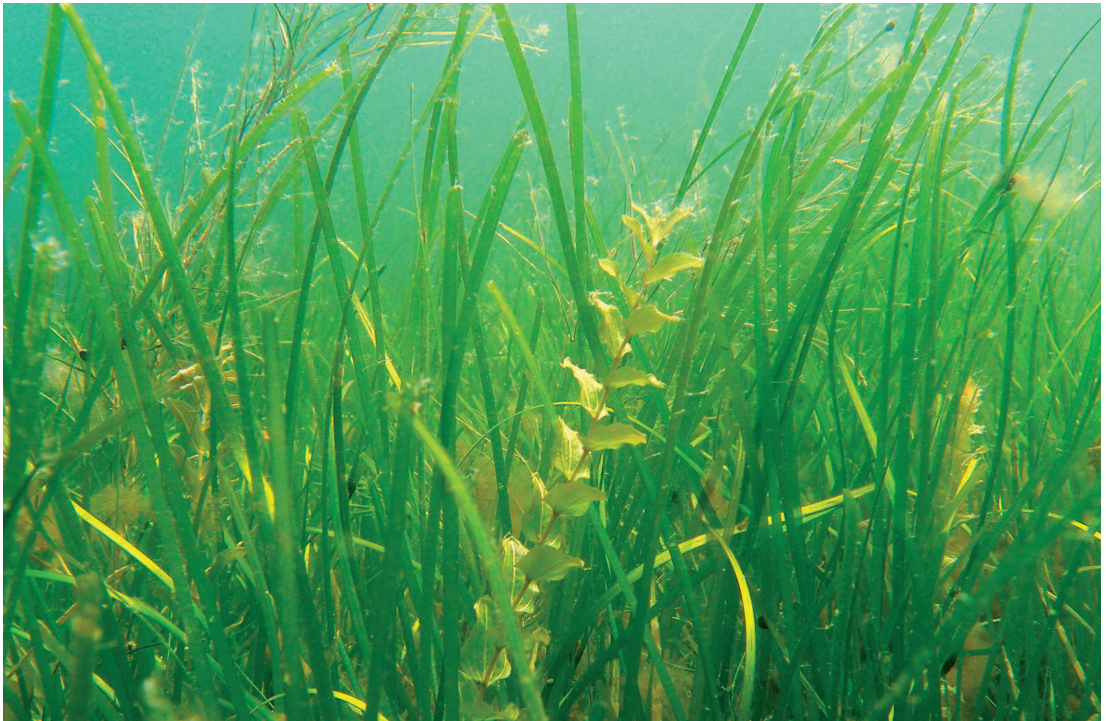


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Biodiversity and ecosystem functioning in angiosperm communities in the Baltic Sea



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Painosalama Oy

Åbo 2013

“We take a tiny colony of soft corals from a rock in a little water world. And that isn’t terribly important to the tide pool.

Fifty miles away the Japanese shrimp boats are dredging with overlapping scoops, bringing up tons of shrimps, rapidly destroying the species so that it may never come back, and with the species destroying the ecological balance of the whole region.
That isn’t very important in the world.

And thousands of miles away the great bombs are falling and the stars are not moved thereby. None of it is important or all of it is.”

John Steinbeck - The Log from the Sea of Cortez (1951)

Abstract

The biological variation in nature is called biodiversity. Anthropogenic pressures have led to a loss of biodiversity, alarming scientists as to what consequences declining diversity has for ecosystem functioning. The general consensus is that diversity (e.g. species richness or identity) affects functioning and provides services from which humans benefit.

The aim of this thesis was to investigate how aquatic plant species richness and identity affect ecosystem functioning in terms of processes such as primary production, nutrient availability, epifaunal colonization and properties e.g. stability of *Zostera marina* subjected to shading. The main work was carried out in the field and ranged temporally from weeklong to 3.5 months-long experiments. The experimental plants used frequently co-occur in submerged meadows in the northern Baltic Sea and consist of eelgrass (*Z. marina*), perfoliate pondweed (*Potamogeton perfoliatus*), sago pondweed (*P. pectinatus*), slender-leaved pondweed (*P. filiformis*) and horned pondweed (*Zannichellia palustris*).

The results showed that plant richness affected epifaunal community variables weakly, but had a strong positive effect on infaunal species number and functional diversity, while plant identity had strong effects on amphipods (*Gammarus* spp.), of which abundances were higher in plant assemblages consisting of *P. perfoliatus*. Depending on the starting standardizing unit, plant richness showed varying effects on primary production. In shoot density-standardized plots, plant richness increased the shoot densities of three out of four species and enhanced the plant biomass production. Both positive complementarity and selection effects were found to underpin the positive biodiversity effects. In shoot biomass-standardized plots, richness effects only affected biomass production of one species. Negative selection was prevalent, counteracting positive complementarity, which resulted in no significant biodiversity effect. The stability of *Z. marina* was affected by plant richness in such that *Z. marina* growing in polycultures lost proportionally less biomass than *Z. marina* in monocultures and thus had a higher resistance to shading. Monoculture plants in turn gained biomass faster, and thereby had a faster recovery than *Z. marina* growing in polycultures. These results indicate that positive interspecific interactions occurred during shading, while the faster recovery of monocultures suggests that the change from shading stress to recovery resulted in a shift from positive interactions to resource competition between species.

The results derived from this thesis show that plant diversity affects ecosystem functioning and contribute to the growing knowledge of plant diversity being an important component of aquatic ecosystems. Diverse plant communities sustain higher primary productivity than comparable monocultures, affect faunal communities positively and enhance stability. Richness and identity effects vary, and identity has generally stronger effects on more variables than richness. However, species-rich communities are likely to contain several species with differing effects on functions, which renders species richness important for functioning. Mixed meadows add to coastal ecosystem functioning in the northern Baltic Sea and may provide with services essential for human well-being.

Key words: Species richness, species identity, primary production, selection effect, complementarity, angiosperm assemblage, multitrophic effects, resistance, recovery, Baltic Sea

Sammanfattning

Biologisk mångfald eller biodiversitet innefattar den naturliga variation som finns från molekyllära skalor till landskap. På grund av antropogena effekter har förlusten av biologisk mångfald ökat och samtidigt också oron över hur detta påverkar ekosystem och kopplingen till ekosystemfunktioner. Diversitet (t.ex. artantal eller artsammansättning) anses allmänt påverka ekosystemfunktioner och således även förse människan med ekosystemtjänster.

Syftet med denna avhandling var att studera hur akvatiska växters artantal och artsammansättning påverkar ekosystemprocesser såsom primärproduktion, kolonisering av epifauna och ekosystemegenskaper såsom stabilitet hos *Zostera marina* under skuggning. Delarbetena bestod av fältexperiment (1 vecka till 3,5 månad långa). Växterterna som användes i experimenten; ålgräs (*Z. marina*), ålnate (*Potamogeton perfoliatus*), borstnate (*P. pectinatus*), trådnate (*P. filiformis*) och hårsärv (*Zannichellia palustris*) är vanligt förekommande arter i undervattensängar i norra Östersjön.

Resultaten visar på att växtartantal endast hade svaga effekter på samhällsvariabler hos epifauna men stor betydelse för antalet arter och funktionell diversitet hos infauna. Växtartsammansättningen däremot påverkade märlkräftors (*Gammarus* spp.) densitet som var högre i växtbestånd där *P. perfoliatus* förekom. Beroende på startstandardiseringsenheten så hade växtartantal olika effekter på primärproduktion. Då skottäthet användes som startstandardiseringsenhet, ökade växtartantalet på skottätheten hos tre av fyra arter och även på växtbiomassaproduktionen. Positiva komplementaritet- och selektionseffekter var bakomliggande mekanismer som påverkade den positiva biodiversitetseffekten för biomassaproduktion. Då startbladbiomassan standardiserades påverkade artantal endast en arts biomassaproduktion. Positiv komplementaritet neutraliserades av negativ selektion och positiva biodiversitetseffekter kunde inte urskönjas. Växtartantalet påverkade stabiliteten hos *Z. marina* i och med att *Z. marina* i flerartsbestånd förlorade mindre biomassa i proportion till *Z. marina* i enartsbestånd och hade därmed en högre motståndskraft mot skuggning. Däremot så ökade *Z. marina* sin biomassa fortare i enartsbestånd än i flerartsbestånd och hade således en snabbare återhämtning efter skuggning. Resultaten tyder på att positiva mellanartsinteraktioner var rådande under skuggning men eftersom *Z. marina* återhämtade sig snabbare i enartsbestånd är det möjligt att mellanartskonkurrens dominerade under återhämtningsperioden.

De erhållna resultaten visar att växtartsdiversitet är viktig för ekosystem och kopplingen till ekosystemfunktioner och de bidrar till den ökande kunskapen om växtartsdiversitet som en viktig komponent i akvatiska ekosystem. Artrika växtsamhällen upprätthåller en högre primärproduktion än jämförbara enartsbestånd, påverkar djursamhällen positivt och ökar stabiliteten. Effekter av artantal och artsammansättning varierar dock och artsammansättningen påverkar fler variabler än artantal. Artrika bestånd innehåller emellertid sannolikt fler arter som kan upprätthålla flera funktioner och utgör därför också en viktig del i hur väl ekosystem fungerar. Undervattensängar med hög växtmångfald har en viktig roll i kustekosystemens koppling till ekosystemfunktioner i norra Östersjön. Således, kan de bidra till upprätthållandet av ekosystemtjänster som är nödvändiga för människans välmående.

Nyckelord: Artantal, artsammansättning, primärproduktion, selektion, komplementaritet, fröväxtbestånd, multitrofiska effekter, motståndskraft, återhämtningsförmåga, Östersjön

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List of original papers

The thesis is based on the following articles, which are referred to by their Roman numerals in the text

- I **Gustafsson C & Boström C** (2009) The effects of plant diversity and composition on epifaunal colonization in brackish angiosperm assemblages. *J Exp Mar Biol Ecol* 382: 8-17
- II **Gustafsson C & Boström C** (2011) Biodiversity affects ecosystem functioning in aquatic angiosperm communities. *Oikos* 120:1037-1046
- III Salo T, **Gustafsson C & Boström C** (2009) Effects of plant diversity on primary production and species interactions in brackish water angiosperm communities. *Mar Ecol Prog Ser* 396: 261-272
- IV **Gustafsson C & Boström C** Neighboring plants influence the stability of eelgrass (*Zostera marina*) subjected to shading. *Manuscript*.

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1. INTRODUCTION

In this thesis, the relationship between biodiversity and ecosystem functioning in aquatic angiosperm communities was investigated. Specifically, the effects of plant species richness and identity on ecosystem processes such as primary production, nutrient availability and epifaunal colonization were scrutinized. In addition, the stability of a plant species subjected to shading was studied. In the following summary biodiversity and ecosystem functioning is discussed, further addressing how this topic links to aquatic plant community functioning in the Baltic Sea.

Biodiversity is defined as all natural variation within and among different biological levels ranging from molecules to biomes (Huston 1994). Thus, diversity components may include genes, traits, species or habitats, although research has mostly focused on species richness (Diaz & Cabido 2001), as it is a simple and convenient measure of biodiversity (Tilman et al. 2001). Diversity can be divided into α diversity, which is defined as local richness, for example populations in patches or communities within-habitats, β diversity, which is the change in diversity in local populations or communities between habitats, and γ diversity that incorporates both α and β diversity and refers to regional diversity (Magurran 2004). Ecosystem functioning is defined as the “activities, processes, or properties of ecosystems that are influenced by its biota” (Naeem et al. 2002) with biota including all living things ranging from specific elements of diversity to the complex web of biotic factors, such as species interactions and community structure. Often, ecosystem functions are defined as being ecosys-

tem processes that are stocks and fluxes of energy and material, e.g. biomass production, resource use and nutrient cycling, ecosystem properties such as stability of ecosystem processes and ecosystem values (goods and services) for example provisioning of food and climate regulation that are beneficial to humans (Naeem et al. 2002, Giller et al. 2004, Paterson et al. 2012).

The relationship between biodiversity and ecosystem functioning is thought to result from species richness and identity effects (Hooper et al. 2005, Stachowicz et al. 2007). A richness effect can be observed as a polyculture performing better or worse than the average performance of its component species in monocultures and it can be divided into selection and complementarity effects. The selection effect can be observed when species with a particular trait or set of traits dominate a certain function through a selective process (Loreau 2000, Diaz & Cabido 2001), thus assuming that there is a positive relationship between competitive success and how dominantly species perform a process (Hooper et al. 2005). Complementarity effects consist of positive interactions between species such as facilitative mechanisms and resource partitioning (Loreau 2000). Resource partitioning may arise from the fact that a diverse community has a larger range of different traits that renders it possible for species to be temporally and spatially more efficient in their resource use (Diaz & Cabido 2001).

Identity (composition) effects occur when species assemblages with equal richness but differing composition, perform differently (Stachowicz et al.

2007). Such effects may arise when a species drives a certain process due to a specific trait. For example, the N_2 -fixing ability among legumes may increase the community biomass production (Hooper & Vitousek 1997, Marquard et al. 2009). Consequently, the presence of such species therefore affects a certain function to a greater extent than species richness in itself (Benedetti-Cecchi & Maggi 2012).

One definition of ecosystem stability is that a system is stable if variables of interest return to an initial equilibrium after a perturbation (Pimm 1984). Stability of ecosystem functioning can be measured in several ways and the most frequently measured are for example the variability in time (temporal stability) or resistance and recovery of processes to perturbations (Griffin et al. 2009). The impact of diversity on stability may be mediated by positive interactions (Hughes & Stachowicz 2011) and facilitative mechanisms in particular, can be important in maintaining stability of individuals of species (Mulder et al. 2001).

1.1 Biodiversity and ecosystem functioning

In the early 1990s, the anthropogenically induced global loss of biodiversity alarmed scientists because the consequences of such loss for ecosystem functioning were unknown. Thus, researchers from various ecological disciplines begun collaborating, and an ecological paradigm on biodiversity and ecosystem functioning (BEF) was born (Naeem 2002, Cardinale et al. 2012).

Experimental findings from microcosms and grasslands showed that primary production and nutrient utiliza-

tion were enhanced by increasing diversity (Tilman et al. 1996, Hooper & Vitousek 1997). Theoretical work included mathematical models that explained mechanistically how plant diversity affects functioning in grassland communities (Tilman et al. 1997, Loreau 1998) and how diversity and ecosystem stability is related (Doak et al. 1998). The stability-relationship was further examined and diversity was proposed to act as insurance in such that species redundancy increases the reliability of a community in case of disturbance or species loss when remaining redundant species step up and continuously maintain a function or a process (Yachi & Loreau 1999).

