

# Baltic Sea shores and climate change

by

Alma Strandmark



## Plants & Ecology

---

The Department of Ecology,  
Environment and Plant Sciences  
Stockholm University

2014/2

# Baltic Sea shores and climate change

by  
Alma Strandmark

Supervisors:  
Peter Hambäck, Sara Cousins and  
Gundula Kolb

## Plants & Ecology

---

The Department of Ecology,  
Environment and Plant Sciences  
Stockholm University

2014/2

Plants & Ecology

Plant Ecology  
Department of Botany  
Stockholm University  
S-106 91 Stockholm  
Sweden

---

© Plant Ecology

ISSN 1651-9248

Printed by FMV Printcenter

Cover: A typical shore meadow in the Stockholm archipelago (Bullerö). Photo: Gustaf Almqvist

## Sammanfattning

Östersjön är ett brackvattenhav med en skarp nord-sydlig gradient i salthalt och temperatur. Klimatförändringen kommer enligt projektioner för Östersjön att innebära; högre vattentemperatur, högre eutrofieringsgrad, ökad förekomst av cyanobakterieblomningar och troliga förändringar i salthalt. Högre vattentemperatur skapar en högre metabolism hos såväl växter som djur vilket i kombination med ökad eutrofiering kommer att gynna snabbväxande, fintrådiga alger och därmed minska utbredningen av blåstång (*Fucus vesiculosus*) i Östersjön.

Östersjöns kustområden är redan starkt exploaterade, speciellt skyddade, flacka vikar där man hittar artrika strandängar. I och med att byggnader längs kusten också kommer att påverkas av havsnivåförändringen så är det möjligt att konflikten mellan mänskliga intressen och bevarande av kustnära ekosystem kommer att trappas upp i framtiden. De terrestra strandekosystemen varierar mycket längs Östersjöns kust men artrika strandängar finns längs med hela kustlinjen. Östersjöregionen påverkas fortfarande av den senaste istiden genom att land höjer sig ur havet i de norra och centrala delarna. I och med klimatförändringen förflyttas jämviktlinjen mellan landhöjningen och havsnivåhöjningen kontinuerligt norrut. Eftersom många arter längs Östersjöns stränder är beroende av en kontinuerlig försörjning av nya habitat som stiger upp ur havet kommer artsammansättningen påverkas markant av stigande havsnivåer. Samtidigt kommer minskad utbredning av havsis, i kombination med ökad vindstyrka under vinterhalvåret över norra Östersjön, troligen att öka isskrapningsintensiteten och störningsfrekvensen i kustnära ekosystem längs norra delen av Östersjöekusten. Skötseln (bete och hö) av strandängar längs Östersjöns kust har också i stort sett övergivits vilket har orsakat en minskning i diversiteten av både växter och insekter. Bristen på skötsel kommer tillsammans med klimatförändringen och ökad fragmentering av värdefulla habitat troligen att skapa ekosystem som i framtiden domineras av några få framgångsrika generalister.

## Summary

The Baltic Sea is a brackish semi-enclosed water volume with a pronounced latitudinal gradient in salinity and temperature. Climate change projections for the Baltic Sea ecosystem include; increased water temperatures, increased eutrophication, increased occurrence of cyanobacteria blooms and a probable change in salinity. Higher water temperature will increase the metabolic rate of plants and animals which, together with eutrophication, will benefit fast growing, filamentous algae and thereby cause a reduction in the population of the important species bladderwrack (*Fucus vesiculosus*).

The coast around the Baltic Sea is heavily exploited by humans, especially the sheltered, shallow areas where shore meadows are usually found. Since human structures and buildings will also be affected by a sea level rise, there might be an intensified conflict between human interests and conservation of coastal habitats in the future. Terrestrial shoreline habitats in the Baltic Sea show large geographic differences but species rich shore meadows are present everywhere along the coastline. The Baltic Sea region is under the influence of the last ice age with isostatic rebound still causing land uplift in the northern and central parts of the area. Climate change is constantly moving the equilibrium line between isostatic rebound and sea level rise northwards. Since many species in shoreline ecosystems depend on that new land continuously rise from the sea the composition of species will likely change radically due to rising sea levels. Further, a decrease in sea ice cover together with increased wind speeds during winter might enhance the ice scouring and disturbance in coastal habitats in the northern Baltic Sea. At the same time the management (grazing and hay making) of shore meadows along the Baltic shoreline has almost stopped which has decreased the diversity of plants and insects. The lack of management together with climate change and further fragmentation of valuable habitats will probably produce ecosystems that in the future will be dominated by relatively few generalist species.

## **Introduction**

The ecosystems that are predicted to be most negatively affected by climate change include many shoreline habitats (Schrum 2001). The combined pressure of habitat fragmentation and climate change (Travis 2003) is likely to lead to increased global homogenization (McKinney & Lockwood 1999) and communities in highly fragmented landscapes, like archipelagos, will probably in the future be dominated by few mobile generalist species even more than today. The world's human population is to a large part concentrated to the coastlines and ecosystem services of coastal habitats are various. Since shorelines are attractive for human exploitation such as for building harbors, tourism and housing there is a conflict between human interests and conservation of natural ecosystems. Shoreline ecosystems are ecotones on the border between two elements. They typically have a high diversity and host many rare species; in Latvia for example more than one third of the rare and endangered vascular plants occur in coastal habitats by the Baltic Sea (Ievinsh 2006). Energy flows between land and water are important in these ecosystems. The flow of energy from land to sea is quite well understood, with run off from farming land and human disposed substances like chemicals and medicine eventually ending up in the oceans. However, processes in the oceans are also changing the conditions in terrestrial systems especially the systems that are closely linked to the sea (Mellbrand et al. 2011). Therefore, climate change impact on marine systems will also affect terrestrial shoreline habitats.

The Baltic Sea is a brackish water enclosure with sharp gradients in salinity and temperature and, thus, species living there have clear distribution limits (Haatela 1974; Bergström & Bergström 1999). The coastlines in the Baltic Sea vary in structure with flat shores that are heavily ice scoured in the north, rocky shores in the central parts and shallow coastlines in the south. The coastline is still influenced by the last ice age with isostatic rebound causing the land to lift in large parts of the sea. In the south the isostatic rebound is already counterbalanced by climate induced rising sea levels which increase the problems with erosion in these areas. Shore meadows are species rich in plants and arthropods and can be found along the whole coastline. My studies will concern the complexity of shoreline ecosystems in the Baltic Sea area, especially shore meadows in the central part, and how the conditions in these systems might change with the ongoing climate change.

