the substrate of streams or ponds, where they exhibit different feeding strategies and play different functional roles in the benthic system. As such, they provide an interesting system to test hypotheses regarding intraguild diversity. Caddisfly larvae, for example, construct silk nets in the pore spaces of the streambed, and passively feed on suspended particulate matter. Their structures generate topographical features, which influence patterns of water flow and therefore food availability (Cardinale et al., 2002). Often, several species with anatomically different feeding structures co-occur. This has led to the hypothesis that increased diversity leads to facilitation of food uptake. The hypothesis has been tested in stream mesocosms, where caddisfly larvae assemblages were established, either with a single species (18 larvae) or with 3 species (6 larvae per species; Cardinale et al., 2002). Results showed that higher diversity led to facilitative interactions and an increase in the uptake of organic matter. However, the species building the largest tubes had the strongest physical impact on streambed water flow.

A follow-up experiment tested whether the diversity-functioning relationship would be different under conditions of regular disturbance (Cardinale & Palmer, 2002). The hypothesis was that disturbance would induce mechanisms that would interfere with ecological processes. Disturbance was simulated by mechanically removing a given number of larvae in randomly selected pore spaces. Three ecological processes were measured at the end of the experiment: respiration of the benthic biofilm, primary productivity of benthic algae and the flux of particulate organic matter (POM) from the water column to the streambed. The disturbance treatment resulted in the suppression of a dominant taxon, which had a particularly low rate of nutrient excretion. This led to a negative correlation between primary production and species richness in the undisturbed streams, as this taxon was included in multi-species treatments. Concordantly, POM flux increased with species richness under disturbance conditions. Disturbance thus favoured the co-existence of competitively superior and inferior species, enhancing ecosystem processes (Cardinale & Palmer, 2002).

Other stream invertebrate larvae feed on leaf litter as "shredders" (Jonsson & Malmqvist, 2000). In a laboratory experiment, three species of stoneflies (*Plecoptera*), belonging to this leaf-eating feeding guild, were placed in one-, two- and three-species treatments to investigate the effect of species richness on leaf mass loss. Ecosystem process rates (leaf mass loss) increased significantly with species richness, but were not dependent on species identity, suggesting that the different species were not functionally redundant (Jonsson & Malmqvist, 2000).

An extension of the previous experiment investigated the effect of intraguild species diversity for other feeding guilds (Jonsson & Malmqvist, 2003). In several controlled laboratory experiments, multiple species of the following functional groups were collected: filter feeders (six blackfly larvae *[Diptera]*), grazers (two species of mayfly larvae *[Ephemeroptera]* and one snail), and predators (two stonefly species *[Plecoptera]* and one caddisfly species *[Trichoptera]*). Each functional group was set up in single-, two- and three species combinations and provided with their respective food source: dry yeast for the filter feeders, algae for the grazers and blackfly larvae for the predators. There was a strong effect of species identity, and species combinations, whereas species richness *per se* did not affect process rates in any of the three functional groups (Jonsson & Malmqvist, 2003).

These four examples show that stream invertebrate larvae form a complex system consisting of different feeding guilds exhibiting many different functions. Apparently the extent to which species richness affects ecosystem functioning depends greatly on the identity and the function of the species present. In general, however, like marine soft-bottom invertebrates, lotic larval communities seem to contain species exhibiting disproportionate effects on the system. The effects of species loss may be predictable when their functional role is accurately ascertained, but can become idiosyncratic when interactions such as competitive behaviour among species occur.

4. Two "special topics" in benthic BEF studies

As mentioned in the former sections, most BEF studies assess ecosystem functioning in terms of biomass production, effects on community composition or element cycling. However, there are other possible effects with important implications for the whole ecosystem. We choose two examples to illustrate this: trophic cascades and invasion success. We chose these two special topics because the former shows that slightly different levels of intraguild diversity can lead to completely opposed effects, whereas the latter illustrates that although experimental approaches meet hypotheses based on theory, they sometimes do not reflect what is actually happening in nature.

