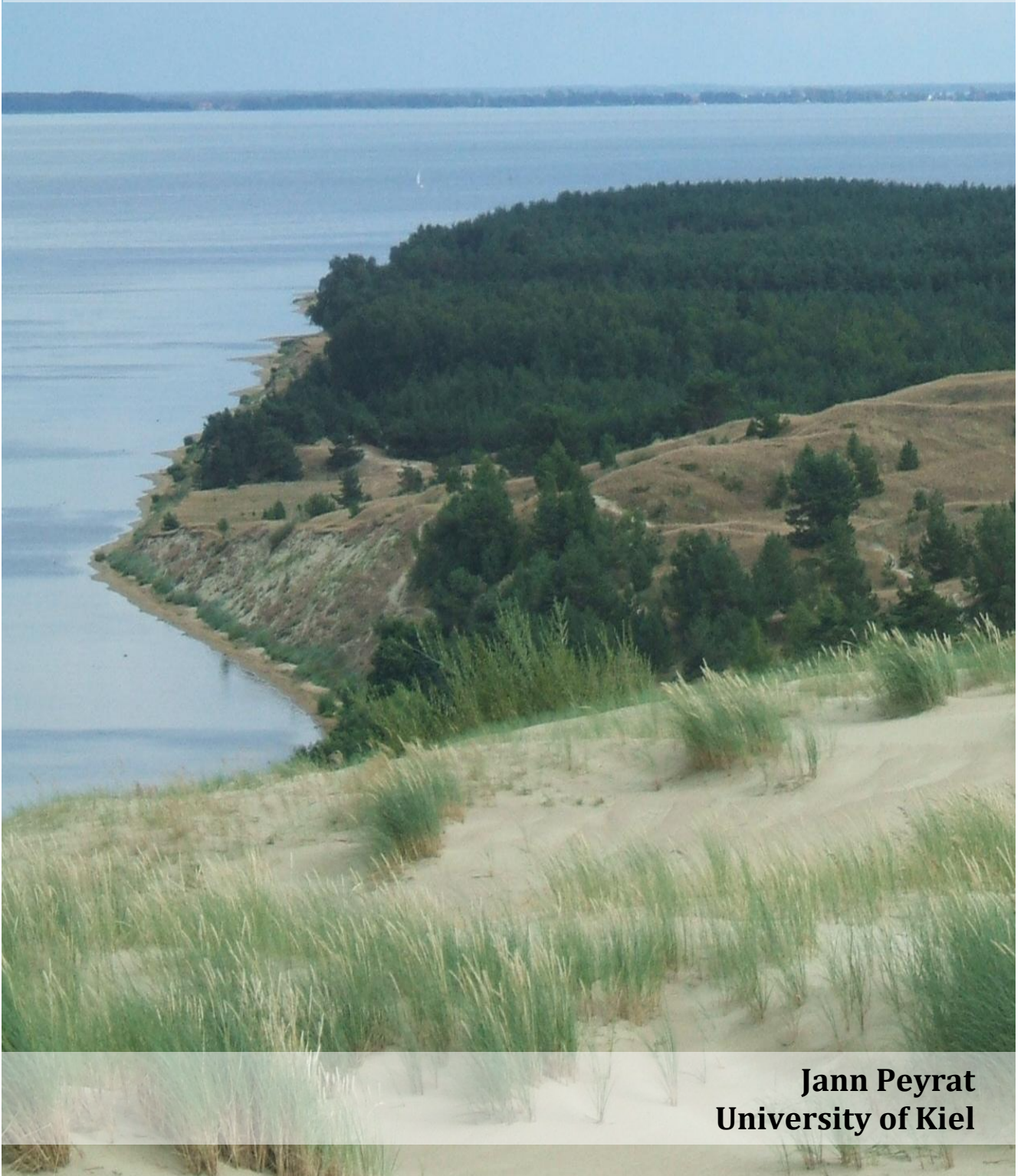


# **Landscape and vegetation of southern Baltic dune systems: diversity, landuse changes and threats**



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Cover: Dune landscape at the Nagliai Strict Nature Reserve, Curonian Spit, LT (Photo: Peyrat 2008).

Aus dem Institut für Natur- und Ressourcenschutz  
der Christian-Albrechts-Universität zu Kiel

# **Landscape and vegetation of southern Baltic dune systems: diversity, landuse changes and threats**

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# Contents

Chapter 1	Introduction.....	9
Chapter 2	Plant communities of the Sundic Baltic Sand Dune..... Vegetation Complex on dry coastal dunes along the southern Baltic coast. Peyrat J. 2010. <i>Botanica Lithuanica</i> 16 (4): 149–167.	35
Chapter 3	Neophytic <i>Corispermum pallasii</i> (Stev.) (Chenopodiaceae) ..... invading migrating dunes of the southern coast of the Baltic Sea. Dolnik C., J. Peyrat, A. Volodina and A. Sokolov. 2011. <i>Polish Journal of Ecology</i> 59 (2): 17-25.	59
Chapter 4	Plant species diversity in dry coastal dunes of the Southern ..... Baltic coast. Peyrat J. and A. Fichtner. submitted. <i>Community Ecology</i> .	73
Chapter 5	Vegetation dynamics on the Łeba Bar/Poland: a comparison ..... of the vegetation in 1932 and 2006 with special regard to endangered habitats. Peyrat J., M. Braun, C. Dolnik, M. Isermann and H. Roweck. 2009. <i>Journal of Coastal Conservation</i> 13 (4): 235–246.	90
Chapter 6	Synthesis .....	111
Summary	.....	127
Zusammenfassung.....		130
Краткий обзор (Russian summary).....		133
Danksagung .....		136
Curriculum vitae.....		138
Erklärungen .....		139



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I carried out the field work and I was responsible for data analyses and writing of the manuscripts of the publications from chapter 2, 4 and 5. A. Fichtner helped me with the statistical data analyses of the publication from chapter 4. C. Braun, C. Dolnik, M. Isermann and H. Roweck contributed to ideas and discussion for the publication of chapter 5. The publication of chapter 3 was written together with C. Dolnik, A. Volodina and A. Sokolov. I provided data material and contributed to ideas and discussion.