Based on several reviews (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006), the conclusion is that biodiversity has positive effects on processes such as primary production and nutrient utilization but responses are variable and usually ecosystem- and disturbance-specific (Balvanera et al. 2006, Cardinale et al. 2011). Diversity also affects food web functioning, but depending on whether top-down or bottom-up mechanisms are considered, the effects are variable (Schmid et al. 2009). Regarding the relationship between biodiversity and stability properties (e.g. stability of ecosystem processes, see Giller et al. 2004), the evidence points to diversity enhancing the temporal stability of communities, while the stabilizing effect of diversity on populations and on resistance and recovery is more equivocal (Griffin et al. 2009). Gradually, the focus of research is switching from species and functional diversity to trait-based research and from within-trophic levels to multi-trophic studies that incorporate diversity effects across

trophic levels (Hector & Bagchi 2007, Naeem et al. 2009a). So far, multifunctionality, which means that species provide multiple ecosystem processes simultaneously, has seldom been incorporated in studies but has increasingly been highlighted as an essential part of future BEF research (Hector & Bagchi 2007, Naeem et al. 2009a).

1.2 Marine biodiversity and ecosystem functioning

The accelerating loss of key ecosystems and species in oceans has increased the demand for marine biodiversity studies. After the beginning of the new millennium, BEF research in marine ecosystems increased (Covich et al. 2004, Worm et al. 2006, Stachowicz et al. 2007) but to date, experimental marine BEF work still lags behind and only constitutes a fraction of the total number of studies (Schmid et al. 2009). Due to the different features of marine (aquatic) and terrestrial ecosystems such as greater openness between and within habitats in terms of material and energy transport and the biogeochemical processes being more dynamic, it was previously believed that biodiversity and ecosystem functioning-relationships would also clearly differ between these systems (Giller et al. 2004). The present consensus is that despite the intrinsic differences between terrestrial and aquatic environments, similar processes underlie BEF relationships (Schmid et al. 2009).

Generalities derived from marine work show that diversity does affect ecosystem functioning but when separating the effects, richness effects are usually weak, while species identity is of greater importance (Stachowicz et al. 2007). According to Gamfeldt &

Bracken (2009), most marine BEF research has focused on consumers; perhaps the role of species identity has been emphasized because a few species such as habitat providers (foundation species) and keystone species have substantial effects on consumers in benthic ecosystems. However, as richness effects become stronger on longer timescales via complementarity mechanisms, generalities have been questioned (Stachowicz et al. 2008), and an increasing need for longer-term experiments has arisen. High richness of diversity entities also affects the stability of marine ecosystems and for example functional group richness enhances the recovery of macroalgal communities subjected to thermal stress (Allison 2004) and genotypic richness increases seagrass resistance and recovery to stress (Hughes & Stachowicz 2004, 2011, Reusch et al. 2005).

1.2.1 The functioning of submerged plant communities

Aquatic plants are considered to be ecosystem engineers because they modify their abiotic surroundings (Jones et al. 1997) and physically affect the environment by, for example, reducing current velocities, wave action and sediment resuspension (Gambi et al. 1990, Boström & Bonsdorff 2000, Madsen et al. 2001). In addition, they enhance biogeochemical processes such as O₂-cycling, nitrification and denitrification rates and thus enhance the biogeochemical cycling in vegetated areas (Caffrey & Kemp 1990, 1991, Borum et al. 2006). Under a changing climate, seagrass beds in particular, have also been recognized as crucial CO₂ sinks (Duarte et al. 2010, Fourquaran et al. 2012).

Seagrasses and other aquatic plants add structural complexity to unvegetated bottoms and increase the primary and secondary production (Duffy 2006, Warfe & Barmuta 2006) through provisioning of substratum for epiphytic growth and shelter for fauna (Orth et al. 1984, Duffy 2006). Diverse macrophyte assemblages (plants and algae) are hypothesized to harbor high faunal diversity through the formation of structurally heterogeneous habitats (Stachowicz et al. 2007). Consequently, structurally complex habitats are likely to sustain high animal diversity by providing more vacant ecological niches to occupy (Parker et al. 2001, Warfe & Barmuta 2006). Structural components of plants e.g. plant biomass, root-rhizome density and shoot area affect the predation pressure and food availability (Orth et al. 1984), as well as increase community attributes such as macroinvertebrate abundances (Warfe & Barmuta 2006, Boström et al. 2010). Complex aboveground plant morphology also increases the accumulation of drift algae (Bell and Hall, 1997) and may thus facilitate both faunal passive settlement and active colonization (Holmquist 1994, Boström & Bonsdorff 2000).

1.3 Interactions in plant communities

Aquatic plants frequently reproduce clonally and compared to terrestrial plants, they are more phenotypically plastic, which has led to a wider array of structural modifications (Sculthorpe 1967, Kautsky 1988). The environmental variables affecting terrestrial and aquatic plant communities differ greatly; terrestrial plants are often water-limited or temperature-stressed, while light availability, nutrient limita-

tion and sediment conditions are more crucial for aquatic plants (Kautsky 1988). Therefore, many aquatic plants are shade-tolerant and adapted to anoxic sediment conditions (Santamaria 2002). However, irrespective of the environment, plants compete for the same basic resources i.e. light, space and nutrients (Kautsky 1991).

Biotic interactions range from competitive to complementary mechanisms that often work simultaneously (Bertness & Callaway 1994, Holmgren et al. 1997, Brooker et al. 2008). As communities are not static, both interactions and biodiversity-functioning relationships are likely to change in strength depending on time and scale for instance during different successional stages or in environments with varying productivity (Tilman 1993, Mouquet et al. 2003). In later successional stages diversity may decrease due to the competition of available resources and only a few dominating species persist (Mouquet et al. 2003). However, after a perturbation, competitive species are usually absent, often due to trade-offs between competitive ability and colonization rate (Tilman 1993) and pioneer species are able to colonize.

Interspecific competition is proposed to be more prevalent in productive environments, whereas positive interactions, such as facilitation, increase in both frequency and strength when the physical environment becomes harsher and disturbances like high grazing pressure or severe drought occur (Bertness & Callaway 1994, Mulder et al. 2001, Brooker et al. 2008). In harsh environments, positive interactions may include habitat amelioration by increasing the oxidization of anoxic sediments or by enhancing the nutrient availability and soil moist-

ness (Brooker et al. 2008). Pioneer species may also facilitate conditions prevailing in primary successional states enabling other species to colonize (Tilman 1993).

The strength of biotic interactions also depends on species traits. Competitive abilities can be enhanced by traits such as individual plant biomass and height (Gaudet & Keddy 1988, Kautsky 1991), while traits such as nitrogen fixation ability can increase species complementarity through resource use (Diaz & Cabido 2001). How these traits are manifested depends on how plants respond to various abiotic and biotic factors i.e. how phenotypically plastic they are (Callaway et al. 2003). Neighboring species can have strong effects on trait plasticity (Callaway et al. 2003), and plastic traits such as resource requirement and uptake (Berg & Ellers 2010), may allow species to co-exist in communities despite resource competition, thus leading to niche complementarity (Ashton et al. 2010). Traits that determine how a species interacts with its environment can be divided into response and effect traits (Violle et al. 2007) e.g. how tolerant a species is to shading or drought (response traits) and which traits in a species reflect its effects on ecosystem processes and properties (effect traits) (Diaz & Cabido 2001, Violle et al. 2007).

1.4 Aquatic plant communities in the Baltic Sea

The seagrass meadows in the Baltic Sea often occur as mixed communities with plant species of both marine and limnic origin (> 10 species) (Kautsky 1988). The high plant diversity makes them more analogous to tropical mead-

ows (Duarte 2000) than to temperate meadows that often consist of mono- or bicultures (Marbá et al. 1996, Duffy 2006).

In the Baltic Sea, only a few seagrass species occur, namely eelgrass (*Zostera marina*), and widgeongrasses (*Ruppia cirrhosa*, *R. spiralis*) but whether *Ruppia* spp. are true seagrass species is unclear (den Hartog & Kuo 2006). Pondweeds (e.g. *Potamogeton perfoliatus*, *P. pectinatus*, *P. filiformis*) and horned pondweeds (*Zannichellia palustris*, *Z. major*) are widespread and often grow mixed with *Z. marina* and *Ruppia* spp. These species differ in their morphological and physiological characteristics (Kautsky 1988) leading to different life strategies ranging from fast-growing competitors (*P. perfoliatus*, *P. pectinatus*) to stress-tolerant biomass storers (*Z. marina*) (Kautsky 1988). However, especially *Potamogeton* spp. are plastic and depending on the exposure they can switch from a competitive to a more stress-tolerant strategy (Kautsky 1987). The different characteristics of the plants also affect interspecific interactions, and species having for example similar rooting depths may compete for nutrients and thus affect each other negatively. On the other hand, the large variation in the rooting depths of species may allow for a wider array of co-existing species and thus promote resource complementarity (Kautsky 1991).

1.5 Anthropogenic threats to benthic vegetation

During the past decades, the Baltic Sea has become increasingly eutrophicated (Bonsdorff et al. 1997). The water transparency in coastal areas has significantly decreased during the past 30

years, while the occurrence of cyanobacterial and macroalgal blooms has increased (HELCOM 2009). The reduced light attenuation has led to severe light-limitation stress for benthic vegetation, and this has been especially noticeable in the changing depth limits of the belt-forming macroalgae, bladderwrack *Fucus vesiculosus* (Törn et al. 2006). Historical data (pre-1950s, Boström & Bonsdorff 1997) on vascular plant distribution from the northern Baltic Sea are non-existing, but data on *Z. marina* from the southern Baltic Sea stretching from the early 20th century to the millennia have shown that eutrophication has decreased the depth limits of *Z. marina* as well, likely due to reduced light attenuation (Boström et al. 2003). The impact of reduced light attenuation has cascading effects on plants, affecting physiology, morphology and biogeochemistry (Fig. 1). For example, the photosynthetic capacity of plants is reduced, which further leads to decreased oxygen-flow from leaves to roots (Hemminga & Duarte 2000). Less oxygen transport in turn, can result in increasing root anoxia and sediment

sulfides (Hemminga 1998, Holmer & Laursen 2002) (Fig. 1). Not only reduced light, but also the increasing amounts of loose-drifting macroalgal mats (Berglund et al. 2003) pose a serious threat for submerged vegetation (den Hartog 1994, Hauxwell et al. 2001). These mats shade (Hauxwell et al. 2001, Rasmussen et al. 2012) and if thick enough (> 9 cm, Rasmussen et al. 2012) suffocate both benthic vegetation and fauna through hypoxia (den Hartog 1994, Norkko & Bonsdorff 1996). In addition to light-limitation, increasing concentrations of ammonium and nitrite in the water column may pose a threat for aquatic vegetation (van Katwijk et al. 1997, Touchette & Burkholder 2007). Submerged plants may not have efficient nitrogen uptake regulation mechanisms in aboveground tissue (van Katwijk et al. 1997). As water column nitrogen concentrations increase, plants must use more carbon (i.e. carbohydrates) to assimilate the accumulated nitrogen and may eventually become carbon-limited, which can ultimately lead to plant death (Touchette & Burkholder 2007).

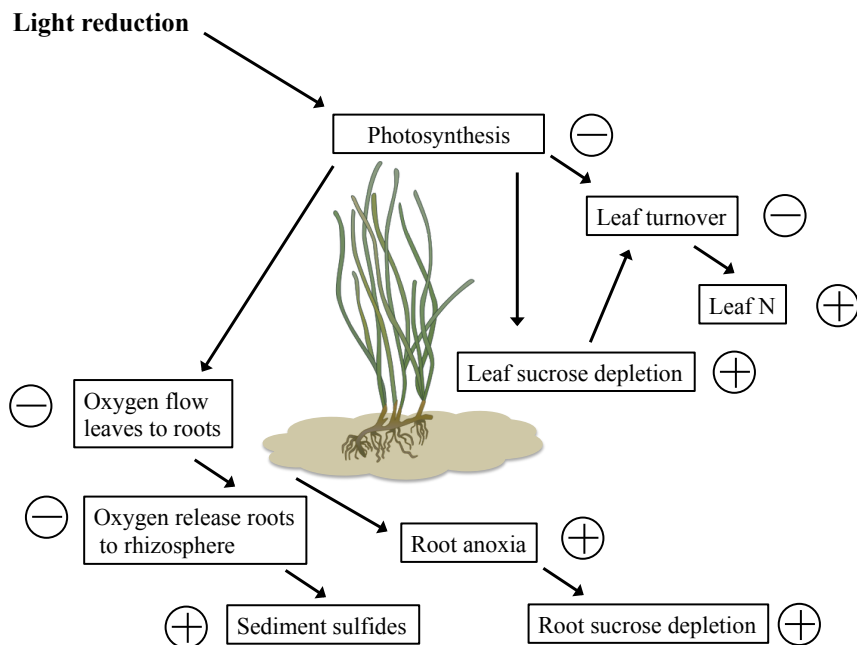


Fig. 1 A schematic picture of plant responses to light reduction. +/- sign denotes general increase/decrease in a variable. Modified from Hemminga (1998). Plant drawing by Tracey Saxby (ian.umces.edu/imagelibrary/).

1.6 Knowledge gaps

BEF studies on marine benthic plant ecosystems to date are few and limited to a couple of studies conducted on seaweeds (Bruno et al. 2005, Boyer et al. 2009) and seagrass (Parker et al. 2001, genetic diversity: Hughes & Stachowicz 2004, Reusch et al. 2005). Thus, there is still a large knowledge gap in how plant diversity affects the functioning of submerged plant communities. Since most of the work concerning plants has been carried out in terrestrial settings, the question whether similar patterns found in terrestrial environments can be observed in submerged grass meadows has risen. The fact that one of the most productive aquatic ecosystems, kelp forests, frequently occur as monospecific stands (Paine 2002) has also brought up the

question whether other aquatic macrophyte communities function analogously. With increasing anthropogenic pressures threatening marine plant communities globally, gaining knowledge of their importance for coastal ecosystem functioning and furthermore for the provisioning of ecosystem services has become an important topic (Waycott et al. 2009). As the Baltic Sea plant meadows most often occur as multi-species assemblages they form a setting that enables experiments to test the relationship between plant diversity and ecosystem functioning in an aquatic ecosystem.

1.7 Aims of the thesis

To fill the abovementioned knowledge gaps, the main aim of this thesis was to investigate how aquatic plant diversity

affects ecosystem functioning in submerged plant communities in the northern Baltic Sea. The overall hypothesis was that plant species rich assemblages have a positive effect on ecosystem functioning. Functioning was measured as several ecosystem processes and as the stability of a plant species subjected to shading. Multitrophic effects of plant diversity, i.e. the influence of plant diversity on epifaunal colonization and infaunal community structure were also investigated.

Specifically, the aims were to investigate:

(1) Whether short-term epifaunal colonization, i.e. the abundance, biomass and diversity of epifauna was affected by plant species diversity (**I**).