4.1 Trophic cascades

Trophic species-level cascades occur when a change in predator abundance induces changes in the biomass of primary producers, due to a control of the abundance of grazers, thereby releasing lower trophic levels from grazing pressure (Polis et al., 2000). Predator diversity may reduce trophic cascades and may therefore be important for the population development of lower trophic levels and primary production. The importance of such intraguild diversity was studied by manipulating predator species richness (1, 2 or 3 species). The predator species pool consisted of several invertebrates such as hunting and web-building spiders preying on an arthropod (planthopper) assemblage inhabiting *Spartina* cordgrass (Finke & Denno, 2005). The occurrence of trophic cascades was

dependent on predator species richness, however the magnitude of the effect depended on whether the predators were a mixture of strict predators only, or of strict and intraguild predators combined. Higher intraguild predator richness led to antagonistic interactions among predators and dampened trophic cascades. As a consequence, it diminished herbivore suppression and therefore reduced primary productivity, indicating that predator diversity indirectly affects primary biomass production via trophic top-down control (Finke & Denno, 2005).

A similar outcome resulted from an experiment containing five species of predators, namely four carnivores (crabs, shrimp, blennies and killifish) and one omnivore (pinfish), preying on a herbivore assemblage dominated by amphipods and isopods, which in turn grazed on five species of macroalgae (Bruno & O'Connor, 2005). In an outdoor experiment, one, three or five predators were randomly assigned to mesocosms containing algae and herbivores. Predator diversity and identity had strong effects on the strength of the trophic cascade: when a generalist carnivore was present, grazers were significantly limited and algal biomass increased, whereas algal biomass decreased with increasing predator diversity, especially when the omnivorous fish was included.

Analogous to the previous examples, field observations in kelp forest ecosystems have revealed that predator diversity is negatively correlated with herbivore abundance and positively correlated with kelp density (Byrnes et al., 2006). To confirm the causality of this observation, predator richness was manipulated experimentally in kelp mesocosms. Accordingly, decreasing predator richness stimulated herbivore grazing leading to a decrease in giant kelp biomass. The underlying mechanism was not antagonistic behaviour among multiple predator species as observed in Finke & Denno (2005); instead, the herbivores changed their behaviour towards the different predators and therefore spent less time grazing.

Duffy et al. (2005) tested the effect of food chain length and trophic cascades on biomass of primary producers and consumers. In outdoor mesocosm tanks, experimental eelgrass communities were assembled in treatments of two (plants, grazers) and three (plants, grazers and predator) trophic levels. Grazer diversity was altered in the different treatments, and one omnivore predator (blue crab) was in- or excluded in order to modify the length of the trophic chain (Duffy et al., 2005). Results showed that the crabs had a strong effect on the grazers, resulting in higher algal biomass.

The results of these studies show that slight changes in predator diversity (e.g., one *versus* two species) can cascade to lower trophic levels. However, the exact outcome depends on the intraguild interactions at the predator's trophic level on one hand, and on the predator-prey response on the other. This implies that the loss of certain species at the top of the food chain can have unprecedented effects inducing fundamental changes to the whole system. In the case of seagrass and macroalgal systems, the loss of predators may induce the loss of key habitat-providing species with harmful consequences for the whole community (e.g. Estes et al., 1998).

4.2 Invasion success

Marine biological invasions are a major issue at regional and global scales. One of the major causes is the large number of transport vectors, like cargo vessels, but it has also been hypothesized that a depauperate native flora and fauna may facilitate the invasion success of exotic species (Elton, 1958). Non-native species can be a threat to regional biota due to competitive advantage, with uncontrollable consequences for the functioning of ecological

processes. To investigate the relationship between native species diversity and invasion success of exotic species, experiments were conducted on marine sessile epibenthic invertebrates of the southern rocky coasts of New England, exposed to the invasion of the colonial ascidian *Botrylloides diegensis*, native of the Pacific Ocean (Stachowicz et al., 1999, 2002). Experimental communities were composed of zero to four native species. Species richness was manipulated by transplanting juveniles or by allowing larvae to settle on 2x2 cm tiles that were (after the successful colonization) combined in a 5x5 grid (i.e., a complete plate consisted of 25 interchangeable subunits). During the course of the experiment all but the five target species were removed regularly. As a result, survival of the invasive species decreased with higher species richness, and it was hypothesized that reduced resource availability may be the underlying mechanism.