This essay is written in four chapters. The first chapter is on island biogeography; in order to understand how shoreline ecosystems might be affected by different climatic factors, it is

important to know the processes behind species composition and diversity. The second chapter briefly describes the special features of the Baltic Sea ecosystem and shoreline ecosystems bordering the Baltic Sea. The third chapter describes the projected climate change scenarios for the Baltic Sea area and the last chapter is a discussion about the possible effects of climate change for both the marine and terrestrial shoreline ecosystems as well as a brief discussion on the effects of coastal climate change for humans and ecosystem services in the Baltic Sea area.

### **Island biogeography**

Island biogeography does not only concern islands but also isolated habitats in heterogeneous landscapes. Thus, when conducting a study in for example an archipelago, the island concept does not only concern island size and isolation (distance to mainland) but can also be used for a single shore meadow or sandy beach.

In the 1960s MacArthur & Wilsons published their “island equilibrium theory” and Preston initiated the theory of “species area-relationship (SAR)”. Both theories agree on that larger areas/islands should host a larger number of species and individuals than smaller areas/islands. The MacArthur & Wilson theory includes the “equilibrium concept”, where equilibrium is achieved when extinction and immigration are in balance. According to the theory, larger islands can be at equilibrium with a higher number of species and individuals than small. However, various researchers have later argued that the equilibrium theory is far from applicable in all situations for describing species distribution and abundance and equilibrium has been suggested to be present only for short time periods (if at all) (Lomolino 2000). Lomolino (2000) argued the need for a model based on the fundamental processes immigration, extinction and evolution that includes not only the features area and isolation but also others like geology and climate. It should further also be species based, and not assume all species to be equal in e.g. spreading capacity and competitive ability. Differences in species traits will influence immigration, speciation and extinction rates and can, together with area and isolation, explain differences in SAR for different locations (Holt et al. 1999; Ricklefs & Lovette 1999). Habitat generalists for example are typically widespread with a low local abundance while specialists may be very common locally (Verberk et al. 2010). Highly specialized organisms are often considered to be more sensitive to fragmentation than habitat

generalists (Summerville et al. 2006) since they are limited to a small part of the habitat-matrix while more generalized species might be able to use the whole matrix. Furthermore, specialized species often have synchronized life cycles, while generalists typically spread their production effort over the season which making them more adaptive to unpredictable conditions (Verberk et al. 2010). In invasion biology, successful invasive species are often found to be generalist species possessing species traits that make them adaptive to a large spectrum of possible habitats and changes to the environment (Parker et al. 2001)

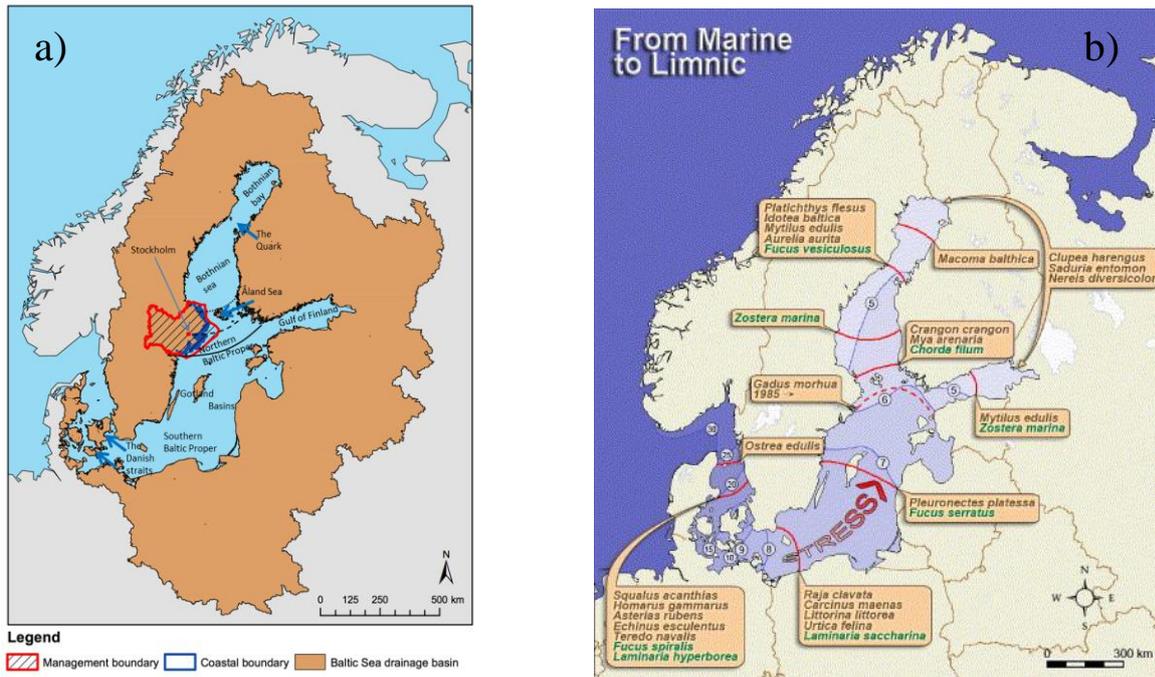
“Species area relationships” are functions of “Density area relationships” which describe the number of individuals of one species or a group of species in relation to area. This relationship diverges among species and groups of species in accordance to different degrees of specialization and other species life history traits. Species with a high degree of habitat specialization and high population density (Ricklef & Lovette 1999) and species with specialized feeding (Holt et al. 1999) usually have a strong density area relationship while generalists, independent of size, have been shown to have a more negative density area relationship (Hambäck et al. 2007; Hambäck et al. 2010). Further, species with different search behaviors have been found to show different density area dependence (Hambäck et al. 2007). The relationship also changes with individual size and mobility, as large and mobile species usually have a negative relationship (Hambäck et al. 2010). For some groups like spiders, that are well known as successful colonizers (Polis & Hurd 1995), small islands can host a very large number of individuals. Really small islands have long been suggested to be independent of the Species area relationship (SAR), a phenomenon that has been called “The small island syndrome” (Mac Arthur 1967) and several studies have shown that SAR is scale dependent (Drakare et al. 2006). Large islands seem to relate to SAR, with really large islands having a very steep relationship, while the relationship for small islands is more depending on the local conditions on the island (Williamson et al. 2001). Lomolino & Weiser (2001) mean that really large islands, with large habitat diversity, should not be treated as islands but rather be divided into different habitats, since differences in species diversity on larger islands is probably more related to habitat-diversity than island size (Ricklefs & Lovette 1999). Knowledge about habitat diversity and connectivity between habitats is important to understand species diversity which is always a matter of scale and which has been divided into alpha-, beta- and gamma-diversity according to the theory of Whittaker (1960 & 1972). In a landscape, alpha-diversity is the diversity in one habitat/site/island/sample and is often measured by making a mean value of diversity in

samples from two or several different habitats (Crist et al. 2003). Beta-diversity is measured as the divergence in diversity between habitats and Gamma-diversity is the diversity in the whole area, landscape or region. In the simplest form  $\alpha + \beta = \gamma$  although there are a large number of other definitions. The border between alpha and gamma-diversity is not absolute and often set according to the data that is available (Crist et al. 2003).