(2) The effects of plant diversity on ecosystem processes (primary produc-

tion and nutrient availability) when standardizing experimental units by initial shoot density. The multitrophic effects of plant diversity, i.e. how plant diversity affected the community structure and functional diversity of secondary producers (macroinfauna) were also assessed (**II**).

(3) Plant diversity effects on primary production and nutrient availability when standardizing experimental units by initial aboveground biomass (**III**).

(4) The influence of neighboring plants on the stability and performance (growth, physiology) of *Z. marina* subjected to shading (**IV**).

More specific aims and hypotheses are found in the published articles and manuscript.

2. MATERIALS AND METHODS

2.1 Study site

The Archipelago Sea in the northern Baltic Sea, SW Finland, is characterized by an extensive amount of islands and skerries (>25,000 islands, Granö et al. 1999) (Fig. 2). Especially in the middle and outer archipelago, the shores are often rocky but sandy beaches also occur. Aquatic vascular plants are common in shallow soft-bottomed inner archipelago areas, but also in sheltered and semi-exposed bays in the middle and outer archipelago. The primary study site Fårö Island

(59° 55, 219' N, 21° 47, 711' E, WGS 84) is located in the transition zone between the middle and outer archipelago (Fig. 2) with annual water temperatures ranging between 0–20°C, and salinity between 6–7 psu. The experimental area is semi-exposed with average water depths of 1.5 (I, II, III) – 2.0 m (IV). The nearshore area consists of a sandy, mostly unvegetated bottom with sediment dominated by fine (~ 70% 0.125 mm) and very fine (~5% 0.0062 mm) sand with low organic content.

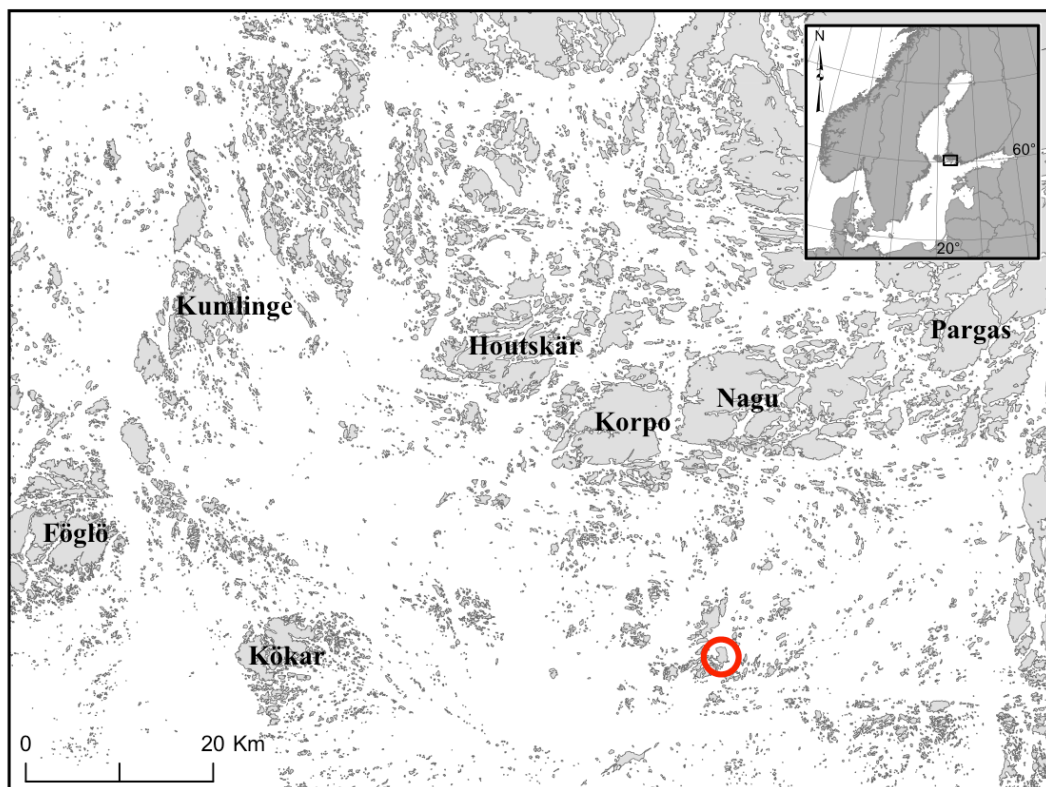


Fig. 2. Map showing the Archipelago Sea, northern Baltic Sea with the red circle marking the experimental site (Fårö Island).

A seagrass meadow dominated by eelgrass *Zostera marina* (L.), perfoliate pondweed *Potamogeton perfoliatus* (L.) and sago pondweed *Potamogeton pectinatus* (L.) grows from 2–5 m depth, while stands of slender-leaved pondweed *Potamogeton filiformis* (Pers.) and horned pondweed *Zannichellia palustris* (L.) grow both within the meadow and as monospecific stands on bare sand. Patchy occurrences of Eurasian water-milfoil *Myriophyllum spicatum* L. and ditchgrass *Ruppia cirrhosa* (Petagna) Grande are also found within the meadow.

2.2 Experimental plant species

Five different vascular plant species were used; *Z. marina*, *P. perfoliatus*, *P. pectinatus*, *P. filiformis* and *Z. palus-*

tris, and all of them propagate through clonal growth in the northern Baltic Sea (Kautsky 1990). These plants were chosen because of their frequent co-occurrence within the depth interval 1–2 m across the study area (pers. obs.), their varying morphologies (Fig. 3), different biomass allocation strategies and productivity patterns (Kautsky 1988). By choosing plant species with such trait differences (Table 1) strong complementary and/or competition effects were expected in **II** and **III**. Differences in above- and belowground structures were also expected to increase the structural diversity of mixed plant assemblages with possible positive effects on colonizing epifauna and infauna (**I**, **II**).

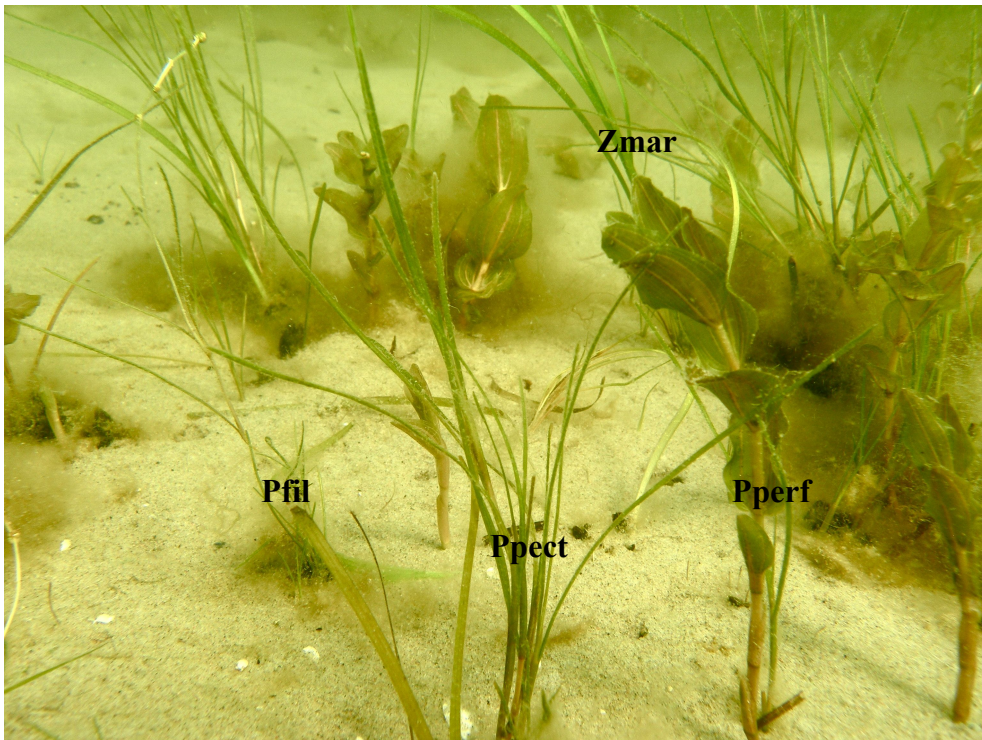


Fig. 3. A polyculture plot consisting of *Zostera marina* (Zmar), *Potamogeton perfoliatus* (Pper), *Potamogeton pectinatus* (Ppect) and *Potamogeton filiformis* (Pfil). The plant abbreviations mark each plant species.

Table 1. Trait differences among the experimental plant species and differences in provisioning of ecosystem processes. Plant species: *Zostera marina*, *Potamogeton perfoliatus*, *Potamogeton pectinatus*, *Potamogeton filiformis* and *Zannichellia palustris*.

Traits/process	<i>Z. marina</i>	<i>P. perfoliatus</i>	<i>P. pectinatus</i>	<i>P. filiformis</i>	<i>Z. palustris</i>
Biomass (g dwt ⁻¹ m ⁻²)	4-33 ¹	0-15 ²	1-28 ^{2,3}	0-18 ²	0-14 ²
Primary production (mg C g dwt ⁻¹ h ⁻¹)	0.2-2.7 ⁴	3.4-7.0 ⁴	0.9-7.2 ⁴	0.9 ⁴	5.0 ⁴
Longevity	Perennial ⁴	Perennial ⁴	Perennial ⁴	Perennial ⁴	Annual ⁴
Canopy height cm	20-100 ^{4,5}	20-200 ^{4,5}	20-200 ^{4,5}	10-30 ^{4,5}	10-30 ^{4,5}
Rooting depth cm	10 ³	10-25 ³	10-25 ³	5-10 ³	2-5 ³
Anchorage	Fast ⁸	Fast ⁸	Fast ⁸	Fast ⁸	Loose ⁸
Reproduction mode	Vegetative growth ^{6,7}	Turions, veg. growth, seeds ⁶	Tubers, veg. growth, seeds ⁶	Tubers, veg. growth, seeds ^{4,5}	Veg. growth, seeds ^{6,8}
Life strategy	Biomass storer ⁴	Competitive ⁴	Competitive ⁴	Ruderal ⁴	Ruderal ⁴
Root oxygen release (μmol O ₂ g dwt ⁻¹ h ⁻¹)	0-9 ^{9,10}	2-99 ⁹	1.5-13 ¹⁰	-	-
Nitrification (nmol cm ⁻³ h ⁻¹)	1-27 ¹¹	0-450 ¹¹	-	-	-

¹Boström et al. 2004, ²Wallentinus 1979, ³Kautsky 1987, ⁴Kautsky 1988, ⁵pers. obs., ⁶Kautsky 1990, ⁷Boström 1995, ⁸Idestam-Almqvist 2000, ⁹Caffrey&Kemp 1991, ¹⁰Sand-Jensen et al. 1982, ¹¹Caffrey&Kemp 1990

2.2.1 *Zostera marina*

Z. marina is a cosmopolitan marine species found in temperate areas. In fully marine areas it often grows in mono- or bicultures (Hughes & Stachowicz 2004), but in the Baltic Sea it co-occurs with numerous limnic plant species (Kautsky 1988). In the south and southwestern parts of the Baltic, *Z. marina* can be found in both exposed and sheltered areas, but in the northern parts it is only found in exposed and semi-exposed sites (Baden & Boström 2001). *Z. marina* has an extensive root-rhizome mat that is used as anchorage (Kautsky 1988). Characteristic for north Baltic populations is the lack of sexual reproduction, i.e. *Z. marina* mainly propagates clonally in this area (Boström 1995, Table 1) The above-ground morphology of *Z. marina* is simple with long ribbon-like leaves, while the belowground parts consist of

a structurally complex rhizome-root mat. It has relatively slower growth (see primary production-rates in Table 1) compared to more competitive species with high production rates such as *Potamogeton* spp. (Table 1). In the northern Baltic Sea, *Z. marina* has the lowest biomass values found throughout its range, which may be due to the low nutrient levels in the sediment (Boström et al. 2004, Baden et al. 2010), low availability of inorganic carbon (Hellblom & Björk 1999) or /and due to lower salinities than the salinity optimum of the species (Nejrup & Pedersen 2008).

2.2.2 *Potamogeton perfoliatus*

P. perfoliatus is a widely distributed species of limnic origin but it survives in salinities up to 12 psu (Wallentinus 1979). In the Baltic Sea, it can be found from sheltered areas with low

wave exposure (Kautsky 1988) to semi-exposed areas. It hibernates with wintering organs, turions that originate from the rhizome (Wallentinus 1979). It reproduces both sexually and vegetatively (Table 1). The morphology of *P. perfoliatus* consists of a robust rhizome with numerous ramets (shoots) having alternate oviform leaves, but morphological characteristics such as branching and rhizome spacer length can vary widely depending on both abiotic and biotic factors (Wolfer & Straile 2004). The extensive rhizome may grow at >20 cm depth in the sediment (Table 1). *P. perfoliatus* is competitive, but it may also be advantageous for neighboring plants due to its elevated capacity of oxygen release to the rhizosphere, which further affects sediment nitrification-denitrification processes (Caffrey & Kemp 1990, Marbá et al. 2006, Table 1). Caffrey & Kemp (1991) showed that the oxygen content in porewater remains high 0.5 mm away from the rhizome and the oxic layer extends to 2 mm from the rhizome, while it only reaches ~ 50 µm around roots of *Z. marina* (Borum et al. 2006). Thus, dense stands of *P. perfoliatus* may oxidize large areas of the immediate rhizosphere.

2.2.3 *Potamogeton pectinatus*

P. pectinatus is a cosmopolitan euryhaline species that is often found in brackish waters with its upper salinity tolerance around 15 psu (Wallentinus 1979). Similarly to *P. perfoliatus*, it hibernates as seeds and tubers (Kautsky 1990) and has various reproduction modes (Table 1). *P. pectinatus* has a robust rhizome with proportionally small roots (Kantrud 1990), but its

aboveground morphology is complex with several branching ramets growing from the rhizome. (Kautsky 1988). The leaves are linearly formed and narrow. *P. pectinatus* is a phenotypically plastic species that can shift its biomass allocation depending on abiotic factors such as wave exposure (Kautsky 1987, Idestam-Almqvist & Kautsky 1995). Thus, when occurring in semi-exposed and exposed sites it allocates proportionally more biomass to its belowground compartments (Kautsky 1987), which in turn may increase the oxygen release from rhizomes and roots (Sand-Jensen et al. 1982), and facilitate the anoxic circumstances found in bottom substrates.