Contrary to the previous example, two observational studies on natural assemblages evidenced the opposite to what had been demonstrated in controlled experiments before. A long-term (11 months) survey of sessile invertebrates on a rocky jetty on the Tasmanian coast revealed a positive relationship between colonization rates of both native and introduced species and natural species richness (Dunstan & Johnson, 2004). Similarly, in a natural riparian assemblage, the most diverse assemblages were the most invaded by exotic plants; the same patterns were evidenced by an *in situ* experiment manipulating local diversity (Levine, 2000). A possible explanation therefore could be the different niche opportunities across varying environmental gradients (Shea & Chesson, 2002). Therefore at a larger observational scale, invasion success will be higher, given that more suitable niches are available, be it for native or exotic species, whereas invasion success would negatively relate to species richness at smaller, i.e. local scales (Shea & Chesson, 2002). On a more individual basis, the specific characteristics and functions of the resident species as well as the interactions among them and with the invasive species, rather than species richness *per se* may be the determinant for the invasion success (Dunstan & Johnson, 2004). These examples show that isolated experiments can sometimes be misleading in their outcomes. Therefore a combination of field observations, and field as well as laboratory experiments would certainly be the best approach to avoid such inherent biases. As this extensive approach is often not feasible, isolated laboratory experiments should be interpreted with caution.

5. Integrating species and genetic diversity in one experiment: an alternative approach

The preceding sections provided an overview of benthic experimental studies that alter either species or genotypic diversity separately. It has been argued that genetic diversity is only important in ecosystems that rely on or are dominated by one or a few key or habitat providing species, such as *Zostera marina* ecosystems (Hughes et al., 2008). However, all living organisms are hierarchically organized: genes make up genotypes, genotypes define populations and populations collectively constitute a species (Reusch & Hughes, 2006). If there is variation and heritability, as well as selection in ecologically important traits such as, e.g., growth rate or resistance to parasites, diversity at any level can have important ecological effects (Hughes et al., 2008). Moreover, it has been shown in terrestrial plant communities that genetic diversity can have direct consequences on species diversity: in a long-term experiment, genetically diverse communities reduced the rate at which species diversity declined (Booth & Grime, 2003), and genetic and species diversity maintained each

other through mutual feedbacks (Lankau & Strauss, 2007). It is therefore fundamental to start to include changes in genetic (population) and species diversity in studies assessing the consequences of biodiversity decline.

Today, *Zostera marina* vegetations probably provide the best systems to investigate species and genetic diversity in concert (Reusch & Hughes, 2006). To our knowledge, it is also the only system where genotypic (seagrass) and species (grazer) diversity have been manipulated simultaneously (Hughes et al., 2010). One big advantage of this system is that seagrasses can reproduce clonally, which means that multiple shoots of one genotype can be handled as one unit when changing genetic (genotypic) richness just like a species is handled as one unit when changing species richness. This makes it possible to alter species and genotypic richness in one experiment. On the other hand, it is a method restricted to clonally reproducing organisms and cannot be applied to sexually reproducing animals. Another major advantage may be that seagrasses consist of relatively few but functionally diverse species. This is very valuable for the manipulation of the experimental units. However, the results cannot be extrapolated to systems with higher species richness, and questions concerning intraguild diversity may be addressed only to a limited extent. Besides, one major disadvantage of the seagrass system is that a lot of space is needed to set up outdoor (or indoor) mesocosms. Moreover, *Zostera marina* has to be available in order to establish the artificial plantings. Yet, its distribution is limited to the northern hemisphere, mainly along European and North American coasts.

As an alternative approach to test effects of species and genetic diversity on ecosystem functioning, we present a setup allowing experimental manipulation of multitrophic assemblages in very small and easy-to-replicate laboratory microcosms (Figure 1a). These comprise small amounts of sediment containing a benthic microbial food web of diatoms (i.e. primary producers), prokaryotes (i.e. decomposers) and nematodes and/or harpacticoid copepods (i.e. grazers of prokaryotes and of diatoms, as well as predators of other nematodes and copepods) (Figure 1b). These organisms dominate all soft sedimentary habitats such as beaches and mudflats around the world. They typically attain high local diversity, species numbers in 10 ml of sediment typically ranging in the order of hundreds to thousands, and several tens for prokaryotes, diatoms and nematodes, respectively. They are highly relevant to basic benthic ecosystem processes such as the decomposition of organic matter and the mineralization of nutrients. They respond more rapidly to environmental changes than most macrofauna (Bolam et al., 2002).