## **The Baltic Sea and coastline**

### *The Baltic Sea*

The Baltic Sea is the world's largest brackish water area. The current brackish state is geologically young and started only 7 500 years before present when Öresund opened up. The coastline of the Baltic Sea is shared between 9 countries and there are about 200 000 islands of varying size within the sea (Leppäranta & Myrberg 2009). The drainage basin covers 1 739 000 km<sup>2</sup> of land area in 13 countries, housing a population of 84 000 000 people in 2002 and is shown in Fig. 1a (Hannerz & Destouni 2006). Thus the Baltic Sea is a resource shared by many people and has been a case of “tragedy of the common”. Untreated waste water has triggered eutrophication and pollutants from the large drainage area along with dumping of chemicals in the Sea are causing toxic effects to many organisms. Further, intensive fishing was for a long time performed with poor and non-enforced regulation which has depleted the fish stock (Lane & Jensen 1996). The first attempt for protection of the Baltic Sea as a cooperation between neighboring states was initiated in the early 1970s, leading to the creation of HELCOM (The Baltic Marine Environmental Protection Commission) in 1980.



**Figure 1.** The Baltic Sea. **1a.** Baltic Sea drainage basin with sub areas. The drainage basin, here including the Danish Straits and Kattegat, is indicated in brown. An example water management district in Sweden, the Northern Baltic Proper, is indicated in red, with the coastal boundary highlighted in blue. Lines across the Baltic Sea illustrate the approximate position of the line of equilibrium between isostatic rebound and sea level rise, for the present situation of a sea-level rise rate of around 3 mm y<sup>-1</sup> (solid line), and potential future higher rates of 4 mm y<sup>-1</sup> (dashed line) and 5 mm y<sup>-1</sup>. **1b.** Distribution limits for a selection of important species in the Baltic Sea (From: Bonsdorff 2006).

The Baltic Sea has pronounced latitudinal gradients in salinity and temperature. In the northernmost areas (Bothnian Bay) surface salinity is low (between 2 and 3 psu); because of the high inflow of fresh water from rivers and surface run off from the large catchment area. In the south, the surface salinity is 8-9 psu, due to inflow of marine deep water through the Danish straits. The long term mean inflow of deep water approximately equals the freshwater supply creating a steady and sharp brackish gradient. Climatic zonation reaches from continental sub-arctic in the north to maritime temperate in the south (Läpperanta & Myrberg 2009) with the northern parts facing long, ice rich winters while winters in the southern parts of the sea are usually mild and free of ice (Rabalais et al. 2009). Because of these large geographical differences, Baltic species typically have clear distribution limits in relation to

salinity and temperature (Fig. 1b). Many species including fish, bivalves, arthropods and algae of marine origin have a northern distribution border in the Quark, where the salinity drops from 5 psu in the south to 3 in the north (Haahtela 1974; Bergström & Bergström 1999). North of the Quark, most species originate from fresh water environments and therefore instead have southern distribution limits in relation to salinity (Segerstråle 1957). The Baltic Sea hosts a moderate number of species, compared to other areas with a longer history of brackish conditions, such as the Ponto Caspian area (Reid & Orlova 2002). There are no endemic species and since brackish conditions are not optimal for either fresh water or marine organisms, Baltic inhabitants are usually considered to be living under constant stress. Marine organisms like the blue mussel (*Mytilus edulis*) for example are much smaller in size in the Baltic Sea than on the Swedish west coast (Tedengren & Kautsky 1986). Although (or perhaps since) the number of species is low, Baltic species occur in very large numbers with a few very important keystone species like bladderwrack (*Fucus vesiculosus*) and the sea grass *Zostera marina*. Sea grass beds are present on soft bottoms in sheltered coastal areas and are essential breeding grounds for a large proportion of the coastal fish assemblage (Baden et al. 2003). *Fucus vesiculosus* is the only perennial, structure-building algae in the Baltic Sea. It is home to a large number of marine arthropods (Wikström & Kautsky 2007) and is also important for coastal fish species, providing shelter for small fish and fry and hunting grounds for larger individuals (Bäck et al. 1992). Due to eutrophication, the depth distribution of *Fucus vesiculosus* decreased after the 1940s with a minimum in the 1980s (Torn et al. 2006). However, there has lately been an improvement of the phytobenthic communities in the Baltic Sea. Today *Fucus vesiculosus* has the same depth distribution as in the 1940s in large parts of the Sea which can be explained by a decrease in inflow of nutrients from terrestrial systems due to increased efficiency of sewage treatment and a decreased leakage from agricultural lands (pers. com. Hans Kautsky). Among the animals *Mytilus edulis* is the most common species in large parts of the sea, constituting up to 90 % of the total animal biomass in coastal areas. The population of *Mytilus edulis* in the Baltic proper is believed to filter the whole water volume about 1.5 times a year which makes this species highly important in the recirculation of nutrients to the Baltic ecosystem.

## *Baltic Sea Shores*

Shoreline habitats are dynamic and change between terrestrial and aquatic over time. Since shorelines are situated on the border between terrestrial and aquatic environments the marine influences to terrestrial systems are substantial. The flow of energy from marine to terrestrial environment includes insects with aquatic larvae, fish eating birds and algal detritus (Kolb et al. 2010). Shoreline habitats depend on the inflow of marine energy to different degrees. When terrestrial productivity is high (e.g. species rich shore meadows) the marine influence is more limited than in places with low terrestrial productivity. Sandy or stony beaches for example can obtain high productivity if substantial amounts of marine energy is provided from algal beds and emerging insects.

The abiotic conditions along a sea coast form a unique environment. Processes like sand burial, high temperature, soil salinity and flooding create a heterogeneous environment (Ievinsh 2006). In the Baltic Sea large geographical differences make the conditions along the coast even more varied (Tyler 1969). The coast is heterogeneous with mainly shallow shores in the north, rocky shores dominating in the central part and sandy shores being common in the southern parts (Poland; Germany and southern Sweden). The steepness of the shore influences the vegetation. On rocky, steep slopes lichens dominate, with plants such as tall tussock grasses and a few herbs like *Allium schoenoprasum* and *Veronica longifolia* in crevices (Jerling 1999). In sheltered more shallow areas, fine grained particles and organic material can accumulate and create species rich shore meadows which can be found everywhere along the Baltic coast and usually occur on fine clay (Tyler 1969).