2.2.4 *Potamogeton filiformis*

A small species found in the northern hemisphere that tolerates moderate salinities (≤ 8 psu, Kautsky 1988). It is more exposure-tolerant than the previously mentioned *Potamogeton* spp. and mainly grows on stony or sandy substrate (Wallentinus 1979). *P. filiformis* hibernates through the formation of tubers (Kautsky 1988) and it reproduces varyingly (Table 1). Morphologically it resembles *P. pectinatus* but it is smaller and more slender, having threadlike leaves and frail belowground parts that only penetrate the upper parts of the sediment (Table 1). It has relatively slow growth and low productivity (Kautsky 1988, Table 1). Due to its shallower rooting depths compared to the other species mixed communities with *P. filiformis* may show for example complementary resource use (Kautsky 1991).

2.2.5 *Zannichellia palustris*

Z. palustris is a euryhaline species that occurs in large parts of the world from brackish to freshwater environments (den Hartog & Kuo 2006). It is a short-lived ruderal species (Table 1) that tolerates disturbances such as ice and wave erosions by reproducing rapidly, shedding its seeds and dying (Kautsky 1988). Thus, it reproduces sexually, but during the growing season it also spreads laterally (Idestam-Almqvist 2000, Table 1). *Z. palustris* is often a pioneer species on bare bottoms, where it modifies the habitat through particle trapping and possibly facilitates the succession of other species (Wallentinus 1979). It has numerous short shoots with threadlike leaves that rise from a slender rhizome and it is only loosely attached to the sediment (Table 1) making it susceptible to wind and wave erosion (Idestam-Almqvist 2000). As *Z. palustris* also has a shallow rooting depth, mixed communities with this species may show complementary resource use (Kautsky 1991).

2.3 Field and laboratory work

Field experiments were conducted to investigate how plant diversity affects different ecosystem processes in natural settings by manipulating plant richness and identity. Specifically, the research focused on how the faunal colonization was affected by varying plant diversity (I), and how primary production and nutrient utilization was related to increasing plant diversity (II, III). In addition, the stability of *Z. marina* when subjected to shading was studied in field settings (IV) (Table 2).

All experimental units were standardized according to a substitutive replacement design (Harper 1977, Table

2). Plants were collected from a nearby meadow, kept submerged during the handling, tied to plastic grids and transplanted within six hours. The plants were tied to a grid in a non-random, spatially even pattern and to avoid groupings of the same species, neighboring plants were always heterospecific. The experimental units were then planted ~ 5 cm deep into the sediment using SCUBA. The plots were positioned in a randomized block (I, II, III) or in a completely randomized design (IV). In I, two experiments were carried out; the first in early July and the second in late August to capture temporal differences in epifaunal colonization. In IV, half of the plots were subjected to shading, which was done by installing shading screens (1m²) 60 cm above the sediment. The shading level was ~ 90 % of ambient levels.

One month prior to the termination of the experiments in II and III, sediment cores were sampled to analyze the sediment organic content. Porewater nutrients were also sampled before biomass harvesting in II, III and IV and analyzed for NH₄⁺ and PO₄³⁻ (II, III) in a certified lab. In addition, water column samples (total N and total P) were sampled during the experimental duration.

At the termination of the experiments in II and III or at each sampling event (see Materials and Methods in IV) all plant material (above- and belowground biomass) was harvested and plants of each species were cleansed, counted, divided into above- (shoots) and belowground biomass (roots, rhizomes) and dried to a constant weight (60°C, 48 h). The youngest parts of different plant compartments were separated for CNP-determination (II, IV), total sulfur content and stable isotopic

composition ($\delta^{34}\text{S}$) (**IV**). Furthermore, to determine carbohydrate concentrations (**IV**), a whole shoot with attached rhizome and roots was separated, freeze-dried, ground to a fine powder and extracted for soluble sugars (sucrose).

In **I**, epifauna was sampled by enclosing whole plots in net bags, and fauna was sieved (0.5 mm), counted, identified and dried to constant weight (dwt, 60°C, 48 h). In **II**, infaunal cores were collected from plots simultaneously with biomass harvesting. Samples were sieved (0.5 mm), sorted and fauna was identified to the lowest taxonomical level. Animal biomass (dwt) was determined after drying (60°C, 48 h).

2.4 Data analysis

In **II**, **III**, **IV** the biomass production was calculated as the relative biomass change (dwt) from the experimental initiation to termination (**II**, **III**) or sampling events (**IV**) by converting percentage values to log-ratios. To partition diversity effects into richness and identity (**I**, **II**) planned comparisons (**I**) or nested ANOVA (**II**) were used (Table 2). Linear regression was used to explore the relationship between plant species richness and response variables (**I**, **II**, **III**) (Table 2). In addition, the multivariate tests ANOSIM and SIMPER were utilized in **I** to describe differences in epifaunal community composition. Response variables in **IV** showed both normal and gamma distributions and generalized linear models that allow for other probability distribution types (Quinn & Keough 2002) were used to investigate the effects of shading on response variables (Table 2). Models with lower deviance values

were chosen and the goodness-of-fit was assessed by checking for AIC and AICC (Norušis 2010). The models were based on the Maximum-Likelihood Method and the hypothesis testing on the Wald χ^2 -test. Normally distributed variables with heterogeneous variances were tested in a 2-way heterogeneous variance model (Littell et al. 2006). Based on lower goodness-of-fit statistics (AIC, AICC) and significantly smaller -2 Residual Log Likelihood-values, heterogeneous variance models were chosen over the original model (Littell et al. 2006).

To investigate how shading and plant richness affected the performance (growth, physiology) of *Z. marina* and how different responses were causally related in **IV**, structural equation modeling (SEM) was conducted (Grace 2006). First, a null model was built without pathways, where after paths were added one at a time. After gaining a model with high fit, it was trimmed to the most parsimonious model by removing pathways based on a χ^2 -test and by comparing goodness-of-fit values (Grace 2006). Statistical analyses were performed on SPSS 13.0, 19.0, Amos 19.0, Primer 6.1.6 and SAS 9.2.

To assess plant performance, proportional deviations, D_i , of plant species' yield from expected values were calculated (Loreau 1998) (**II**, **III**) and to partition net biodiversity effects, the additive partitioning method by Loreau & Hector (2001) was used (**II**, **III**, Table 2). Both calculations were based on the above- and belowground and total biomass production. In the additive partitioning method, the expected yields of species in polycultures are compared to observed yields of species in polycultures. The expected values are derived from monoculture yields.

The method identifies to what extent complementarity and selection effects underlie a net biodiversity effect and all mechanisms can be either positive or negative (Loreau & Hector 2001), e.g. a positive net effect implies that the production is higher in polycultures than expected from the production in monocultures. In **IV**, the stability of *Z. marina* subjected to shading was assessed by calculating the resistance to shading and recovery after shading

(van Ruijven & Berendse 2010) (Table 2) when growing in mono- and polycultures, respectively.

To investigate how plant diversity affected the functions of the infaunal community, species were divided into functional groups (Pearson & Rosenberg 1987) (**II**). Species were classified according to their feeding habit, feeding mode and mobility type.

Table 2. Summary of the experimental settings of the different field experiments and the numerical analyses of results from papers I-IV

	Paper I	Paper II	Paper III	Paper IV
Standardization unit	18 g aboveground biomass	24 individual ramets	30 g aboveground biomass	24 individual ramets
Plant species	<i>Zostera marina</i> <i>Potamogeton perfoliatus</i> <i>Potamogeton pectinatus</i>	<i>Z. marina</i> <i>P. perfoliatus</i> <i>Potamogeton filiformis</i> <i>Zannichellia palustris</i>	<i>Z. marina</i> <i>P. perfoliatus</i> <i>P. pectinatus</i>	<i>Z. marina</i> ³ <i>P. perfoliatus</i> <i>P. pectinatus</i> <i>P. filiformis</i>
Experimental duration	I: 7 d II: 6 d	15 weeks	14 weeks	11 weeks
Response variables	Epifaunal abundance Epifaunal species number Shannon's index H' Pielou's evenness index J' Epifaunal community composition <i>Gammarus</i> spp. abundance <i>Gammarus</i> spp. biomass	Shoot density production Biomass production Porewater nutrient concentration Tissue nutrient conc. Infaunal species abundance Epifaunal species biomass Infaunal species diversity Infaunal functional diversity	Shoot density production Biomass production Porewater nutrient conc.	Biomass production Leaf growth Tissue carbohydrate conc. Tissue sulfide conc. Tissue nutrient conc. Porewater nutrient conc.
Factors	Richness (3 levels) Composition (7 levels)	Richness (3-4 levels) ¹ Composition (14 levels)	Richness (3-4 levels) ² Composition (7 levels)	Shading (2 levels) Richness (2 levels)
Numerical analyses	1-way ANOVA Linear regression Randomization analysis 1-way ANOSIM SIMPER Planned comparisons (Duffy et al. 2005)	1-sample T-test 2-way mixed ANOVA Nested ANOVA Linear regression Proportional deviation D _i (Loreau 1998) Additive partitioning (Loreau & Hector 2001)	1-sample T-test 1-way ANOVA Linear regression Proportional deviation D _i Additive partitioning	Generalized Linear Models 1-way ANOVA Structural equation modeling Resistance, recovery (van Ruijven & Berendse 2010)

¹ = 3 (plant responses), 4 (infauna, porewater nutrients), ² = 3 (plant responses), 4 (porewater nutrients),

³ = responses measured of this species

3. MAIN FINDINGS

Plant richness and identity both affected the functioning of angiosperm communities and for most ecosystem processes, the effects were positive (Fig. 4). Some response variables e.g. total shoot density of plots, amphipod population structure and plant community biomass production were strongly affected by the identity of plants (**I**, **II**, **III**), while plant richness was of more importance for the individual shoot

densities of species and for the structural and functional diversity of infauna (**II**). Plant diversity (not separated into richness or identity effects) also had a positive effect on the resistance of *Z. marina* to shading (**IV**). The results demonstrate that both plant richness and identity have important effects on plant community functioning and both play a role in maintaining these processes

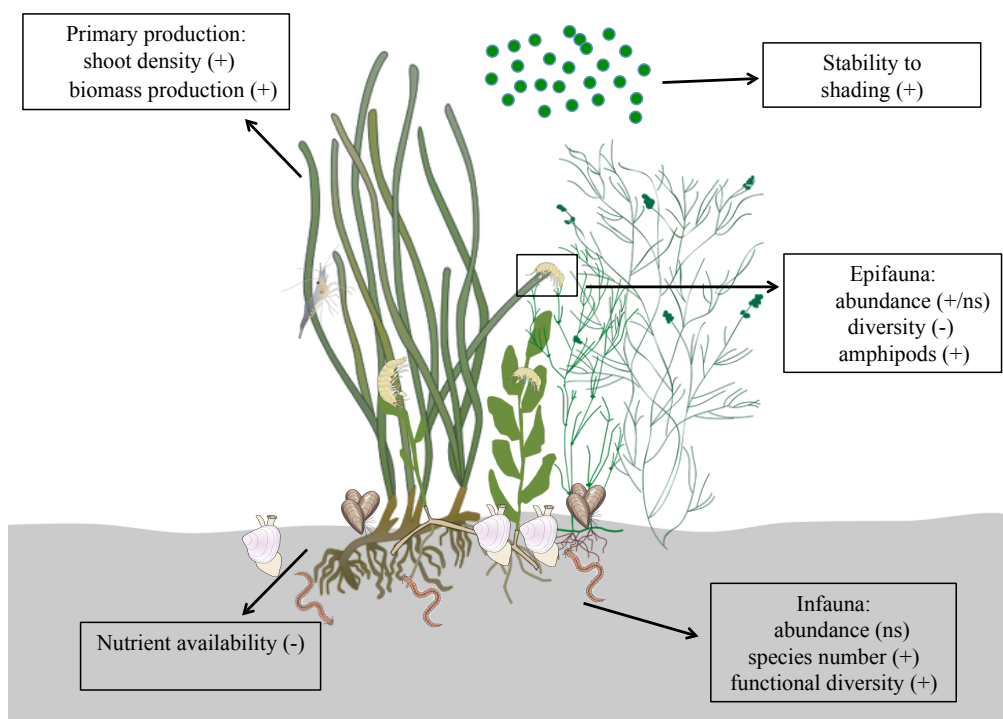


Fig. 4. Effects of plant diversity (richness or identity or both) on ecosystem processes and properties. + = significantly positive effect, - = significantly negative effect, ns = non-significant. Stability refers to resistance to shading of *Zostera marina* growing in polycultures (**IV**). Epifaunal abundance only showed a significantly positive relationship to plant richness during one time event (August, see Fig. 1 in **I**). Plant species in the drawing represent *Z. marina*, *Potamogeton perfoliatus*, *P. pectinatus* and *Zannichellia palustris*. Plant and animal drawings from www.ian.umces.edu/imagelibrary/.

3.1 Plant growth in species-rich plant assemblages

The investigated plant species showed varying effects on increasing plant diversity. Depending on whether the standardized start unit was above-ground biomass or shoot density, the additive partitioning of diversity mechanisms revealed that the net biodiversity effects differed in strength (Fig. 5).

When initial starting biomass was used as a standardization unit (III), negative selection effects were prevalent, counteracting the positive complementarity effects resulting in no significant net effects (Fig. 5a,b). Based on biomass production, plant species performance (D_i) showed positive values for some treatments but the significance disappeared after correcting for multiple comparisons (see Table 3 in III). In general, richness effects were species-specific, affecting biomass and vegetative propagule production of only specific species, while species identity affected total community performance and e.g. *Z. marina* increased both the belowground and the total biomass production in plant assemblages (III).

In II, three of four investigated plant species had a higher change in

shoot densities in polycultures compared to monocultures. Thus, richness had strong effects on the species-specific ramet production, while the total shoot density in plots was determined by species identity. However, richness did not enhance the change in above- and belowground biomass production of individual species. Nevertheless, when pooling bi- and triculture biomasses, both complementarity and selection effects lead to significantly positive net effects in tricultures (Fig. 5d). Based on biomass production, the individual species performed differently (D_i) and *Z. marina* showed a significantly better performance, while the performance of *Z. palustris* was lower than expected (see Table 2 in II). *P. perfoliatus* also showed positive values but these differences became borderline significant after correcting for multiple comparisons. The significant values indicated that *Z. marina* and *P. perfoliatus* to some extent benefited from growing with heterospecifics, while the opposite was true for *Z. palustris*. Possibly, some of the species had higher production in polycultures than expected because of less competition among heterospecifics compared to conspecifics.