Former experiments with similar setups have proven to be very useful to study benthic processes. De Mesel et al. (2003, 2004, 2006) studied the impact of bacterivore nematodes on the bacterial community and the decomposition of cordgrass leaves. They found that four different bacterivore nematode species have a significant top-down effect on the structure of the bacterial community (De Mesel et al., 2004). However, species richness within the guild of bacterivore nematodes did not enhance decomposition rates, rather the process depended on species identity and on unexpected inhibitory and facilitative interactions among species within the same guild (De Mesel et al., 2003, 2006). Hubas et al. (2010) investigated the influence of microbial organisms, i.e., bacteria, diatoms and bacterivore nematodes, on the production of extracellular polymeric substances (EPS), a major sediment-stabilizing product (Stal, 2010). The results evidenced that the presence of bacterivore nematodes had a positive impact on microbial abundance and EPS production, which was highest at the highest community complexity, i.e., involving nematodes, diatoms and bacteria (Hubas et al., 2010). Dos Santos (2009) studied bottom-up and top-down controls of nematodes on the

bacterial community. They established closed microcosms with bacterivore nematode species that colonize decaying organic matter, revealing that intraguild species interactions depend on food availability (Dos Santos et al., 2009). They also worked with semi-closed microcosms of sandy beach sediments with more natural diversity levels (up to 24 species). Results showed that bacterivore nematodes did not have a more pronounced effect on the structure of the bacterial community than nematodes from other trophic guilds; however, nematode species richness (across trophic levels) did (Dos Santos, 2009). Moreover, processes such as carbon production increased with species richness, and the most species-rich nematode assemblage had a positive effect on bacterial diversity (Dos Santos, 2009).
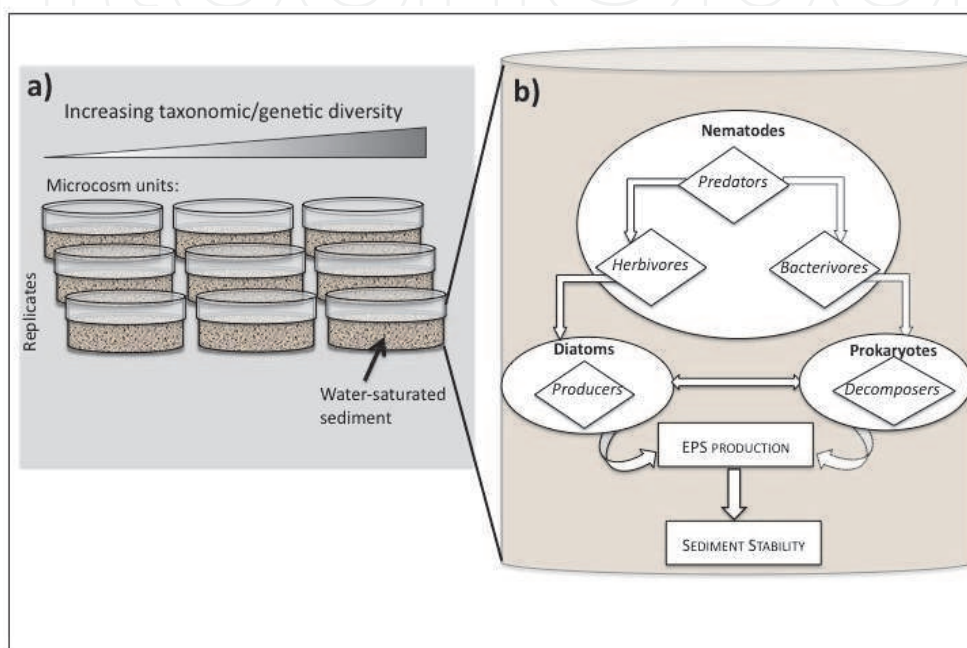

Fig. 1. The experimental system. a) The experimental unit. Microcosms can be setup in a variety of containers; for the illustration we chose a relatively small glass or plastic jar with a thin, water-saturated layer of sediment, covered by a plastic film or lid to avoid desiccation. Experimental microcosms contain increasing levels of nematode taxonomic and/or genetic diversity b) A schematic view of the benthic food web contained in the sediment of the microcosm. Predatory nematodes prey on herbivorous and bacterivore nematodes, which, in turn, graze on diatoms and prokaryotes respectively. In different experimental units, nematode genetic and species diversity are modified. The effects of the different diversity levels on the functioning of the food web are measured in terms of the production of extracellular polymeric substances (EPS) and sediment stability.