The coastlines of the Baltic Sea are still under the influence of the last ice age, with the strongest effect in the northern part of the Bothnian Sea where the isostatic rebound is 9 mm/year while the southernmost shorelines of the Baltic Sea are slowly sinking into the sea (Jerling 1999). Today the equilibrium line between eustatic sea level rise and isostatic rebound crosses the Baltic Sea in a west-east-directed arch from around Norrköping in Sweden to around Hanko in Finland (Fig. 1a). North of this line land is still rising and different successional stages of vegetation are found on the shores. Early successional stages (close to the water) are dominated by stress tolerant, clonal and usually wind pollinated species, including many grasses while long lived perennials that are usually insect pollinated dominate higher up on the shores. At older parts of the shores (close to the forest) woody plants can be found like alder, willows or rowan and in some places shores are dominated by

sea-buckthorn. In the Bothnian Bay and Bothnian Sea where isostatic rebound is high and ice scouring is intense, vegetation is typically low growing (Fig 2.). Many of the species living on these shores are also found in freshwater environments e.g. *Carex nigra* (Dijkema 1990). You also find many relicts from the last ice age that have been isolated from other water bodies because of the land uplift; examples are *Juncus gerardii*, *Silene uniflora*, and *Veronica longifolia*, as well as a few species that are endemic to the area, including *Deschampsia bottnica* and *Euphrasia bottnica* (Ås et al. 1997).



**Figure 2.** A typical shoreline habitat in the Bothnian Bay (northern Baltic Sea). Vegetation is typically low growing and marks from earlier ice scouring can be seen on the trees.  
Photo: Peter Hambäck

The largest proportion of the 200 000 islands in the Baltic Sea are present in archipelagoes in the Baltic proper (or Main Basin). The islands are of various sizes and include everything from quite large islands (i.e. Gräsö, Mörkö, Nämö, and Möja) with lots of habitats including large forest and lakes to a huge number of very small islands with no vegetation or only very small areas covered with vegetation. The salinity in these areas is moderate (5-6 psu) but plants growing close to the sea still need adaptations to saline soils. Historically, even small islands in the archipelagos were used for grazing livestock for a long time period (von Nümers & Korvenpää 2007; Aggemyr & Cousins 2012; Auffret et al. 2012) while agriculture took place on larger islands. Nowadays much management has been abandoned but in some parts of the archipelago the land is still kept open for natural preservation. Shore meadows in Baltic archipelagoes are typically small, isolated habitats surrounded by rocky areas and forest (Fig. 3).



**Figure 3.** Shore meadows in the archipelagoes of the Central Baltic Sea are usually small and isolated habitats in a heterogeneous landscape. Photo: Alma Strandmark (from the Stockholm archipelago).

Coastal areas in the southern Baltic Sea are generally very flat with long shallow sandy beaches and sea meadows (Fig. 4) that often border arable land. Since the salinity is high (Baltic Standard), the vegetation is comprised of many true sea shore species with adaptations for living in saline soils. Different adaptations to cope with the salt include excretion of  $\text{Na}^+$  through roots or salt glands or transportation to older leaf or leaf surface (Ievinsh 2006). On shore meadows there is typically a gradient inland with species tolerant to salinity closest to the sea, like sea reeds and sedges, more salinity sensitive species further inland and eventually trees and bushes longer from the water. Shore meadows in the south have traditionally been used for grazing and hay making (Jerling 1999). These human induced processes favor halophytes (e.g. *Puccinella maritima*, *Aster tripolium*, *Plantago maritima*, *Triglochin maritima*, *Spergularia media*, *Salicornia europaea*) by eliminating competitors for light and making the soil compact, keeping the salinity at high levels (Dijkema 1990). Nowadays however most grazing land has been abandoned, opening up the areas for other higher growing species like tall grasses (e.g. *Calamagrostis stricta*, *Agrostis stolonifera*, *Phragmites australis*) and bushes (Jutila 2001) and halophytes are predominantly found in wave exposed sites (Dijkema 1990).



**Figure 4.** Shore meadows along the coastline of the southern Baltic Sea are usually flat and continuous and often bordered by arable land. Photo: Gundula Kolb (a grazed shore meadow on the southern part of the island Öland).

The zonation of plants on shores mainly depends on changes in water levels (area of the shore that is flooded) salinity and soil properties (Jutila 2001). There is no tide in the Baltic Sea (only 1-4 cm in the main basin) and thus the daily fluctuations in water level are limited. The seasonal variations in sea levels are never the less large. In spring, water levels are low and at the end of summer they tend to rise, continuing to do so during autumn to reach the highest levels during winter (Tyler 1969). The largest fluctuations are found in the Gulf of Bothnia with an annual mean of 300 cm while the rest of the Baltic Sea fluctuates in the order of 160 cm (Ekman 1996). The salinity in the soil of shore meadows and other habitats varies over time in accordance with fresh water inflow, flooding, draught etc. Most shoreline plants are not able to germinate in soils with high salinity but need some kind of freshening of the soil, like heavy rain or run off during spring. As low water levels in late winter and spring coincide with high surface run off, favorable conditions for germination of sea shore plants are created on the Baltic coast (Dijkema 1990).

Baltic shoreline ecosystems are species rich in arthropods even though it is a highly fragmented landscape since the large majority is found in shore meadows where higher vegetation thrives. The arthropod community structure is different from mainland communities. Among herbivore species, lepidopterans are notably less abundant on the exposed shore meadows compared to coleopterans. Several ecological factors may underlie this difference, both connected to plant community structure and to physical factors such as wind and ice scouring. The predator community is dominated by generalist spiders, predatory heteropterans and coleopterans, and the by far most common predators in Baltic shoreline are wolf spiders, especially *Pardosa* sp (Mellbrand & Hambäck 2010). Wolf spiders are generalist feeders but a large percentage of their diet has been shown to be comprised of

insects with aquatic larvae, most commonly chironomids (Mellbrand et al. 2011). Spiders are typically successful colonizers, known to aggregate along coasts, and are often not depending on the terrestrial plant and insect community for food since they instead use energy of marine origin (Polis & Hurd 1995). The most successful carabid species on Baltic shorelines are also generalist predators with low degree of habitat specialization (Ås et al. 1997) although they might prefer one kind of habitat when available. The preference for special habitats is apparent in the distribution of individuals on islands of different size, with species on small islands being present in a larger variety of vegetation types than on larger islands (Kotze 2008). Usually species with good flying ability should be most common in fragmented landscapes (Kotze 2008), on islands in the Baltic Sea however *brachypterous* carabid species, which are poor flyers, are more common than expected (Ås 1984). Part of their success might be due to that they mainly migrate by floating, and thereby they can allocate more energy to growth and reproduction (instead of features such as wings and flight muscles) (Ås 1984).