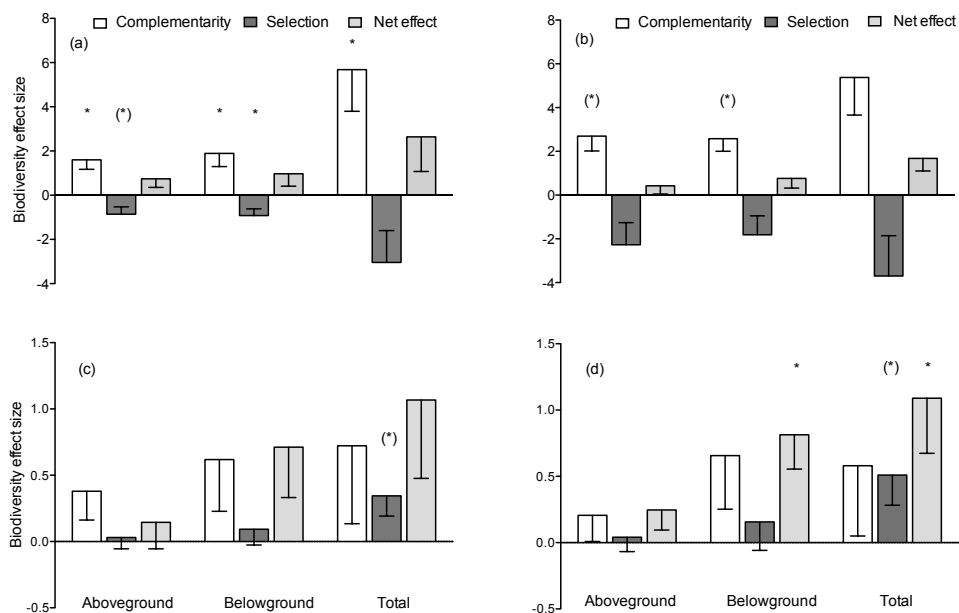


Fig. 5. Additive partitioning of aboveground, belowground and total biomass production in the biomass standardized experiment (III) in (a) bicultures and (b) tricultures and in the shoot density standardized experiment (II) in (c) bicultures and (d) tricultures. Asterisks denote significant deviations from 0 ($p < 0.016$, corrected for multiple comparisons), while asterisks in parentheses show borderline significant differences ($0.05 < p < 0.016$) after multiple comparisons.

3.2 Effects of plant diversity on nutrient availability and resource use

The porewater NH_4^+ availability decreased with increasing richness, suggesting that the resource uptake was more efficient in diverse plant assemblages (II). However, the relationship was curvilinear and the lowest average nutrient concentration was found in bicultures (Fig. 4 in II). Despite a curvilinear relationship in III, the lowest nutrient availability was found in monocultures, thus implying that plant richness had no clear effect on the sediment ammonium concentrations (Fig. 7 in III). The PO_4^{3-} -availability did not decrease with richness in either study, though there was a decreasing trend in porewater concentrations in II.

For three of four plant species, the leaf tissue became more depleted in nutrients (N, P) with increasing richness, suggesting less available nutrients for the plants. The leaf tissue of *Z. marina*, however, showed an opposite pattern, and increased in N and P with increasing richness (II), suggesting that nutrients became more available for this species with increasing richness.

3.3 Multitrophic responses to increasing plant diversity

Plant richness weakly affected epifaunal community variables and showed strong temporal variability. The epifau-

nal community composition did not vary between treatments but differed temporally and two dominating taxa; *Cerastoderma glaucum* and *Hydrobia* spp., contributed most to the temporal dissimilarity (17% and 13 % respectively). In general, epifaunal diversity (H') decreased with increasing richness. This was mainly due to the numerical domination by the two above-mentioned taxa during each experiment (>80 %, see Table 2 in I). In July, the colonization study coincided with the settlement of *C. glaucum* and in August, faunal abundances were dominated by *Hydrobia* spp. (see Fig. 2 in I). Total abundance showed a positive trend in July and increased in August (Fig. 1 in I). In contrast to plant richness and community variables, plant identity had strong effects on amphipods (*Gammarus* spp.), of which abundances were higher in plant assemblages with *P. perfoliatus* (see Fig. 4 and Table 4 in I).

Infaunal abundance and biomass were unaffected by plant richness and identity, but total species and taxon richness increased with increasing plant richness (Fig. 5a in II). Likewise, the total number of functional groups responded to plant richness, having higher number of functional groups present in bicultures compared to monocultures (11 % increase). The average number of species and taxa per functional group ranged from 1.38 in unvegetated treatments to 1.46 in bi- and tricultures, with no significant differences between treatments (nested ANOVA: species richness $F_{3,60} = 1.21$, $p > 0.05$, species identity $F_{12,60} = 0.65$, $p > 0.05$). This was incorrectly shown in Fig. 5c in II (erratum Fig. 5c in beginning of II), which in fact shows the sum of species and taxa representing functional

groups. The sum of species and taxa increased with plant richness in such that the pool of species and taxa comprising the functional groups found was higher in polycultures than monocultures. The sum of species and taxa was higher than the total species and taxon richness because some species represented several functional groups (e.g. *Macoma baltica*, which is both a suspensivore and a surface-feeding detritivore). As plant richness did not increase the average number of species and taxa per functional group, infaunal species redundancy was not enhanced. Hypothetically, this could occur when increasing plant richness would support a higher infaunal diversity, and thus increase the chance of more species belonging to the same functional groups

3.4 Stability of *Z. marina* subjected to shading

Z. marina grown in both mono- and polycultures lost biomass during shading (Fig. 3 in IV) but in mixed assemblages *Z. marina* had a greater resistance to shading than monoculture plants. However, after a recovery time of 4 weeks, the monoculture plants had gained biomass faster, i.e. their recovery was faster than the recovery of polyculture plants (Fig. 4 in IV). Shading reduced plant carbohydrate contents in both diversity treatments by 80-95 % (Fig. 5 in IV). However, the recovery to pre-shading levels was discernible after 4 weeks, suggesting that the plants recovered fast from shading.

The SE model demonstrated that shading affected several response variables both directly and indirectly, while plant richness only had a direct effect on root sulfide content (Fig. 6 in IV).

Shading increased the rhizome sulfide content, which had a strong negative effect on shoot density. Plant species richness had a negative effect on root sulfide content, thus suggesting that

positive interactions such as increased oxygenation of the rhizosphere occurred, which may have reduced the sulfide invasion into the roots.

4. DISCUSSION

4.1 Plant diversity and ecosystem functioning

4.1.1 Effects of plant diversity on plant-related processes

Plant diversity in submerged assemblages affected several ecosystem processes positively (Fig. 4). Plant identity had a strong effect on the total plot shoot density, while richness affected species-specific densities (**II**). However, the change in biomass production was not affected by richness, which may have been due to the fact that for three of four species, the average shoot biomass showed a negative slope in relation to shoot density, indicating that the plants were close to reaching their constant final yield (White & Harper 1970, Weiner & Freckleton 2010). Plant biomass and shoot density are only positively related up to a certain point, where after biomass does not increase despite increasing shoot density. Starting shoot densities used in **II** and **IV** were in the range of natural shoot densities (*Z. marina*: 70–500 shoots m^{-2} , *P. perfoliatus*: 10–200 shoots m^{-2} , *P. pectinatus*: 40–500 m^{-2} and *Zannichellia palustris*: 50–700 m^{-2} respectively, Idestam-Almqvist 2000, Wolfer & Straile 2004, Boström et al. 2006) and were thus expected to produce realistically dense communities and reach their constant final yield. In monocultures, constant final yield may lead to self-thinning. This is a density-dependent mechanism, which occurs

when the mortality of individuals increase because of intraspecific competition for resources (e.g. light and nutrients) (Wolfer & Straile 2004). Populations of *P. perfoliatus*, *P. pectinatus* and *Z. marina* all show some form of self-thinning (Wolfer & Straile 2004, Olesen & Sand-Jensen 1994). When a mixed plant stand has reached its constant final yield, plant species use all available resources (Weiner & Freckleton 2010) and thus, species likely interact, whether through competition or complementarity (Harper 1977). The partitioning of diversity effects for biomass production in **II** and **III** show that both kinds of interactions occurred in bi- and tricultures (Fig. 5).

Negative selection effects were more common in **III** compared to **II**, which may have been due to the different initial standardizing units (Table 2). Aboveground biomass and related traits such as plant height are strongly linked to a plant's competitive ability (Gaudet & Keddy 1988). The increase in both shoot density and biomass production of *P. perfoliatus* with increasing richness may have caused negative selection effects on biomass production. *P. perfoliatus* had low monoculture biomass, which resulted in lower-than-average monoculture biomass (see Loreau & Hector 2001 and **III**). As this species is a very competitive species that develops high biomass rapidly (Kautsky 1988), it likely caused negative selection effects in polycultures.

However, as strong positive complementarity effects also affected biomass production, some form of complementary and/or positive interactions also occurred despite dominance by one species. Because the net biodiversity effects were stronger in **II** compared to **III**, this could indicate that planting density may have had an effect on how biodiversity effects were manifested. Planting density has been shown to influence biodiversity effects (He et al. 2005, Marquard et al. 2009, Stachová et al. 2012) through for example changes in plant composition that further result in altered competitive interactions (He et al. 2005). Thus, it is not surprising that the patterns differed somewhat between **II** and **III** (Fig. 5) and apparently the net biodiversity effects became stronger when including an additional diversity level (4 species in **II** vs. 3 species in **III**).

Despite including species with differing morphological traits (e.g. rooting depth, Table 1), which hypothetically could have lead to increased nutrient uptake in the plant community and decreasing nutrient availability due to resource complementarity (van Ruijven & Berendse 2005), no strong linear relationship between increasing plant diversity and ammonium availability could be discerned (**II**, **III**). This suggests that: 1) plant richness effects on sediment porewater nutrient concentrations are weak because plants in diverse assemblages do not use available nutrients more completely than in monocultures or 2) they use different nutrient forms acquired from both leaves and roots (Hemminga & Duarte 2000), thus complementing their resource use by the uptake of both nitrate and ammonium (Touchette & Burkholder 2000). Plants growing in

sandy sediments such as the experimental site are often N-limited (Touchette & Burkholder 2000), though phosphorus may also be a limiting nutrient in the northern Baltic Sea (Boström et al. 2004). The C:P ratios increased with richness for all plant species except for *Z. marina* (**II**), which could indicate P-depletion. However, freshwater plants often have greater C:P ratios than seagrasses even though their tissue P-concentrations are similar (Duarte 1992). The C:N content of *Z. marina* decreased with increasing richness (**II**) suggesting that more N was available in polycultures, possibly enhancing its production. This could have been due to for example increased rhizosphere oxidation by neighboring species that ameliorated the nutrient uptake of *Z. marina* (Sand-Jensen et al. 1982). The other plant species showed slightly enhanced C:N ratios with increasing richness, indicating less available nitrogen. However, the C:N ratios were still in the normal range for Baltic Sea plants (Kautsky 1988) and were thus not likely N-depleted.

Although it is clear that angiosperm assemblages perform many functions, it is unclear as to which species traits are important for certain processes. Some species can have higher oxygen release capacity to the sediment due to root porosity and different root morphologies (Jespersen et al. 1998) and also lower root-rhizome respiratory demands (Caffrey & Kemp 1991, Hemminga 1998). Trait differences also add to positive interactions such as facilitation between species, cf. N₂-fixing legumes facilitating other species in terrestrial ecosystems e.g. Tilman et al. 1997. Especially under stressful conditions, such as during light deprivation, neighbor facilitation may play an important

role for the stability of both individuals of species (Mulder et al. 2001) and of communities (Bertness & Callaway 1994). The enhanced resistance of polyculture *Z. marina* to shading-induced changes in **IV** gives evidence of plant diversity having positive effects on the stability of a plant species. Therefore, it is likely that *Z. marina* growing together with efficient oxygen releasers such as pondweeds (Sand-Jensen et al. 1982, Caffrey & Kemp 1991, Table 1) had an increased resistance to shading because of facilitative mechanisms. Facilitation could arise from an amelioration of sediment anoxia, which, in turn, could lead to lower sulfide intrusion and thus, lower root sulfide concentrations due to the reoxidization of sulfides (Holmer et al. 2005, Marbá et al. 2006) (see Fig. 6 in **IV**). In seagrass meadows, increased rhizosphere oxidization also increases nitrogen mineralization, thereby affecting the N-dynamics (Touchette & Burkholder 2000, Marbá et al. 2006), and possibly increasing the primary production (Romero et al. 2006). The positive effect of plant diversity however, had disappeared after a recovery time of 4 weeks, and monoculture plants recovered faster than *Z. marina* growing in polycultures. This could have been due to a shift from facilitation to interspecific competition of a resource (Holmgren et al. 1997). However, as porewater nutrient concentrations did not differ between mono- and polycultures (Table 1 in **IV**) which resource plants were competing for remains a puzzle and requires further study. Due to some of the experimental plant species being canopy-forming and having high primary production rates (Kautsky 1988), they may have responded rapidly to increasing light during recovery. This could have re-

sulted in shading of *Z. marina*, and thereby slower recovery in polycultures.

4.1.2 Effects of plant diversity on faunal communities

Positive relationships between plant diversity and faunal diversity have frequently been discovered in different systems (Duffy et al. 2012), with especially clear patterns found between herbivore arthropod diversity and plant diversity in terrestrial settings (Murdoch et al. 1972, Knops et al. 1999). In aquatic environments, the relationships are often weaker and this is hypothesized to be due to less frequent faunal host-specificity compared to terrestrial environments (Hay & Steinberg 1992, Vesakoski et al. 2008). The null response of epifaunal species number in **I** can be due to the fact that the Baltic Sea is characterized as being species poor with various generalist species that are capable of using several ecological niches (Dahl 1973) and thus, strong host-specificity is lacking (Vesakoski et al. 2008). Total epifaunal abundances varied temporally but were on average higher in more diverse plant assemblages (Fig. 1a, b in **I**). The same factors hypothesized to affect the positive relationship between faunal and plant diversity e.g. increased structure (Orth et al. 1984, Murdoch et al. 1972, Stachowicz et al. 2007, Hansen et al. 2011), chemical cues attracting fauna (Brönmark 1985) and palatability of epiphytic communities (Bologna & Heck 1999) may also affect faunal community variables such as abundance. Plants with complex leaf architecture generally have a greater surface area per unit weight, with important effects on several community attributes

and specific species such as amphipods (Orth et al. 1984, Parker et al. 2001). In addition to plant surface area, complex aboveground morphological structures provide shelter from predators (Orth et al. 1984) and trap settling fauna (Boström et al. 2010) and drifting algae (Bell & Hall 1997). Drift algae are important transport elements for both actively and passively moving fauna (Brooks & Bell 2001, Boström & Bonsdorff 2000) and many of the numerically abundant taxa in **I** e.g. *Cerastoderma glaucum* and *Hydrobia* spp. commonly settle and raft in drift algae (Norkko et al. 2000, see Fig. 2 in **I**).