To address the BEF subject at different organizational levels simultaneously (i.e., species *and* genetic diversity) across different trophic guilds (i.e., grazers, bacterivores and predators), we follow the microcosm approach as applied in the study by Hubas et al. (2010). We suggest assessing components affecting directly the physical integrity of the habitat as a proxy of the functionality of our microcosms, i.e. the production of EPS and its effect on sediment stability (Figure 1b). However, other functions, such as community respiration, prokaryote enzymatic activities or the decomposition of a specific substrate, may be assessed in the same setup. Microbial EPS are increasingly recognized as a major stabilising factor. They are an ubiquitous component of aquatic ecosystems composed

primarily of carbohydrates and proteins. They have multiple roles and functions: attachment to substrata, flotation and locomotion, feeding, protection against environmental factors such as desiccation, UV radiation and pollution, as well as the development of biofilms (Decho, 1990). Perhaps the most striking feature of these compounds is their ability to bind sediment grains together, enhancing their cohesive strength and thereby increasing resistance to erosion. Particularly diatoms are the major ecosystem engineers of this sediment bio-stabilisation (Stal, 2010), and prokaryotes are increasingly recognised as playing a key role in enhancing sediment surface adhesion and cohesive strength (Gerbersdorf et al., 2008, 2009; Lubarsky et al., 2010). The advantage of this alternative approach is that it offers the possibility of testing both effects of species and genetic diversity on ecosystem functioning.

5.1 Methodology
5.1.1 Microcosm setup
To setup the microcosm, a variety of small containers can be suitable, depending on the exact aim of the study. First, a specified amount of non-cohesive sedimentary substrate needs to be placed on the bottom. For example, acid-washed marine sand (Hubas et al., 2010) or non-cohesive glass beads (Lubarsky et al., 2010) can be used. The sediment needs to be fully hydrated by sterile seawater of a specific salinity (which depends on the organisms). Whether or not the seawater needs to cover the sediment depends on the specific aims of the study. Prokaryote and diatom cultures can be established by sampling sediment surface (0 – 5 mm) from natural tidal flats, and re-suspending the sediment slurry in culture media. Alternatively, or additionally, prokaryote and diatom strains can be obtained from established culture collections. Microbial assemblages should then be incubated for several weeks (e.g., Ribalet et al., 2008). The resulting assemblages can then be used for the experiment. An appropriate culture medium, which favours algal rather than bacterial growth, should be applied. F/2 medium is, for instance, widely used for growing marine algae, especially diatoms (Guillard, 1975). If the use of antibiotics cannot be avoided, a proper test of the effect of each antibiotic on the natural assemblage culture should be conducted.

Finally, nematodes can be placed into the microcosms, according to the experimental groups. There are two different approaches in order to obtain different taxonomic (i.e. species richness) diversity levels across trophic groups of nematodes: either from the field or from cultures. For the former, nematode assemblages can be sampled along diversity gradients from, e.g., an intertidal sandy beach (Gingold et al., 2010) or from different beaches (Dos Santos, 2009). They are extracted live through decantation over a 32µm sieve to obtain stock suspensions of different diversity levels. For the latter, different nematode species can be raised under artificial conditions (Moens & Vincx, 1998). Unfortunately, only a limited number of marine nematode species have hitherto been maintained in permanent monospecific cultures, and most of these belong to the same feeding guild, i.e. bacterivores. However, a majority of species from intertidal sediments can be easily extracted from freshly collected sediment and remain active in a variety of laboratory incubation conditions for several weeks (Moens & Vincx, 1998).