### **Climate scenarios for the Baltic Sea area**

Climate projections for the Baltic Sea include higher water temperature (1-4 degrees Celsius), longer cyanobacteria blooms and a large reduction in ice-cover until 2100 (the ice cover in 2100 is predicted to be only one third of the current) (Neumann 2010). Reduction in length of the ice-cover season, particularly in the central Baltic, is projected by several models (Graham et al. 2008). In particular, the change in frequency of severe ice winters is expected to be large. At the same time cyclonic circulation is projected to increase in both the North Sea and the Baltic Sea due to more intense westerly winds, caused by intensification of NAO (North Atlantic oscillation) (Schrum 2001). Climate model simulations for wind speed vary between climate models (Graham et al. 2008) although it seems very likely that there will be an increase in average winter wind speed over the northern Baltic Sea (Graham et al. 2008; their figure 3.24) while the future wind speed during summer is more uncertain (Graham et al. 2008; their figure 3.25).

Sea levels are for most climate scenarios expected to rise between approximately 50 and 100 cm until 2100 (IPCC) and will be caused by a combination of thermal expansion of the oceans and a melting of glaciers and polar ice. In the southern Baltic, the isostatic uplift is already counterbalanced by the global eustatic sea level rise. The rate is presently about 3 mm y<sup>-1</sup>

(Church & White 2011) and Baltic values have shown little divergence to the global projections. Meier et al. (2004) simulated future Baltic sea level change for different climate scenarios and found that for Stockholm the change would be -480, -30 and 460 mm for global SLR of 90, 480 and 880 mm, respectively, until year 2100. According to the IPCC however, the rate is very likely to increase during the 21st century (Church et al. 2013) and in the Fifth Assessment Report (AR5), the 95% confidence estimates of global sea level rise vary from 260 mm to 970 mm for different emission scenarios (Church et al. 2013). Other recent estimates are even higher (AMAP 2012) and it is thus reasonable to believe that future sea level rise will be in the upper end of the IPCC projections which implies a northward shift in the line of equilibrium between isostatic rebound and sea level rise. In areas south of this line, even today shore erosion is a major problem which will be enhanced with increased sea levels.

The future salinity of the Baltic Sea is somewhat uncertain. Projections show a decreased salinity due to increased precipitation, and corresponding runoff in the northern Baltic while the case of the southern Baltic Sea is more uncertain. Global runoff forecasts, by the IPCC, must be interpreted with caution due to high internal runoff variability (Collins et al. 2013; their figure 12.24) and thus changes in salinity are indefinite. However since the Danish straits will deepen and become wider it is reasonable to believe that salt water intrusions will become more common in the future and thus the salinity in the southern parts of the sea could in fact increase.

## **Discussion**

### *Climate change and the Baltic Ecosystem*

A lower salinity in the northern parts of the Baltic Sea would move the latitudinal borders for many aquatic organisms. Plants and animals with marine origin, such as *Fucus vesiculosus* and *Mytilus edulis*, would probably move their distribution limit south from the Quark to the Åland Sea. Species like *Zostera marina*, with a higher salinity limit and a more southern distribution, would probably be found only in the southernmost parts of the Baltic Sea. In the Bothnian Sea and Bay, the large algal belts and the associated animals would disappear and the area would be dominated by fresh water organisms even more than today. A possible higher salinity in the south would favor marine organisms and most likely increase the number of species with more marine members. There are many invasive species that are on

the edge to enter the Baltic Sea, including several Ponto Caspian gobids, which would be favored by higher temperature and salinity and be more likely to establish in Baltic waters. Invasive species that are present already today, but are not able to breed due to the low salinity e.g. the Chinese mitten crab (*Eriocheir sinensis*) might be able to establish viable populations in the future (Ojaveer et al. 2007).

Higher water temperatures and more frequent episodes of extremely high water temperatures will have large consequences for many aquatic organisms. Except for favoring warm water species over cold water species, higher water temperatures will also increase the metabolic rates of all plants and animals. Filamentous and fast growing algae will have advantage over more slow growing species like *Fucus vesiculosus* when competing for space. For animals higher temperatures might be disastrous if food availability does not increase correspondingly. For example, *Mytilus edulis* showed a large reduction in species number following a long period of extremely high water temperature when primary production was also low. High water temperatures concurring with high primary production on the other hand did not affect the population (pers com Hans Kautsky). If *Mytilus edulis* would decrease substantially in numbers the consequences would be large since it is a very important species for the recirculation of nutrients in the Baltic ecosystem.

Eutrophication of the Baltic Sea will be boosted by higher water temperatures, with prolonged summer periods intensifying the phosphorous-recycling from sediments. Changed precipitation regimes and increased surface run off, in some areas, will also result in a higher release of nutrients to coastal waters. Higher primary production due to increased availability of nutrients will decrease the Secchi depth, and thereby also the depth at which algae can grow and the algal belts will thus narrow. New substrate will be made available by sea level rise and the algal belts will move upwards. In the competition for space on the newly submerged substrate, filamentous and fast growing species will have an advantage over more slowly growing species like *Fucus vesiculosus*. Higher nutrient loading will further lead to more hypoxia in coastal areas due to enhanced stratification, decreased oxygen solubility, increased metabolism and remineralization rates and higher production of organic matter (Rabalais et al. 2009). Vertical mixing of the water in the Baltic Sea is forced by the wind and has a clear seasonal cycle and the projected changes of wind pattern will influence the water circulation and vertical mixing and affect the stagnation in deep waters due to increased stratification (Rabalais et al. 2009). Temperature in itself might also increase the stratification in the Baltic Sea, especially in the north due to the freshening of the surface water. Less

dissolved oxygen in the bottom waters with decreased oxygen diffusion from the upper layers to the bottom will have large effect on biological communities, cause less secondary production and disrupted biochemical cycles (Rabalais et al. 2009).

Cyanobacterial blooms are expected to become more frequent and prolonged with increased eutrophication, and climate change will further boost the blooms since rising temperatures, enhanced vertical stratification and alterations in seasonal weather patterns (draught storms, floods etc.) are all favorable changes for cyanobacteria in eutrophic waters (Paerl & Huisman 2009). Warmer temperature benefit cyanobacteria by increasing their growth rate, dominance, persistence, geographical distribution and activity. After a bloom, cyanobacteria sink to the sea floor and are consumed by benthic organisms. The hepatotoxin nodularin from *Nodularia spumigena*, which is often a dominating species in algal blooms during summer, has been shown to accumulate in bottom dwelling organism and continue up in the food chain through trophic transfer (Nascimento et al. 2009). Since the inflow of marine energy to shoreline ecosystems is so large, it seems fairly likely that the same signal can be traced also in terrestrial food chains. The impact of increased algal blooms to terrestrial shore species is uncertain although some species of cyanobacteria have been shown to contain an insecticide (Becher & Jüttner 2005) and in marine habitats they can cause oxygen depletion, kill fish and suppress the establishment and growth of macro algae (Paerl & Huisman 2009).

For many shoreline ecosystem the inflow of marine energy is very important and if the species composition in the sea changes so will the composition (and quality?) of shoreline algal beds. It seems that terrestrial arthropods are not as common and wolf spiders are almost absent on the filamentous algal beds compared to algal beds that are dominated by *Fucus vesiculosus* (pers obs from Öland and Stockholm archipelago). Even though filamentous algae might provide sufficient nutrients for terrestrial species they do not possess the same structural benefits (for e.g. hiding) as *Fucus*-beds.