Epifauna can also be affected by chemical cues excreted by plants to increase grazing of epiphytes (Brönmark 1985) and the chemical properties of plants that determine their nutritional value (Vesakoski et al. 2008). Plants and perennial algae may produce chemical defenses deterring herbivores (Hay & Steinberg 1992) and generally have lower nutritional quality than epiphytes and filamentous algae (Orth & Montfrans 1984). Thus, plant epiphytes and filamentous algae are likely the primary food source of Baltic grazers (Boström & Mattila 2005, Hansen et al. 2011), though isopods also readily feed on low nutrient quality perennial macroalgae (Jormalainen et al. 2001). Due to differences in colonization-available surface area, plant species may have differing epiphytic species composition (Orth & Montfrans 1984), leading to grazers being able to consume a more diverse epiphytic diet in species-rich plant assemblages. Mixed diets can have a higher nutritional value, which subsequently increase grazer fitness (Worm et al. 2006, Vesakoski et al. 2008). Hence, nutritional effects may also explain why higher faunal

abundances were found in more diverse plant assemblages in **I**. Even though plant species richness did not have strong effects on the epifaunal community, plant identity was important for species-specific responses, and amphipod abundance was significantly higher in treatments containing *P. perfoliatus* (Fig. 4 and Table 4b in **I**). Amphipods may actively choose structurally complex plants due to increasing microhabitat availability (Parker et al. 2001), food availability (trapped drift algae and epiphytes, Goecker & Kåll 2003) and shelter (Duffy & Hay 1991).

The higher infaunal species richness and functional diversity in polycultures (**II**) could be due to structural factors. Complex aboveground structures can trap more particles, and plant meadows typically accumulate organic material (Boström & Bonsdorff 2000), which could benefit infauna. However, the sediment organic content in **II** did not differ between treatments, suggesting that increased deposition of organic matter alone cannot explain the patterns found. Differences in complex root-rhizome structures (e.g. rhizome morphology and rhizome depth) are other possible factors explaining increasing infaunal diversity in mixed plant assemblages. Complex root-rhizome mats are known to stabilize the sediments and provide shelter from predation (Orth et al. 1984, Boström & Bonsdorff 1997). The difference in infaunal functional groups was due to some feeding types being absent in less diverse plant assemblages or in treatments lacking vegetation all together (Fig. 5 in **II**). For example, herbivores such as the beetle *Macrolea mutica*, spend their larval time in the sediment feeding on roots and rhizomes of *Z. marina* and *P. pectinatus* (Nilsson 1996, BioInfo UK),

possibly accumulating in plant patches consisting of preferable host plants. Species numbers per functional group are generally low in the Baltic (Bonsdorff & Pearson 1999) and as the available pool of species and taxa constituting functional groups was lower in low plant diversity treatments (erratum Fig 5c in beginning of **II**), the low diversity treatments lacked representative species of several functional groups and thus functional groups altogether.

Moreover, positive feedbacks from fauna to plants are also likely to occur. Epiphyte grazing for example, can reduce epiphytic growth, which in turn reduces the competition for light and nutrients and thus stimulates plant production (Duffy et al. 2005). Positive infaunal effects could include bioturbation, where fauna rework the sediment and simultaneously both oxidize and increase the nutrient availability for plants both directly and indirectly by increasing microbial processes related to nutrient mineralization (Kristensen et al. 2012). Infaunal communities composed of efficient bioturbator species such as *Nereis diversicolor* (Kristensen et al. 2012), could hypothetically increase plant productivity through an infaunal species identity effect. As *N. diversicolor* was a ubiquitous member of the infaunal species community in **II**, it could have had a beneficial effect on the plant production.

4.2 Diversity patterns in time

The fact that most marine BEF studies have been conducted on short temporal (average 90 d) and small spatial-scales (average 0.3 m²) (Crowe et al. 2012) makes it difficult to predict large-scale changes in the real world based on extrapolation of results (Bengtsson et al.

2002, Crowe et al. 2012). Longer-term studies conducted in aquatic (Stachowicz et al. 2008) and terrestrial settings (van Ruijven & Berendse 2005) and meta-analyses including both (Cardinale et al. 2007) have shown that diversity mechanisms may become stronger with time and thus possibly have a temporally stabilizing effect on communities (Allan et al. 2011). In plant communities, the spatial heterogeneity may be high during primary succession, which allows for high species diversity, but strong diversity-functioning relationships may be lacking because communities have not reached density-dependent phases (Weis et al. 2007). However, over successional time, diversity-functioning relationships may become stronger because of selection effects when the most productive species dominate due to resource competition (Tilman 1993, Weis et al. 2007) or through complementary effects when biomass allocation patterns change through time and result in enhanced nutrient-uptake efficiency among species (van Ruijven & Berendse 2005). In addition, high species turnover from year to year enables complementary interactions to occur and thereby, a greater provisioning of functioning over time (Allen et al. 2011). To follow diversity patterns of plant assemblages over a growing season, experiments in **II** and **III** were conducted on a short-time scale (~ 100 d). Due to the high seasonality, these plant communities are dynamic and disturbances such as storms, water fluctuations and ice scouring may rapidly change species abundances and composition at shallow depths (~ 1-2 m) (Kautsky 1988, Idestam-Almqvist 2000). At deeper depths (> 3 m) low light availability may become of more importance for

species community structure (Kautsky 1988), but species abundance and composition may also change due to herbivory or drift algal mat-induced mortality (pers. obs.). Such stochastic changes in species abundance and composition may thus affect diversity patterns in plant communities from year to year. Hence, when investigating diversity effects on plant productivity in highly seasonal environments like the Baltic Sea, short-term experiments (**II**, **III**) only provide a snapshot of successional and diversity patterns. It would therefore be more informative, but also riskier, to conduct long-term experiments that extend over several seasons and generations (Duffy et al. 2012).

As communities may be considered stable during a growth season, during several years, decades or even centuries, temporal scale is inevitably linked to stability. To define when a community is stable is difficult as most communities are dynamic and in constant motion and plant composition may be shifting due to natural succession or environmental factors such as declining salinity. Plant communities are often considered to be in a non-equilibrium state (Huston 1994). This means that competitive exclusions when plants become extinct due to competition are avoided because of different abiotic and biotic disturbances (Huston 1994). Therefore, it is possible that plant communities in the northern Baltic Sea that grow in a highly dynamic environment do not reach competitive exclusion during a growing season because of different factors (fluctuations in water temperature, drift algal mats, herbivory among others). The positive complementarity among plants in **III** suggests that on the scale of a growing

season, positive interactions between plants affect plant performance positively (D_i , Table 2 in **II** and Table 3 in **III**), thus suggesting that competitive exclusion did not occur. However, regardless of the possible non-equilibrium state of plant communities, when assessing stability such as resistance and recovery, an equilibrium state of a community must be defined (Pimm 1984). Stress events such as shade-inducing algal blooms (mimicked in **IV**), or transient drift algal mats, are usually short-term in relation to the entire growing season in such that they occur from days to weeks (pers. obs., Norkko & Bonsdorff 1996), but especially algal blooms often form during peak growing season i.e. July–August (pers. obs., Hansson & Öberg 2011). Thus, to mimic natural temporal occurrences of algal blooms in **IV**, plants were shaded in July and assumed to be in equilibrium pre-shading (see Materials and Methods in **IV**). Shading likely influenced interspecific competition and therefore added to the maintenance of a non-equilibrium state. Even though interspecific competition increased during recovery (**IV**), it is unlikely that it would have caused competitive exclusion because of the dynamical environment. Despite the slower recovery of *Z. marina* growing in polycultures, the results indicate that positive interactions, whether through complementary resource use or facilitation enhanced plant stability during stress events (**IV**), but also affected plant growth positively during more stable circumstances (**II**, **III**). Positive species interactions may thus enhance the stability of plant communities in terms of growth and biomass accumulation. Diverse assemblages may also have a higher probability of containing

species that respond differently to environmental perturbations, which can further influence community stability (Hughes et al. 2002).

4.3 Food webs and plant community functioning

High regional diversity can maintain high local diversity and increase local community stability through dispersal (Bengtsson et al. 2002) with mediating effects on diversity-functioning patterns (Bengtsson et al. 2002, Gonzalez et al. 2009). Such effects may vary depending on food web complexity, i.e. whether single- or multitrophic systems are investigated, and whether active or passive dispersal is the primary dispersal mode of the studied organisms (France & Duffy 2006). As mobile species can choose their habitats and move if local resource depletion occurs, this may lead to higher variability of ecosystem processes on spatial and temporal scales (France & Duffy 2006). The Baltic Sea may not have high regional faunal diversity, but plant and faunal dispersal mechanisms likely play a role in how plant and faunal diversity affect processes such as primary and secondary production. Many epifaunal species are found in several habitat types: in *Fucus vesiculosus*-belts (Wikström & Kautsky 2007), drift algal mats (Norkko et al. 2000), angiosperm communities (Boström & Bonsdorff 1997, **I**) and blue mussel beds (Norling & Kautsky 2008). Thus, dispersal between different habitat types is likely to be high and may show similar patterns to the results by France & Duffy (2006), but so far, this remains untested.

Food web structure (diversity among and within trophic levels) can

strongly affect biodiversity and ecosystem functioning (Duffy 2006). High diversity on one trophic level can decrease the function performed by the underlying trophic level, while bottom-up diversity effects are more often null (Schmid et al. 2009). Although increasing bottom-up diversity effects are generally weak, plant diversity may increase the herbivore diversity and have cascading effects on higher trophic levels as shown in terrestrial ecosystems (Knops et al. 1999, Scherber et al. 2010) though no clear patterns have been found in aquatic settings (Parker et al. 2001, Bates & DeWreede 2007, **I**). The increase in infaunal species and functional diversity with plant richness (**II**) shows that infauna may benefit from bottom-up diversity (i.e. plant richness). While bottom-up diversity did not affect epifaunal diversity, it affected epifaunal abundance positively (**I**). This in turn, may have had positive effects on predatory fish that feed on these epifaunal species (Bobsien 2006). Low-diversity systems such as the Baltic Sea can have strong trophic cascades due to the occurrence of simple food chains (Duffy 2006). In Baltic seagrass meadows however, strong top-down (predators) or bottom-up (nutrients) forces do not affect plant productivity (Baden et al. 2010), suggesting that trophic interactions involving epifauna are less important for diversity-productivity relationships. The patterns in **II** suggest that bottom-up diversity can by means of increasing infaunal diversity, possibly affect species on higher trophic levels (intermediate predators) that feed on these infaunal species (Nordström et al. 2009). Despite not being the case in **II**, infaunal diversity may correlate with infaunal biomass, which in turn, can enhance

nutrient fluxes and so have positive effects on primary production (Emmer-son & Huxham 2002). In conclusion, a feedback between diverse plant communities and higher trophic levels is likely to occur. Changes in food web structure caused by anthropogenic pressures can affect plant communities and their functioning profoundly (Baden et al. 2012, Eklöf et al. 2012).

4.4 The future of angiosperm meadows in the northern Baltic

Most marine organisms in the Baltic Sea are locally adapted to the special conditions that are prevalent but many populations show low genetic variability. This can lead to a lowered adaptive capacity to, for example, climate change (Reusch et al. 2005, Johanneson et al. 2011). In the northern Baltic Sea, *Z. marina* has low genetic diversity and many of the local populations consist of genetically distinct old clones (Reusch et al. 1999, Olsen et al. 2004). The populations are locally adapted to low salinity, and have so far shown no decreased fitness due to low genetic variation (Reusch & Boström 2010). However, the long-term survival of *Z. marina* may be at risk because of its low genetic variability and lack of sexual reproduction. The populations already live at their lower salinity limit (~ 5 psu, Baden & Boström 2001). The possibly low adaptive capacity together with future predictions of lowered salinity due to climate change (BACC 2008) may lead to regional extinctions of these old and locally adapted populations of *Z. marina*. The lack of sexual reproduction also renders it dispersal-limited and once it has become locally extinct it will most likely not be able to re-colonize.

Though *Z. marina* alone may not have profound effects on the above-ground biomass production in plant assemblages, its presence increases the community belowground biomass (III). In contrast to the other plant species, its root-rhizome mat is extensive and occurs year-around so it enhances sediment stabilization (Boström & Bonsdorff 2000). If *Z. marina* goes locally and regionally extinct, other species such as *P. perfoliatus* may be able to maintain some processes such as aboveground biomass production, (Table 1 in III), and habitat provisioning for epifauna (I), but due to the intrinsic differences in the root-rhizome characteristics of the species (see Material and Methods), it is unlikely that *P. perfoliatus* can maintain for example, sediment stabilization processes to the same extent as *Z. marina*. Thus, multifunctionality is important as species may have varying and even unique effects on certain processes (Hector & Bagchi 2007).

With increasing climate change the precipitation and runoff is predicted to increase, which may result in increased eutrophication and decreased salinity (BACC, 2008). Some eutrophication-tolerant and limnic species e.g. *Potamogeton* spp. and *Myriophyllum* spp. (Wallentinus 1979) may be positively affected. As *P. perfoliatus* is eutrophication-tolerant, it may be one of the prospective “winners” in the future and thus, epifaunal species that are positively affected by its presence may continuously thrive (I). Other “winners” such as *Myriophyllum spicatum*, can also harbor high epifaunal abundances (Hansen et al. 2011), but it also releases allelopathic substances that have negative effects on phytoplankton (Körner & Nicklish 2002) and different faunal

groups (Lindén & Lehtiniemi 2005). Despite these negative effects, it also increases the light attenuation in the water column by reducing the amount of phytoplankton (Gross 1999, Körner & Nicklish 2002), with a possible positive feedback on benthic vegetation. Thus, shifts in plant species composition may strongly affect plant community functioning of the future Baltic Sea.

4.5 Issues in BEF research

Debate concerning the use of certain experimental designs (replacement or additive designs) in BEF research has been heated at times as both designs have been accused of confounding intra- with interspecific interactions (Sackville Hamilton 1994, Jolliffe 2000). A suggestion of circumventing these problems has, for example, been to use additive-replacement designs and thus have a range of differently standardized units (Duffy et al. 2012). However, this calls for a large experiment with the number of treatments high, which in turn may become logistically difficult. Thereby, in all papers (I–IV), a trade-off between feasibility and experimental design had to be made, with a replacement design ultimately being chosen. Richness effects may be separated from density-dependent processes by treating abundance and richness as separate factors or by using the additive partitioning method by Loreau & Hector (2001) (II, III), which may also reduce the problem of confounding species density with richness effects (Benedetti-Cecchi & Maggi 2012).