In order to establish microcosms containing nematodes of different genetic diversity, lab cultures and field-collected specimens of the same bacteria-feeding species from which permanent cultures exist can be used. Bacteria feeding nematode species such as *Rhabditis marina, Diplolaimelloides meyli, D. oschei,* and *Diplolaimella dievengatensis* have been cultured

for over 15 years now (T. Moens, unpublished data). Therefore, the premise is that cultured nematodes have low genetic diversity due to inbreeding, unlike natural populations, which are expected to exhibit higher genetic diversity levels. This approach implies that the level of genetic difference has to be assessed before the experiment, which in view of the substantial cryptic diversity (e.g., Derycke et al., 2005) is not necessarily evident. Alternatively, contrasting genetic diversity levels can be obtained experimentally with cultures of selected nematode species. Cultures of species of the *Rhabditis marina* species complex, for instance, can be raised from single gravid females, yielding highly inbred lineages, which can be maintained easily for many generations. It is therefore possible to raise a culture collection of many inbred lineages and to establish experimental populations of very low to high genetic diversity. The advantage of this approach is that similar to the study by Gamfeldt & Kallstrom (2007), "families" can be obtained, and the level of genetic diversity (i.e. the "number of families") for each experimental group can be determined *a priori*.

5.1.2 Measuring EPS production and sediment stability

The main ecosystem function we concentrate on in this approach is measured in terms of EPS production (concentration and composition), and the stability of the sediments. To assess EPS concentration and composition, sediment samples are mixed with distilled water. Exopolymers are very diverse and complex molecules that are found in a wide variety of forms and structures in aquatic ecosystems. The selection of the protocol for their extraction, purification and subsequently for the measurement of their concentration in any sample will depend ultimately on the type of exopolymer studied (e.g., Panagiatopoulos & Sempéré, 2005; Danovaro, 2010). Exopolymers can be found dissolved in the water column or as gels in biofilms and aggregates so that their extraction and quantification is a primary step in assessing their potential availability (Decho, 1990). A description and evaluation of different methods and protocols is well beyond the scope of this paper, hence we will only briefly mention methods that are commonly used in the literature and which offer an acceptable ratio of information obtained to amount of time invested.

The water-extractable fraction (i.e. dissolved or colloidal EPS which are already present in pore-water and unbound to sediment grains) can be analyzed for carbohydrates and proteins following the phenolsulphuric acid protocol (DuBois et al., 1956) and the modified Lowry procedure (Raunkjaer et al., 1994). Carbohydrate and protein concentrations can be measured with a UV/VIS spectrophotometer and their concentrations are deduced from calibration curves assessed from glucose and bovine serum albumin, respectively.

Sediment stability can be estimated through the measurement of the erosion shear stress of the biofilm. Typically, it is possible to measure this using flumes (Jonsson et al., 2006) or *in situ* devices such as the Cohesive Strength Meter (CSM). This device has been used extensively in marine ecosystems since the pioneering work of Paterson (1989) and is an efficient way to estimate sediment erodibility. Mechanical properties of the biofilms in terms of surface adhesion have been developed relatively recently. The method is based on the magnetic attraction of magnetic particles (Magnetic Particle Induction - MagPI; Larson et al., 2009) and is both relatively easy to set up and inexpensive. Specifically, a known volume of ferromagnetic fluorescent particles is spread onto a defined area of the sediment surface. The particles are then recaptured by an overlying electromagnet and the force (magnetic flux) needed to retrieve the particles is determined as a measure of the retentive capacity of the substratum, a proxy for adhesion. This method is suitable for sensitive recording of changes of the surface adhesion of sediments or biofilms.