#### *Climate change and Baltic shoreline ecosystems*

Since many insect species are limited by cold temperature (and not heat), a warmer climate, with a longer period of suitable condition, should be favorable. But herbivorous insects, that are associated to one or a few plant species, both depend on successful adaptation to their host plant and the climate. Thus in a changing climate they are also affected by how their host

plant reacts to climate factors like higher temperature. If the host plants are negatively affected by high temperature (or even disappear) the herbivores depending on them naturally would be affected too. Additionally, even if the host plant is favored by warmer temperature it is possible that a faster life cycle of the plant would make it available for insects for a shorter time or too early in the year (Bale et al. 2002). Temperature and changed precipitation regimes are expected to be the main climate factors affecting plant species (Thuiller et al. 2005) since they affect the soil moisture dynamics with higher temperature enhancing evapotranspiration and accelerating the hydrological cycle (Dòdorico et al. 2010). Temperature and water supply are critical drivers for seed germination. In the Baltic Sea, low water levels and high freshwater inflow during spring produce favorable conditions for the germination of sea shore plants (Jerling 1999). Rising sea levels and more and larger fluctuations might jeopardize these favorable conditions with consequences for many sea shore plants and their associated insects. Further, although flooding of shore meadows during parts of the year help to keep them open, by making it impossible for higher vegetation to settle, flooding during the wrong time of year (during some critical point of development) and during too long periods (creating long periods of oxygen depletion in the soil), might be disastrous.

Rising sea levels are continuously moving the border north where the expanding water equals the rise of new land by the isostatic rebound (Fig. 1a). Successful migration is of course depending on the organism's dispersal ability but also on physical properties in the surroundings. Dispersal is affected by the size of patches and distances to the next suitable habitat, but also on the occurrence of dispersal barriers and corridors and network dimensionality (Englund & Hambäck 2007). Some shoreline habitats might move upwards when water levels are elevated, whereas in other cases the shoreline habitat might be bordered by dispersal barriers like steep rocks or forests and species will have to rely on their ability to colonize other areas. Upwards migration of shoreline plants may also be limited because land uplift has concentrated fertile habitats to low lying parts of the islands. The shore-line vegetation in large parts of the Baltic Sea, and the associated arthropod community, depends on the continuous supply of fresh land to colonize combined with a regular physical disturbance that limits domination of higher plants. Pioneer species are usually bad competitors for space and resources and are depending on new areas that have not yet been colonized by other species. There is a possibility that the northern shoreline ecosystems will change towards becoming more similar to those in the south with a domination of higher

vegetation. However, although shorter winters will prolong the growing period for northern species and make it possible for new species to establish populations, the projected decrease in sea ice might together with increased wind speed during winter in the northern Baltic Sea produce more challenging conditions for sea shore plants. If conditions shift between mild and cold weather, ice drift and ridge formation might increase and together with stronger winds change the timing and occurrence of ice scouring. Exactly which species that will suffer most and which species that will be favored is hard to guess but I believe that shoreline ecosystems in the Bothnian Sea and Bay will have a very different species composition in the future.

With an increased sea level many of the already small and isolated habitats in Baltic archipelagos will be further diminished or disappear completely. These areas function as refuges for meadow plants that decreased following farmland abandonments (Löfgren & Jerling 2002). The lack of grassland management is today of great concern for nature conservation as species diversity and grassland quality depend on continuous management (Jerling 1999; Jutila 2001; Cousins & Eriksson 2001) important both for plant species richness and many rare birds and amphibians (Helle et al. 1988; Sammull et al. 2012). The combination of eutrophication and cessation of grazing together with climate change is a great threat to the plant species diversity of islands in the archipelago (Aggemyr & Cousins 2012) and on Baltic Sea shorelines. Conservation of halophytic communities should be managed with grazing, without this management shoreline ecosystems in brackish conditions will no longer host halophytes (Dijkema 1990). Since generalist species are usually less dependent on the size of the habitat they are believed to cope better with fragmentation and highly mobile species are more likely to be able to find other habitats in a landscape of increasing fragmentation. Spiders are good colonizers (Polis & Hurd 1995), and spiders on Baltic Sea shores are predominantly generalist species like wolf spiders. Together with other generalist predators like carabids, the spiders will probably cope with climate induced habitat fragmentation quit well. Wolf spiders are also not totally depending on terrestrial energy for their survival. Chironomids are predicted to be favored by higher temperatures and wolf spiders would thereby not suffer from shortage of food even if some terrestrial prey species might be negatively affected by temperature and fragmentation.

Though shore meadows in the southern Baltic are typically large and continuous, they are often bordered by arable land, houses, roads or other areas of human interest making it hard for species to move upwards when water levels become higher. If the salinity in the southern

Baltic Sea increase, the species living in these areas will be forced to cope with an even larger salinity stress than today and thus, species that are sensitive to high salinity might move further from the water (where competition for space might be greater). A higher sea level and larger fluctuations will also cause longer periods of flooding which will increase the salinity stress even more. Salt tolerant species will probably be able to colonize larger proportions of the shoreline habitats and the zonation of plants in southern Baltic shoreline habitats might be very different in the future.

Naturally the effects on shoreline ecosystems due to different aspects of climate change will depend on how fast the changes are and how long the different species will have to adapt but also on the life history traits of the different species. Baltic shoreline habitats are dynamic and heterogeneous and there is no way of predicting how they will react to such large changes in abiotic conditions but, no species will be affected without affecting its environment and other species. Already Darwin said that higher trophic levels increase the diversity of lower trophic levels by preventing competition and thereby the dominance of one species (top-down effect). The bottom up effect on diversity was also initiated by Darwin by saying that the plant community might influence the predators by changing the diversity of herbivores. So if one species is affected the effects will cascade up or down the food chain in different ways.