The lack of spatial replication between-sites can be considered a shortcoming of the work in I–IV, mainly

relating to the question how valid the results are to Baltic Sea plant communities and submerged meadows in general. Increasing the within-site as well as the between-site spatial replication is recognized as an important part of diversity and ecological studies in general, and the observed patterns can become stronger and generalities of results increased (Crowe et al. 2012). Thus, by conducting similar experiments on different sites, the generality of the results from I–IV could have been tested. In addition, repeating experiments between years would have revealed temporal patterns of diversity effects. Similarly to extending the experimental design to additive-replacement, increasing the spatial replication in I–IV would however, have involved logistical trade-offs between treatment numbers and plot replication (Raffaelli 2006), and this trade-off was considered worse than the lack of spatial replication. Nonetheless, the way forward is to carefully design experiments with as few trade-offs as possible. Future experiments should also include spatial and temporal replication more frequently than at present. Despite these possible shortcomings of the work, spatial and temporal replication was beyond the scope of the thesis and spatial and temporal differences in diversity patterns were not the aim. Rather, the aim was to investigate whether diversity patterns exist in submerged angiosperm communities and whether diversity has any effects on certain ecosystem processes and properties. The fact that the work was conducted in the field increases the realism of the results. Increasing the number of field experiments has been called for as they include more temporal variation in environmental conditions than laboratory

or mesocosm studies and make the results more applicable to real-world situations (Crowe et al. 2012). In conclusion, in the future, scaling-up on both spatial and temporal scales will be one of the most important tasks of BEF research.

5. CONCLUSIONS AND LOOKING AHEAD

The results from papers I-IV show that plant diversity affects several ecosystem processes positively (Fig. 4). As field experiments on aquatic plant diversity-ecosystem functioning are few, the presented work contributes to the growing knowledge of diversity being a very important component of aquatic ecosystems. Diverse plant communities in the northern Baltic Sea sustain higher primary production than comparable monocultures, have positive effects on faunal communities and enhance stability. Richness and identity effects vary, with identity being the best descriptor for more variables than richness. However, species-rich communities are likely to contain several species with differing effects on functions, i.e. multifunctionality, which also renders species richness important for functioning. The functioning of ecosystems is further intimately linked to the provisioning of important services and goods that affect human well-being. Even though specific services and goods were not investigated in this work, the results give implications of the importance of diverse plant assemblages for multiple services such as fisheries, (secondary production) water clarity (particle trapping by complex above-ground structures) and erosion control (sediment stabilization through below-ground biomass) (Duarte 2000).

What has become clear from this work is that several knowledge gaps still exist, for example, recognizing which plant traits are important for the maintenance of certain processes, how processes may change due to species extinctions and whether plant diversity and ecosystem functioning relationships change during future environmental change and if so, how. Furthermore, scaling up is the next step to be taken in future BEF research to be able to answer questions on how matter and energy is transferred between local communities, and how community diversity sustain functioning on larger-scales such as seascapes. An important notion for future research is to include both α - and β -diversity and look at them on larger scales, i.e. on landscape-levels, γ -diversity (Magurran 2012). For example, the plant community at the site where the fieldwork for this thesis was conducted could comprise a plant community within a habitat (α -diversity) with the effects of plant diversity on functioning quantified locally. Whether plant diversity changes when moving to plant communities in other habitats at other sites some islands away make up the β -diversity. Simultaneously, this evokes the question whether plant diversity effects on functioning also changes. Combining these two diversity measures add to the seascape diversity, γ -diversity, relating to how well different habitats can deliver functions within a seascape (e.g. Archipelago Sea) both as local or joint entities (Magurran 2012).

As Thrush & Lohrer (2012) suggested, future investigations should take an integrative approach in such that results derived from manipulative experiments could be used jointly with data obtained from observational stud-

ies (e.g. inventory studies). Inventory studies often constitute the basis for coastal mapping and mapping could for example be used to report the probable extent of plant assemblages along a coastal stretch. Thus, if diverse plant assemblages can be assumed to provide processes to approximately the same extent, a numerical evaluation of performed processes could be done on a seascape scale. This could make it possible to assess the monetary value of sustained services and goods. BEF-researchers have acknowledged the abovementioned issues and prospective solutions have been proposed (see

Naeem et al. 2009b and references therein).

Nonetheless, both this thesis work and other BEF work have shown that the complexities involved in nature and the context-dependency can obscure diversity-ecosystem relationships. Scientists are increasingly required to predict how biodiversity change will affect ecosystem functioning but face great difficulties in doing so due to the complexities of nature. Ultimately, the best way to assure that ecosystems continue to function is to preserve as many biodiversity components as possible.

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References

- Allan E, Weisser W, Weigelt A, Roscher C et al. (2011) More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc Natl Acad Sci USA* 108: 17034-17039.
- Allison G (2004) The influence of species diversity and stress intensity on community resistance and resilience. *Ecol Monogr* 74: 117-134.
- Ashton IW, Miller AE, Bowman WD, Suding KN (2010) Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* 91: 3252-3260.
- BACC Author Team (2008) Assessment of Climate Change for the Baltic Sea Basin. Springer-Verlag, Berlin Heidelberg, 473 pp
- Baden SP, Boström C (2001) The leaf canopy of seagrass beds: faunal community structure and function in a salinity gradient along the Swedish coast. In: Reise K (ed) *Ecological comparisons of sedimentary shores*, Ecological Studies 151. Springer-Verlag, Berlin, p 215-236
- Baden S, Boström C, Tobiasson S, Arponen H et al. (2010) Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: A broad-scale field experiment in the Baltic-Skagerrak area. *Limnol and Oceanogr* 55: 1435-1448
- Baden S, Emanuelson A, Pihl L, Svensson C-J et al. (2012) Shift in seagrass food web structure over decades is linked to overfishing. *Mar Ecol Prog Ser* 451: 61-73
- Balvanera P, Pfisterer AB, Buchmann N, He J-S et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9: 1146-1156
- Bates CR, DeWreede RE (2007) Do changes in seaweed biodiversity influence associated invertebrate epifauna? *J Exp Mar Biol Ecol* 344: 206-214
- Bell S, Hall MO (1997) Drift macroalgal abundance in seagrass beds: investigating large-scale associations with physical and biotic attributes. *Mar Ecol Prog Ser* 147: 277-283
- Benedetti-Cecchi L, Maggi E (2012) The analysis of biodiversity-ecosystem functioning experiments: partitioning richness and density-dependent effects. In: Solan M, Aspiden RJ, Paterson DM (eds) *Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration*. Oxford University Press, Oxford, p 73-84
- Bengtsson J, Engelhardt K, Giller P, Hobbie S et al. (2002) Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning rela-

tions. In: Loreau M, Naeem S & Inchausti P (eds) Biodiversity and ecosystem functioning- Synthesis and perspectives. Oxford University Press, Oxford, p 209–222

Berg MP, Ellers J (2010) Trait plasticity in species interactions: a driving force of community dynamics. *Evol Ecol* 24:617–629

Berglund J, Mattila J, Rönnerberg O, Heikkilä J et al. (2003) Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. *Estuar Coast Shelf Sci* 56: 1167-1175

Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9: 191-193

BioInfo UK, http://www.bioinfo.org.uk/html/Macroplea_mutica.htm, (last accessed 5.10.2012)

Bobsien IC (2006) The role of small fish species in eelgrass food webs of the Baltic Sea. Dissertation, Christian-Albrechts-Universität zu Kiel, Germany, 184 pp

Bologna PAX, Heck KL Jr (1999) Macrofaunal associations with seagrass epiphytes. Relative importance of trophic and structural characteristics. *J Exp Mar Biol Ecol* 242: 21-39

Bonsdorff E, Blomqvist EA, Mattila J, Norkko A (1997) Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanol Acta* 20: 319-329

Bonsdorff E, Pearson TH (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Aust J Ecol* 24: 312-326

Borum J, San-Jensen K, Binzer T, Pedersen O et al. (2006) Oxygen movement in seagrasses. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht, p 255-270

Boström C (1995) Flowering and fruit-bearing *Zostera marina* in Åland, northern Baltic Sea. *Memoranda Soc Fauna Flora Fennica* 71: 7-9

Boström C, Bonsdorff E (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* L. beds in the northern Baltic Sea. *J Sea Res* 37: 153–166

Boström C, Bonsdorff E (2000) Zoobenthic community establishment and habitat complexity—the importance of seagrass shoot density, morphology and physical disturbance for faunal recruitment. *Mar Ecol Prog Ser* 205: 123-138

- Boström C, Baden S, Krause-Jensen D (2003) The seagrasses of Scandinavia and the Baltic Sea. In: Green EP, Short FP, Spalding MD (eds) World Atlas of Seagrasses: Present status and future conservation. UNEP, California Press, p 27-37
- Boström C, Roos C, Rönnerberg O (2004) Shoot morphometry and production dynamics of eelgrass in the northern Baltic Sea. *Aquat Bot* 79: 145-161
- Boström C, Mattila J (2005) Effects of isopod grazing: an experimental comparison in temperate (*Idotea balthica*, Baltic Sea, Finland) and subtropical (*Erichsonella attenuata*, Gulf of Mexico, U.S.A.) ecosystems. *Crustaceana* 78: 185-200
- Boström C, O'Brien K, Roos C, Ekebom J (2006) Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. *J Exp Mar Biol Ecol* 335: 52-73
- Boström C, Törnroos A, Bonsdorff E (2010) Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape. *J Exp Mar Biol Ecol* 390: 106-117
- Boyer KE, Kertesz JS, Bruno JF (2009) Biodiversity effects on productivity and stability of marine macroalgal communities: the role of environmental context. *Oikos* 118: 1062-1072
- Brooker RW, Maestre FT, Callaway RM, Lortie CL et al. (2008) Facilitation in plant communities: the past, the present, and the future. *J Ecol* 96: 18-34
- Brooks RA, Bell SS (2001) Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones. *J Exp Mar Biol Ecol* 264: 67-84
- Bruno JF, Boyer KE, Duffy JE (2005) Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol Lett* 8: 1165-1174
- Brönmark C (1985) Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* 45: 26-30
- Caffrey JM, Kemp WM (1990) Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. *Mar Ecol Prog Ser* 66: 147-160
- Caffrey JM, Kemp WM (1991) Seasonal and spatial patterns of oxygen production, respiration and root rhizome release in *Potamogeton perfoliatus* and *Zostera marina*. *Aquat Bot* 40: 109-128
- Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology* 84: 1115-1128

- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989-992
- Cardinale BJ, Wright JP, Cadotte MW, Carroll JT et al. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc Natl Acad Sci USA* 104: 18123–18128
- Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE et al. (2011) The functional role of producer diversity in ecosystems. *Am J Bot* 98: 572-592
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486: 59-67
- Covich AP, Austen M, Bärlocher F, Chauvet E et al. (2004) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54: 767–775
- Crowe TP, Bracken MES, O'Connor NE (2012) Reality check: issues of scale and abstraction in biodiversity research, and potential solutions. In: Solan M, Aspiden RJ, Paterson DM (eds) *Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration*. Oxford University Press, Oxford, p 185-199
- Dahl E (1973) Ecological range of Baltic and North Sea species. *Oikos* 15: 85-90
- den Hartog C (1994) Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. *Aquat Bot* 47: 21-28
- den Hartog C, Kuo J (2006) Taxonomy and biogeography of seagrasses. In: Larkum AWD, Orth RJ, Duarte CM (eds) *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, p 1-23
- Diaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16: 646-655
- Doak DF, Bigger D, Harding-Smith E, Marvier MA et al. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *Am Nat* 151: 264–276
- Duarte CM (1992) Nutrient concentration of aquatic plant: Patterns across species. *Limnol Ocenogr* 37: 882-889
- Duarte CM (2000) Marine biodiversity and ecosystem services: an elusive link. *J Exp Mar Biol Ecol* 250: 117-131
- Duarte CM, Marbà N, Gacia E, Fourqurean JW et al. (2010) Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeo-*

chem Cycles 24: GB4032

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72: 1286-1298

Duffy JE, Richardson JP, France KE (2005) Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol Lett* 8, 301-309

Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. *Mar Ecol Prog Ser* 311: 233-250

Duffy JE, Stachowicz JJ, Bruno JF (2012) Multitrophic biodiversity and the responses of marine ecosystems to global change. In: Solan M, Aspden RJ, Paterson DM (eds) *Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration*. Oxford University Press, Oxford, p 164-184

Eklöf JS, Alsterberg C, Havenhand, JN, Sundbäck K et al. (2012) Experimental climate change weakens the insurance effect of biodiversity. *Ecol Lett* 15: 864-872

Emmerson M, Huxham M (2002) How can marine ecology contribute to the biodiversity-ecosystem functioning debate? . In: Loreau M, Naeem S & Inchausti P (eds) *Biodiversity and ecosystem functioning- Synthesis and perspectives*. Oxford University Press, Oxford, p 139-146

Fourqurean JW, Duarte CM, Kennedy H, Marbà N et al. (2012) Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5: 505-509

France KE, Duffy JE (2006) Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* 441: 1139-1143

Gambi MC, Nowell ARM, Jumars PA (1990) Flume observations on flow dynamics in *Zostera marina* (L.) beds. *Mar Ecol Prog Ser* 61: 159-169

Gamfeldt L, Bracken MES (2009) The role of biodiversity for the functioning of rocky reef communities. In: Wahl M (ed) *Marine hard bottom communities, Ecological Studies* 206. Springer-Verlag Berlin Heidelberg, p 361-373

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334: 242-243

Giller PS, Hillebrand H, Berninger U-G, Gessner MO et al. (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104: 423-436

Goecker, ME, Kåll SE (2003) Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. *J Sea Res* 50: 309-314

- Gonzalez A, Mouquet N, Loreau M (2009) Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) Biodiversity, ecosystem functioning and human wellbeing. – An ecological and economic perspective. Oxford University Press, Oxford, p 134-146
- Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge
- Granö O, Roto M, Laurila L (1999) Environment and land use in the shore zone of the coast of Finland. *Publ Inst Geogr Univ Turkuensis* 160: 40-49
- Griffin JN, O’Gorman EJ, Emmerson MC, Jenkins SR et al. (2009) Biodiversity and the stability of ecosystem functioning. In: Naeem S, Bunker DE, Hector A, Loreau M et al. (eds) Biodiversity, ecosystem functioning and human wellbeing. – An ecological and economic perspective. Oxford University Press, Oxford, p 78-93
- Gross EM (1999) Allelopathy in Benthic and Littoral Areas: Case Studies on Allelochemicals from Benthic Cyanobacteria and Submersed Macrophytes. In: Inderjit, Dakshini KMM, Foy CL (eds) Principles and practices in plant ecology. CRC Press, Boca Raton, Florida, p 179-199
- Hansen JP, Wikström SA, Axemar H et al. (2011) Distribution differences and active habitat choices of invertebrates between macrophytes of different morphological complexity. *Aquat Ecol* 45: 11-22
- Hansson M, Öberg J (2011) Cyanobacterial blooms in the Baltic Sea. HELCOM Indicator Fact Sheets 2011. www.helcom.fi/environment2/ifs/en_GB/cover (last accessed 2.10.2012).
- Harper JL (1977) Population Biology of Plants. Academic Press, London
- Hauxwell J, Cebrián J, Furlong C et al. (2001) Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82: 1007-1022
- Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) Herbivores. Their Interactions with Secondary Plant Metabolites. Vol II, Ecological and Evolutionary Processes. Academic Press, San Diego, p 371-413
- He J-S, Wolfe-Bellin KS, Schmid B, Bazzaz FA (2005) Density may alter diversity–productivity relationships in experimental plant communities. *Basic Appl Ecol* 6: 505-517

Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–191

HELCOM (2009) Eutrophication in the Baltic Sea - An integrated thematic assessment of the effects of nutrient enrichment and eutrophication in the Baltic Sea region. Balt Sea Environ Proc No 115B

Hellblom F, Björk M (1999) Photosynthetic responses in *Zostera marina* to decreasing salinity, inorganic carbon content and osmolality. *Aquat Bot* 65: 97-104

Hemminga MA (1998) The root/rhizome system of seagrasses: an asset and a burden. *J Sea Res* 39: 183-196

Hemminga MA, Duarte CM (2000) *Seagrass Ecology*. Cambridge University Press, Cambridge

Holmer M, Laursen L (2002) Effect of shading of *Zostera marina* (eelgrass) on sulfur cycling in sediments with contrasting organic matter and sulfide pools. *J Exp Mar Biol Ecol* 270: 25-37

Holmer M, Fredriksen MS, Møllegaard H (2005) Sulfur accumulation in eelgrass (*Zostera marina*) and effect of sulfur on eelgrass growth. *Aquat Bot* 81: 367-379

Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78: 1966-1975

Holmquist JG (1994) Benthic macroalgae as a dispersal mechanism for fauna: influence of marine tumbleweed. *J Exp Mar Biol Ecol* 180: 235-251

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305

Hooper DU, Chapin FSI, Ewel JJ, Hector A et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75: 3–35

Hughes JB, Ives AR, Norberg J (2002) Do species interactions buffer environmental variation (in theory)? In: Loreau M, Naeem S & Inchausti P (eds) *Biodiversity and ecosystem functioning- Synthesis and perspectives*. Oxford University Press, Oxford, p 92-101

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc Natl Acad Sci USA* 101: 8998-9002

Hughes AR, Stachowicz JJ (2011) Seagrass genotypic diversity increases disturbance response via complementarity and dominance. *J Ecol* 99: 445-453

Huston MA (1994) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge

Idestam-Almquist J, Kautsky L (1995) Plastic responses in morphology of *Potamogeton pectinatus* L. to sediment and above-sediment conditions at two sites in the northern Baltic proper. *Aquat Bot* 52: 205-216

Idestam-Almquist J (2000) Dynamics in submersed aquatic vegetation on shallow softbottoms in the Baltic Sea. *J Veg Sci* 11: 425-432

Jespersen DN, Sorrell BK, Brix H (1998) Growth and root oxygen release by *Typha latifolia* and its effects on sediment methanogenesis. *Aquat Bot* 61: 165-180

Johanneson K, Smolarz K, Grahn M et al. (2011) The Future of Baltic Sea Populations: Local Extinction or Evolutionary Rescue? *Ambio* 40: 179-190

Jolliffe P (2000) The replacement series. *J Ecol* 88: 371–385

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957

Jormalainen V, Honkanen T, Heikkilä N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar Ecol Prog Ser* 220: 219-230

Kantrud HA (1990) Sago pondweed (*Potamogeton pectinatus* L.), a literature review. US Fish Wildl Serv, Res Publ 176: 1-89

Kautsky L (1987) Life-cycles of three populations of *Potamogeton pectinatus* L. at different degrees of wave exposure in the Askö area, northern Baltic Proper. *Aquat Bot* 27: 177-186

Kautsky L (1988) Life strategies of aquatic soft bottom macrophytes. *Oikos* 53: 126–135

Kautsky L (1990) Seed and tuber banks of aquatic macrophytes in the Askö area, northern Baltic proper. *Holarct Ecol* 13: 143-148

Kautsky L (1991) In situ experiments on interrelationships between six brackish macrophyte species. *Aquat Bot* 39: 159–172

Knops JMH, Tilman D, Haddad NM, Naeem S et al. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol Lett* 2: 289-293

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T et al. (2012) What is bio-turbation? The need for a precise definition for fauna in aquatic sciences. *Mar Ecol Prog Ser* 446: 285-302

Körner S, Nicklisch A (2002) Allelopathic growth inhibition of selected phytoplankton species by submerged macrophytes. *J Phycol* 38: 862-871

Lindén E, Lehtiniemi M (2005) The lethal and sublethal effects of the aquatic macrophyte *Myriophyllum spicatum* on Baltic littoral planktivores. *Limnol Oceanogr* 50: 405-411

Littell RC, Milliken GA, Stroup WW, Wolfinger RD et al. (2006) SAS for Mixed Models. 2nd ed, SAS Institute Inc, Cary NC

Loreau M (1998) Separating sampling and other effects in biodiversity experiments. *Oikos* 82: 600–602

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3–17

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76

Madsen JD, Chambers PA, James WD, Koch EW et al. (2001) The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444: 71-84

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford

Magurran AE (2012) Biodiversity in the context of ecosystem function. In: Solan M, Aspiden RJ, Paterson DM (eds) Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration. Oxford University Press, Oxford, p 16-23

Marbá N, Cebrian J, Enríques S, Duarte CM (1996) Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. *Mar. Ecol. Prog. Ser.* 133, 203-215

Marbá N, Holmer M, Gacia E, Barrón C (2006) Seagrass beds and coastal biogeochemistry. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht, p 135-157

Marquard E, Weigelt A, Roscher C, Gubsch M et al. (2009) Positive biodiversity–productivity relationship due to increased plant density. *J Ecol* 97: 696-704

Mouquet N, Munguia P, Kneitel JM, Miller TE (2003) Community assembly time

- and the relationship between local and regional species richness. *Oikos* 103: 618-626
- Mulder CPH, Uliassi DD, Doak DF (2001) Physical stress and diversity-productivity relationships: the role of positive interactions. *Proc Natl Acad Sci USA* 98: 6704-6708
- Murdoch WW, Evans FC, Peterson CH (1972) Diversity and pattern in plants and insects. *Ecology* 53, 819-829
- Naeem S (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* 83: 1537-1552
- Naeem S, Loreau M, Inchausti P (2002) Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. In: Loreau M, Naeem S & Inchausti P (eds) *Biodiversity and ecosystem functioning- Synthesis and perspectives*. Oxford University Press, Oxford, p 3-11
- Naeem S, Bunker DE, Hector A, Loreau M et al. (2009a) Introduction: the ecological and social implications of changing biodiversity. An overview of a decade of biodiversity and ecosystem functioning research. In: Naeem S, Bunker DE, Hector A, Loreau M et al. (eds) (2009) *Biodiversity, ecosystem functioning and human wellbeing. – An ecological and economic perspective*. Oxford University Press, Oxford
- Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) (2009b) *Biodiversity, ecosystem functioning and human wellbeing. – An ecological and economic perspective*. Oxford University Press, Oxford
- Nejrup LM, Pedersen MF (2008) Effects of salinity and water temperature on the ecological performance of *Zostera marina*. *Aquat Bot* 88: 239-246
- Nilsson A (ed) (1996) *Aquatic Insects of North Europe. A Taxonomic Handbook*, Vol. 1. Apollo Books, Stenstrup
- Nordström M, Aarnio K, Bonsdorff E (2009) Temporal variability of a benthic food web: patterns and processes in a low-diversity system. *Mar Ecol Prog Ser* 378: 13-26
- Norkko A, Bonsdorff E (1996) Rapid zoobenthic community responses to accumulations of drifting algae. *Mar Ecol Prog Ser* 131: 143-157
- Norkko J, Bonsdorff E, Norkko A (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. *J Exp Mar Biol Ecol* 248: 79–104
- Norling P, Kautsky N (2008) Patches of the mussel *Mytilus* sp. Are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. *Aquat Biol* 4: 75-87

Norušis MJ (2010) PASW Statistics 18 Advanced Statistical Procedures Companion. Prentice Hall Inc., New Jersey

Olesen B, Sand-Jensen K (1994) Biomass-density patterns in the temperate seagrass *Zostera marina*. Mar Ecol Prog Ser 109: 283-291

Olsen JL, Stam WT, Coyer JA, Reusch TBH et al. (2004) North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. Mol Ecol 13: 1923-1941

Orth RJ, van Montfrans J (1984) Epiphyte-seagrass relationships with an emphasis on the role of micograzing.- A review. Aquat Bot 18: 43-69

Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339-350

Paine RT (2002) Trophic control of production in a rocky intertidal community. Science 296: 736-739

Parker JD, Duffy JE, Orth RJ (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Mar Ecol Prog Ser 224: 55-67

Paterson DM, Defew EC, Jabour J (2012) Ecosystem function and co-evolution of terminology in marine science and management. In: Solan M, Aspden RJ, Paterson DM (eds) Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration. Oxford University Press, Oxford, p 24-33

Pearson TH, Rosenberg R (1987) Feast and famine: structuring factors in marine benthic communities. In: Gee JHR, Giller PS (eds) Organization of communities past and present. Blackwell Scientific Publications, Oxford

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307: 321-326

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Raffaelli D (2006) Biodiversity and ecosystem functioning: issues of scale and trophic complexity. Mar Ecol Prog Ser: 311: 285-294

Rasmussen JR, Olesen B, Krause-Jensen D (2012) Effects of filamentous macroalgae mats on growth and survival of eelgrass, *Zostera marina*, seedlings. Aquat Bot 99: 41-48

Reusch TBH, Boström C, Stam WT, Olsen JL (1999) An ancient eelgrass clone in the Baltic Sea. Mar Ecol Prog Ser 183: 301-304

- Reusch TBH, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc Natl Acad Sci USA* 102: 2826-2831
- Reusch TBH, Boström C (2010) Widespread genetic mosaicism in the marine angiosperm *Zostera marina* is correlated with clonal reproduction. *Evol Ecol* 25: 899-913
- Romero J, Lee K-S, Pérez M, Mateo MA et al. (2006) Nutrient dynamics in seagrass ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, p 227-254
- Sackville Hamilton NR (1994) Replacement and additive designs for plant competition studies. *J Appl Ecol* 31: 599-603
- Sand-Jensen K, Prahl C, Stokholm H (1982) Oxygen release from roots of submerged aquatic macrophytes. *Oikos* 38: 349-354
- Santamaría L (2002) Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecol* 23: 137-154
- Scherber C, Eisenhauer N, Weisser WW, Schmid B et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553-556
- Schmid B, Balvanera P, Cardinale BJ, Godbold J et al. (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M ET AL. (eds) (2009) *Biodiversity, ecosystem functioning and human wellbeing. – An ecological and economic perspective*. Oxford University Press, Oxford, p 14-29
- Sculthorpe CD (1967) *The biology of aquatic vascular plants*. Spottiswoode, Ballantyne and Co, London
- Stachová T, Fibich P, Lepš J (2012) Plant density affects measures of biodiversity effects. *J Plant Ecol*, doi: 10.1093/jpe/rts015
- Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. *Annu Rev Ecol Evol Syst* 38: 739-766
- Stachowicz JJ, Best RJ, Bracken MES, Graham MH (2008) Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. *Proc Natl Acad Sci USA* 105: 18842-18847

Thrush SF, Lohrer AM (2012) Why bother going outside: the role of observational studies in understanding biodiversity-ecosystem function relationships. In: Solan M, Aspiden RJ, Paterson DM (eds) Marine biodiversity and ecosystem functioning - Frameworks, methodologies and integration. Oxford University Press, Oxford, p 200-214

Tilman D (1993) Community diversity and succession: the roles of competition, dispersal and habitat modification. In: Schulze ED, Mooney HA (eds.) Biodiversity and ecosystem function. Springer-Verlag, Berlin, p 327-344

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718-720

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94: 1857-1861

Tilman D, Knops J, Wedin D, Reich P (2001) Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands. In: Loreau M, Naeem S & Inchausti P (eds) Biodiversity and ecosystem functioning- Synthesis and perspectives. Oxford University Press, Oxford, p 21-35

Torn K, Krause-Jensen D, Martin G (2006) Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. *Aquat Bot* 84: 53-62

Touchette B, Burkholder J (2000). Overview of the physiological ecology of carbon metabolism in seagrasses. *J Exp Mar Biol Ecol* 250: 169-205

Touchette B, Burkholder J (2007) Carbon and nitrogen metabolism in the seagrass, *Zostera marina* L.: Environmental control of enzymes involved in carbon allocation and nitrogen assimilation. *J Exp Mar Biol Ecol* 350: 216-233

van Katwijk MM, Vergeer LHT, Schmitz GHW et al. (1997) Ammonium toxicity in eelgrass *Zostera marina*. *Mar Ecol Prog Ser* 157: 159-173

van Ruijven J, Berendse F (2005) Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc Natl Acad Sci USA* 102: 695-700

van Ruijven J, Berendse F (2010). Diversity enhances community recovery, but not resistance, after drought. *J Ecol* 98: 81-86

Vesakoski O, Boström C, Ramsay T, Jormalainen V (2008) Sexual and local divergence in host exploitation in the marine herbivore *Idotea baltica* (Isopoda). *J Exp Mar Biol Ecol* 367:118-126

- Violle C, Navas M-L, Vile D, Kazakou E et al. (2007) Let the concept of trait be functional! *Oikos* 116: 882-892
- Wallentinus I (1979) Environmental influences on benthic macrovegetation in the Trosa-Askö area, northern Baltic Proper II. The ecology of macroalgae and submerged phanerogams. *Contr Askö Lab Univ Stockholm* 25: 1-210
- Warfe DM, Barmuta LA (2006) Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia* 150: 141-154
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106: 12377-12381
- Weiner J, Freckleton RP (2010) Constant final yield. *Annu Rev Ecol Evol Syst* 41:173-92
- Weis JJ, Cardinale BJ, Forshay KJ, Ives AR (2007) Effects of species diversity on community biomass production change over the course of succession. *Ecology* 88: 929-939
- White J, Harper JL (1970) Correlated changes in plant size and number in plant populations. *Ecology* 58: 467-485
- Wikström SA, Kautsky L (2007) Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Est Coast Shelf Sci* 72: 168-176
- Wolfer SR, Straile D (2004) Density control in *Potamogeton perfoliatus* L. and *Potamogeton pectinatus* L. *Limnologica* 34: 98-104
- Worm B, Barbier EB, Beaumont N, Duffy JE et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787-790
- Yachi S, Loreau M (1999) Biodiversity and ecosystem functioning in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci USA* 96: 1463-1466

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Biodiversity and ecosystem functioning in angiosperm communities in the Baltic Sea

This PhD-thesis describes the effects of submerged plant diversity on ecosystem functioning in angiosperm communities in the Baltic Sea. It shows that diverse plant communities sustain higher primary production than comparable monocultures, affect faunal communities positively and enhance stability. Thus, diverse meadows add to coastal ecosystem functioning and may provide with services essential for human well-being.

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