5.1.3 Assessing community composition

We suggest assessing nematode, prokaryote, and diatom community diversity and composition at a genetic and taxonomic level. Most studies identify nematode species morphologically, nematodes first being mounted on permanent slides (Platt & Warwick, 1988). Species are identified with a microscope, using pictorial (Platt & Warwick 1983, 1988; Warwick et al., 1998) taxonomic keys and primary literature on species descriptions, which is becoming increasingly available in online public databases such as NeMys (Deprez et al., 2005). Morphology based identification of diatoms is achieved by fixing the sampling cores in 4% glutaraldehyde and then embedding in Naphrax after chemically removing organic matter using potassium permanganate. The species composition of the microalgal community is assessed by light microscopy using identification keys (Krammer & Lange-Bertalot, 1986-1991; Lange-Bertalot, 1997; Pankow, 1990; Simonsen, 1962; Underwood et al., 1998; Witkowski et al., 2000). However, species diversity can be assessed using a metagenetic approach as well. The three sets of taxa (nematodes, prokaryotes and diatoms) may be pyrosequenced after distinct sampling procedures. Nematodes are extracted from sediment by sieving (45 μm mesh) and floatation techniques and genotyped using both small and large rDNA subunits (Creer et al., 2010; Porazinska et al., 2009, 2010) and/or mitochondrial genes such as part of the cytochrome oxidase subunit I gene (Derycke et al., 2010). Diatoms are collected on a filter before DNA extraction and amplification using the small rDNA subunit (Cuvelier et al., 2010; Medinger et al., 2010; Quaiser et al., 2010). Prokaryotes are assessed from direct DNA extractions of sediment samples and genotyped using 16S rDNA (Coolon et al., 2010; Xu, 2006). When studying well-documented communities, where sequence data is available for a majority of species, such an approach can yield information on species composition, relative abundances and diversity. In the absence of such a reference database (currently unavailable for any marine assemblage, but this will undoubtedly change in the near future), it can still provide an estimate of diversity in terms of both species richness and evenness. Metagenetic analyses yield information on the different genotypes present, and thus allow simultaneous assessment of species as well as intraspecific diversity, pending proper knowledge on barcoding gaps in the taxa of interest.

5.1.4 Advantages/disadvantages of our system

As a model system for BEF research, our setup combines many advantages. One major advantage from the practical point of view may be that it can be manipulated in small containers and yet contain diversity levels representative of natural communities. The microcosms can easily be incubated under controlled conditions and sufficiently replicated. Nematodes, diatoms and prokaryotes are key players in almost any coastal or stream soft sediment, performing similar essential ecosystem functions across a range of habitats. Therefore they are easily collectable, either at a sandy beach or tidal flat at seashore or from a stream or lake when working with freshwater organisms. A whole experimental setup fits in any average-sized laboratory. If enough space is available, it can even be expanded to bigger mesocosm units including macrofauna as an additional trophic and functional level, which is likely to impact on nematodes, diatoms and prokaryotes through trophic as well as physical interactions (Austen & Widdicombe, 1998; Braeckman et al., 2011). Other extensions are also possible, for example a temperature treatment can be applied to simulate temperature rise as a consequence of climate change. Although the duration of such a short

experiment would not reflect absolute temporal scales of climate change, it may well reflect and therefore be representative for the rates of temperature change long-lived organisms might experience (Petchey et al., 1999). Knowing that genetic diversity enhanced resistance of seagrass *Zostera marina* to climate extremes (Reusch et al., 2005), it would be particularly interesting to plan hypotheses involving genetic diversity of nematodes and increased temperature of the environment.

A further advantage of our system is that it includes different trophic levels, from decomposers (prokaryotes) and producers (diatoms) to grazers (bacterivorous and herbivorous nematodes) and their predators (predatory nematodes), some of the latter being omnivorous rather than strictly predacious (Moens et al., 2004). Moreover, for some setups, we can integrate species of a natural community and not only the dominant species of a given habitat. This is important because even weak interactions can have important stabilizing effects on communities (Berlow, 1999). Contrary to the seagrass system, which alters diversity at the primary-producer level, we can assess the effect of species and genetic diversity also at the consumer level. This is important, as it has been suggested that the stronger top-down control in the sea relative to terrestrial habitats (Shurin et al., 2002) implies that in marine systems ecosystem functions such as primary production may be influenced more by herbivores and predators than by plant diversity (Duffy, 2003; Paine, 2002). In order to track and quantify trophic pathways, pulse-chase experiments which label a particular component and trace transfer to consumers can be designed (Middelburg et al., 2000; Moens et al., 2002; Van Oevelen et al., 2006). Such a characterization and quantification of the relationships among the different components of the community would be an additional improvement, since experimental research on multi-level food webs should not only assess the consequences of species richness and identity on ecosystem processes, but also evaluate trophic cascades and the distribution of interaction strengths within natural communities and how they change with community composition (Duffy, 2002).

However, there are probably three major disadvantages that have to be taken in account when planning the experiments: first, only a limited number of species of nematodes can be cultured with the present methods. Second, the identification of nematodes and diatoms needs considerable expertise, especially when working with field samples containing many different species. And third, the design essentially relies on closed microcosms, hence excluding the role of immigration and emigration. Moreover, by bottling aqueous sediments, a system is created which accumulates end products of decomposition and depletes oxygen. As a consequence, the microcosms can only be used for a limited duration, after which treatment effects are likely to become confounded by bottling effects.