### *Climate change and Ecosystem services*

During recent years the most profound consequences of climate change on coastlines and islands have been extensively discussed. The world's population is to a large part concentrated to the coastlines and ecosystem services provided by coastal systems are many and valuable. Ecosystem services include fish breeding habitats and habitat for other source of sea food, areas for harbors and trade at sea, storm shelter, as well as recreational values like swimming, sun bathing, different water sports and scenic views. Coastal habitats like shore meadows and salt marshes also provide cleaning of water and productive grazing-land. Further, many coastal ecosystems provide protection against catastrophic events caused by a warmer climate and when the natural ecosystems are lost reconstruction of this protection by buildings or restoration of ecosystems is often very expensive and sometimes not even possible (Barbier et al. 2008). Despite all the benefits of coastal ecosystems, there is a conflict between human interests and conservation since coastlines are so attractive for human settlement and activities. This conflict will probably be intensified when natural ecosystems

as well as human constructions and interests are affected by climate change. Precast for the Baltic Sea include flooding of coastal areas, erosion of sandy beaches and destruction of harbor buildings. Climate change will also put enormous pressure on a large number of valuable ecosystems both on land and in sea, like many habitats for rare vascular plants and breeding habitats for birds. Many sandy beaches in the southern Baltic Sea that are intensively used for recreational values will disappear (Kont et al. 2003) and people with houses close to the water will be forced to move. Intrusion of seawater to groundwater is already a large problem for many house owners close to the Baltic Sea. Higher sea levels can increase the inflow of salt water further inland. The distribution of sea intrusion vulnerability, in terms of proximity to spatiotemporal and managerial thresholds, around the Baltic remains to be assessed (Mazi et al. 2014). A general conclusion, however, is that appropriate management of pumping and/or artificial recharge of coastal groundwater is needed and must uphold some minimum discharge of fresh groundwater to the sea in order to control seawater intrusion under rising sea level and climate change. To deal with the increasing problem of seawater intrusion, connection to municipal water and wastewater handling for house owners who currently rely only on private wells and sewage systems close to the sea may be part of a solution.

Humans might need to move some structures and buildings to new places when sea levels increase. Since humans often prefer to place the buildings in sheltered areas with a shallow coastline the most heavily exploited areas are also where species rich shore meadows are found, as well as valuable habitats like sea grass beds under the surface. With possible further exploitation combined with fragmentation caused by sea level rise and other impacts of climate change these areas will be under enormous pressure in the future. To preserve valuable species or habitats in the face of climate change it might be necessary to preserve areas close to the location of the intended object that represent the suitable climate conditions of the future. By conservation biologists this approach is called the “Climate envelope”. This approach is hard to follow in reality, since areas of possible future biological value are often occupied by humans. In Sweden the 100 meters closest to the shoreline is protected from new buildings. However, large proportions of this area are already exploited and dispensations for buildings within this zone are common. This shoreline protection should be more heavily enforced in the future and management of coastal shore meadows should be made a priority

## References

- Aggemyr, E. & Cousins, S.A.O. (2012) Landscape structure and land use history influence changes in island plant composition after 100 years. -*Journal of Biogeography* 39: 1645-1656.
- AMAP (2012) Arctic Climate Issues 2011: Changes in Arctic Snow, Water, Ice and Permafrost. SWIPA 2011 Overview Report, Oslo: Arctic Monitoring and Assessment Programme (AMAP).
- Ås, S. (1984) To fly or not to fly? Colonization of Baltic islands by winged and wingless carabid beetles. -*Journal of Biogeography* 11: 413-326.
- Ås, S., Bengtsson, J. & Ebenhard, T. (1997) Archipelagoes and theories of insularity. -*Ecological Bulletins* 88-116.
- Auffret, A.G., Schmucki, R., Reimark, J. & Cousins, S.A.O. (2012) Grazing networks provide useful functional connectivity for plants in fragmented systems. -*Journal of Vegetation Science* 23: 970-977.
- Bäck, S., Collins, J. C. & Russell, G. (1992) Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. -*British Phycological Journal* 27: 39-47.
- Baden, S., Gullström, M., Lundén, B., Pihl, L. & Rosenberg, R. (2003) Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. -*AMBIO: a Journal of the Human Environment* 325: 374-377.
- Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C. et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. -*Global Change Biology* 8: 1-16.
- Barbier, E. B., Koch, E. W., Silliman, B. R., Hacker, S. D. et al. (2008) Coastal ecosystem-based management with nonlinear ecological functions and values. -*Science* 319: 321-323.
- Becher, P. G. & Jüttner, F. (2005) Insecticidal compounds of the biofilm forming cyanobacterium *Fischerella* sp.(ATCC 43239). -*Environmental toxicology* 20: 363-372.
- Bergström, L. & Bergström, U. (1999) Species diversity and distribution of aquatic macrophytes in the Northern Quark, Baltic Sea. -*Nordic Journal of Botany* 19: 375-383.

Bonsdorff, E. (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology* 330: 383-391.

Church, J.A., Clark, P.U., Cazenave, A., Gregory, J.M. et al. (2013) *Sea Level Change*. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Church, J.A. & White, N. J. (2011) Sea-Level Rise from the Late 19th to the Early 21st Century. *-Surveys in Geophysics* 32: 585–602.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L. et al. (2013) *Long-term Climate Change: Projections, Commitments and Irreversibility*. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Cousins, S. A. & Eriksson O. (2001) Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. *-Ecography* 24: 461-469.

Crist, T. O., Veech, J. A., Gering, J. C. & Summerville, K. S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity. *-The American Naturalist* 162: 734-743.

Dijkema, K. S. (1990) Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: their vegetation and management. *-Biological Conservation* 51: 191-209.

D'Odorico, P., Laio, F., Porporato, A., Ridolfi, L., Rinaldo, A. & Rodriguez-Iturbe, I. 2010. Ecohydrology of terrestrial ecosystems. *-BioScience* 60: 898-907.

Drakare, S., Lennon, J. J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *-Ecology letters* 9: 215-227.

- Ekman, M. (1996) A consistent map of the postglacial uplift of Fennoscandia. -*Terra Nova* 8:158–165.
- Englund, G. & Hambäck, P. A. (2007) Scale dependence of immigration rates: models, metrics and data. -*Journal of animal ecology* 76: 30-35.
- Graham, L. P., Chen, D., Christensen, O. B., Kjellström, E. et al. (2008) *Assessment of Climate Change for the Baltic Sea Basin. Projections of future anthropogenic climate change.* Springer Berlin Heidelberg.
- Haahtela, I. (1974) The marine element in the fauna of the Bothnian Bay. -*Aquatic Ecology* 8: 232-241.
- Hambäck, P. A., Summerville, K. S., Steffan-Dewenter, I., Krauss, J., Englund, G. & Crist, T. O. (2007) Habitat specialization, body size, and family identity explain Lepidopteran density–area relationships in a cross-continental comparison. -*Proceedings of the National Academy of Sciences* 104: 8368-8373.
- Hambäck, P. A., Bergman, K. O., Bommarco, R., Krauss, J., Kuussaari, M., Pöyry, J. & Öckinger, E. (2010) Allometric density responses in butterflies: the response to small and large patches by small and large species. -*Ecography* 33: 1149-1156.
- Hannerz, F. & Destouni, G. (2006) Spatial characterization of the Baltic Sea drainage basin and its unmonitored catchments. -*AMBIO: A Journal of the Human Environment* 35: 214-219.
- Helle, E., Helle, P. & Väisänen, R. A. (1988) Population trends among archipelago birds in the Krunnit sanctuary, northern Gulf of Bothnia, in 1939–1985. -*Ornis Fennica* 65: 1–12.
- Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. (1999) Trophic rank and the species-area relationship. -*Ecology* 80: 1495-1504.
- Ievinsh, G. (2006) Biological basis of biological diversity: physiological adaptations of plants to heterogeneous habitats along a sea coast. -*Acta University Latvia* 710: 53-79.
- Jerling, L. (1999) Sea shores. -*Acta Phytogeographica Suecica* 84: 169-185.
- Jutila, H. (2001) How does grazing by cattle modify the vegetation of coastal grasslands along the Baltic Sea? -*Annales Botanici Fennici* 38: 181-200.