6. Conclusions

Our experimental system provides a good alternative to investigate effects of species and genetic diversity in concert. It is easy to setup and contains organisms that are easily accessible. Moreover, it provides the possibility to be extended and address current challenges of BEF experiments. One of these challenges consists in that future BEF studies must go beyond experiments relating some selected species, singly and in combination, to some ecosystem process. Rather, they must address environmental heterogeneity in space or time, which can be captured in long-term studies on one hand, and working with natural communities on the other. Our experimental units as described here are closed systems, however, they can possibly be converted to semi-closed systems and be setup outdoors. Like

this they would not suffer from the bottling effect, therefore allowing longer-term studies, and capturing the natural variation of environmental conditions. The exact methodology for this has still to be established, but such a system may yield promising results. As the experiment of, e.g., Cardinale & Palmer (2002), very elegantly shows, disturbance may dampen strong single-species effects. It is more probable that changing environmental conditions allow resource partitioning among species, and that under natural conditions, such disproportionate key species effects are greatly reduced allowing stronger diversity effects *per se* (Stachowicz et al., 2008). Moreover, there are many possibilities to include more organisms, species and/or trophic levels and functional groups in an extended version of our setup. Especially when including macrofauna, the system would more accurately reflect the complex interactions among species and trophic levels as they occur in nature.

Our experimental approach will contribute to the understanding of indirect mechanisms leading to biodiversity effects on ecosystem processes. The integrative insight in the interactions among the different levels and the consequences that changes in one level may have on the others and on the system as a whole, may offer the possibility for adequate decisions about conservational priorities. As shown by the experiment by Lankau & Strauss (2007), genetic and species diversity are inherently linked to one another. Therefore, conservation of species diversity may also depend on the maintenance of the processes that sustain genetic diversity. Although BEF studies are designed to understand general patterns and processes, rather than provide solutions to applied conservation problems (Duffy, 2009), they have provided fundamental inputs. The many studies on plant systems for example provided the background at Tijuana River National Estuarine Research Reserve, where a functional ecosystem needed to be restored (Callaway et al., 2003). Just as in many plant studies experimental plantings of differing species diversity were set up, and as a result, biomass and accumulation of nitrogen increased with increasing species diversity (Callaway et al., 2003). As such, our experimental system may offer valuable input for new conservation strategies.

We think that the integrative experimental system as we propose it can be a promising direction for future BEF studies focusing on benthic systems and potential applications for conservational efforts. Today's conservational effort concentrates mainly on identifying and protecting hotspots of species diversity. However, results of such integrative studies will show if the consideration of all organizational levels, as well as the functioning of the whole system, may provide an alternative approach in order to take the best conservation decision under given circumstances. Although BEF experiments conducted to date are likely to underestimate the importance of biodiversity to ecosystem functioning and the provision of ecosystem services in the real world (Duffy, 2009), they could offer constructive inputs for the sustainable management of entire communities and ecosystems.

7. Acknowledgements

8. References

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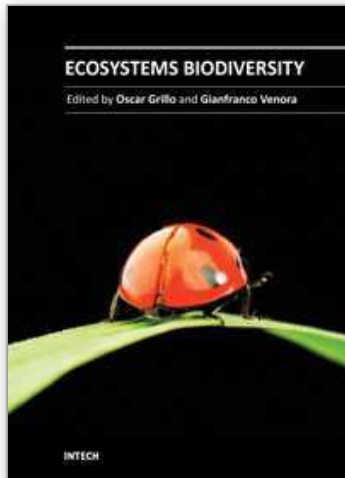
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Ecosystems Biodiversity

Edited by PhD. Oscar Grillo

Ecosystems can be considered as dynamic and interactive clusters made up of plants, animals and micro-organism communities. Inevitably, mankind is an integral part of each ecosystem and as such enjoys all its provided benefits. Driven by the increasing necessity to preserve the ecosystem productivity, several ecological studies have been conducted in the last few years, highlighting the current state in which our planet is, and focusing on future perspectives. This book contains comprehensive overviews and original studies focused on hazard analysis and evaluation of ecological variables affecting species diversity, richness and distribution, in order to identify the best management strategies to face and solve the conservation problems.

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