- Kolb, G. S., Jerling, L. & Hambäck, P. A. (2010) The impact of cormorants on plant–arthropod food webs on their nesting islands. *-Ecosystems* 13: 353-366.
- Kont, A., Jaagus, J. & Aunap, R. (2003) Climate change scenarios and the effect of sea-level rise for Estonia. *-Global and Planetary Change* 36: 1-15.
- Kotze, D. J. (2008) The occurrence and distribution of carabid beetles (*Carabidae*) on islands in the Baltic Sea: a review. *-Journal of insect conservation* 12: 265-276.
- Lane, J. E. & Jensen, S. T. (1996) States and common pool resources. *-Scandinavian Political Studies* 19: 95-109.
- Leppäranta, M. & Myrberg, K. (2009) *Physical Oceanography of the Baltic sea*. Praxis Publishing Ltd Chichester, UK, Germany.
- Löfgren, A. & Jerling, L. (2002) Species richness, extinction and immigration rates of vascular plants on islands in the Stockholm Archipelago, Sweden, during a century of ceasing management. *-Folia Geobotanica* 37: 297-308.
- Lomolino, M. (2000) A call for a new paradigm of island biogeography. *-Global Ecology and Biogeography* 9: 1-6.
- Lomolino, M. V. & Weiser, M. D. (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *-Journal of Biogeography* 28: 431-445.
- MacArthur, R. H. (1967) *The theory of island biogeography* (Vol. 1). Princeton University Press.
- Mazi, K., Koussis, A. D. & Destouni, G. (2014) Intensively exploited Mediterranean aquifers: resilience to seawater intrusion and proximity to critical thresholds. *-Hydrology and Earth System Sciences*. In press.
- McKinney, M. L. & Lockwood, J. L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *-Trends in ecology & evolution* 14: 450-453.
- Meier, H.M., Broman, B. & Kjellstrom, E. (2004) Simulated sea level in past and future climates of the Baltic Sea. *-Climate Research* 27: 59–75.

- Mellbrand, K., & Hambäck, P. A. (2010) Coastal niches for terrestrial predators: a stable isotope study. -*Canadian Journal of Zoology* 88: 1077-1085.
- Mellbrand, K., Lavery, P. S., Hyndes, G. & Hambäck, P. A. (2011) Linking land and sea: different pathways for marine subsidies. -*Ecosystems* 14: 732-744.
- Nascimento, F. J., Karlson, A. M., Näslund, J. & Gorokhova, E. (2009) Settling cyanobacterial blooms do not improve growth conditions for soft bottom meiofauna. -*Journal of Experimental Marine Biology and Ecology* 368: 138-146.
- Neumann, T. (2010) Climate-change effects on the Baltic Sea ecosystem: A model study. *Journal of Marine Systems* 81: 213-224.
- Nümers von, M. & Korvenpää, T. (2007) 20th century vegetation changes in an island archipelago, SW Finland. -*Ecography* 30: 789-800.
- Ojaveer, H., Gollasch, S., Jaanus, A., Kotta, J. et al. (2007) Chinese mitten crab *Eriocheir sinensis* in the Baltic Sea - a supply-side invader? -*Biological Invasions* 9: 409-418.
- Paerl, H. W. & Huisman, J. (2009) Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. -*Environmental Microbiology Reports* 1: 27-37.
- Parker, M., Thompson, J. N. & Weller, S. G. (2001) The population biology of invasive species. -*Annales Rev. Ecol. Syst* 32: 305-32.
- Polis, G. A., & Hurd, S. D. (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. -*Proceedings of the National Academy of Sciences* 92: 4382-4386.
- Rabalais, N. N., Turner, R. E., Díaz, R. J. & Justić, D. (2009) Global change and eutrophication of coastal waters. ICES Journal of Marine Science: -*Journal du Conseil* 66: 1528-1537.
- Reid, D. F. & Orlova, M. I. (2002) Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. -*Canadian Journal of Fisheries and Aquatic Science* 59: 1144-1158.

- Ricklefs, R. E. & Lovette, I. J. (1999) The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. -*Journal of Animal Ecology* 68: 1142-1160.
- Sammul, M., Kauer, K. & Köster, T. (2012) Biomass accumulation during reed encroachment reduces efficiency of restoration of Baltic coastal grasslands. -*Applied Vegetation Science* 15: 219-230.
- Schrum, C. (2001) Regionalization of climate change for the North Sea and Baltic Sea. -*Climate Research* 18: 31-37.
- Segerstråle, S. G. (1957) Baltic Sea. -*Geological Society of America Memoirs* 67: 751-800.
- Summerville, K. S., Wilson, T. D., Veech, J. A. & Crist, T. O. (2006) Do body size and diet breadth affect partitioning of species diversity? A test with forest Lepidoptera. -*Diversity and Distributions* 12: 91-99.
- Tedengren, M. & Kautsky, N. (1986) Comparative study of the physiology and its probable effect on size in blue mussels (*Mytilus edulis* L.) from the North Sea and the northern Baltic proper. -*Ophelia* 25: 147-155.
- Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T. & Prentice, I. C. (2005) Climate change threats to plant diversity in Europe. -*Proceedings of the National Academy of Sciences of the United States of America* 102: 8245-8250.
- Torn, K., Krause-Jensen, D. & Martin, G. (2006) Present and past depth distribution of bladderwrack (< i> *Fucus vesiculosus*</i>) in the Baltic Sea. -*Aquatic Botany* 84: 53-62.
- Travis, J. M. J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. -*Proceedings of the Royal Society of London. Series B: Biological Sciences* 270: 467-473.
- Tyler, G. (1969) Regional aspects of Baltic shore-meadow vegetation. *Vegetatio* 19: 60-86.
- Verberk, W. C., Van Der Velde, G. & Esselink, H. (2010) Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. -*Journal of Animal Ecology* 79: 589-601.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. - *Ecological Monographs* 30: 279-338

Whittaker, R. H. (1972) Evolution and measurement of species diversity. -*Taxon* 21:213-251.

Wikström, S. A. & Kautsky, L. (2007) Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. -*Estuarine, Coastal and Shelf Science* 72: 168-176.

Williamson, M., Gaston, K. J. & Lonsdale, W. M. (2001) The species–area relationship does not have an asymptote! -*Journal of Biogeography* 28: 827-830.