The migrating dune 'Roterwald Berg' on the Curonian Spit, RU/LT (Photo: Peyrat 2008).



Chapter 1

# **Introduction**

## Introduction

Coastal sand dunes form a narrow ecocline between two extremely contrasting biocoenoses, sea and land (Westhoff 1985). In North-West Europe, they form extensive dune systems along the exposed coasts from Portugal through France and the Netherlands to North Denmark and along the southern Baltic Sea with large barrier islands and spits. Although covering less than 1 % of the land surface of Europe, a length of 80,000 km is estimated for coastal dunes (Klijin 1994). Coastal dunes are of high ecological value: Their spatial and temporal dynamics support a wealth of habitats with many endangered or endemic plant and animal species. More than 50 % of all indigenous species in Western Europe (van der Meulen and de Haes 1996) and 20 % of all European endemics (van der Maarel and van der Maarel-Versluys 1997) are found in the coastal zones. Although the contribution by these rare and endangered species to ecosystem function may be small, they form the pillars of many conservation programs promoted by the EU Directive 92/43 (Acosta et al. 2009). The high species richness and diversity in coastal dunes is the result of environmental heterogeneity and variability of species composition (van der Maarel 2003). Thus, coastal dunes are among the most valuable still extant elements of natural environment and natural resources in Europe (Isermann in press). Since the 19<sup>th</sup> century they have been subjected to important ecological research resulting with theories about vegetation succession and ecological system functions in these coastal dunes.

Despite their high ecological value, many coastal dune systems in Europe and worldwide have been heavily degraded over the last centuries following exploitation of their natural resources, demographic expansion and industrial growth (Martinez et al. 2004). A huge expanse of previously well preserved coastal ecosystems has been deteriorated or is in advanced stages of degradation, both resulting in a loss of biodiversity (Van der Meulen and de Haes 1996). It is estimated that 25 % of European coastal dunes have been lost since 1900 (Heslenfeld et al. 2004). At the Convention of Biological Diversity in Rio de Janeiro (1992), it was established that human intervention was responsible for the decline in biodiversity. In order to protect coastal ecosystems along the European coastlines, national parks or nature reserves were established; for example the Waddensea Nationalpark of the North Sea, Nationalpark Vorpommersche Boddenlandschaft Slowinski Nationalpark and Curonian Spit Nationalpark in the Baltic. Furthermore, a number of coastal habitats are protected under the European Habitats Directive (Council Directive 92/43/EEC of 21 May 1992, Council of the European Commission 1992). The principal aim of this directive is for the preservation and restoration of the biological diversity as well as the creation of a favorable conservation status of the natural habitats and their associated fauna and flora. Ten coastal dune habitats of the “Sea Dunes of the Atlantic, North Sea and Baltic coasts”, are considered as priority habitats, such as “Shifting dunes along the shore-

line with *Ammophila arenaria* 2120", "Fixed coastal dunes with herbaceous vegetation \*2130" or "Decalcified fixed dunes with *Empetrum nigrum* \*2140" (Houston 2005). Additionally, many coastal dunes are listed in the CORINE biotope classification as Nature 2000 sites stating that these habitats deserve special conservation attention and are a target of nature conservation in Europe (Herrier and Killemaes 1998).

This research work focuses on coastal dune systems along the southern Baltic coast, where dunes are a common feature and occupy large stretches of the coastline. Important examples of dune systems are found along the German Baltic coast, such as on the Darß peninsula and on the Islands of Rügen and Usedom. In Poland, extensive dunes systems exist on the Łeba Bar, the Hel peninsula and along the Vistula Spit. Eastwards large dune systems dominate the Curonian Spit (Russian Oblast of Kaliningrad and Lithuania). Almost half of the total Latvian coastline is composed of embryonic, yellow and brown dunes; the largest areas are on the open Baltic coast and on the South coast (Kabucis and Aunins 1998, Laima and Tjarve 2009). Along the Danish and Swedish Kattegat coastline and its archipelago, dune fields are not as extensive as on the Danish Island of Anholt, where they are outstanding by European standards due to their relatively authentic nature and extensive lichen-rich coastal heath vegetation (Andersen 1998, Johansson 1998, Christensen and Johnsen 2001).

## **Coastal dunes along the Southern Baltic coast**

### **Geology and dune formation**

The Baltic Sea, with an area of about 415,000 km<sup>2</sup>, is the world largest brackish water system and is geologically a young area (Winterhalter et al. 1981). Its evolution was initiated by the melting of the ice-sheet during the last glacial period 15,000 years ago. This process was associated with a rapid rise of the sea level, which caused a simple drowning of the relief resulting in lesser sediment relocations (Lampe et al. 2005). With the ending of the Littorina transgression 5,700 years ago, hydrodynamic processes started to shape the southern Baltic coastlines (Janke et al. 1993). The reduction of the rise in the sea level with increasing influence of sediment dynamics and sedimentary transport along the shore reshaped large parts of the coast. Holocene structures such as spits and barriers with their systems of beachridges and dunes at the front and peatlands at the back evolve between the Pleistocene cores (Schumacher 2002). Important examples for spits and barriers along the southern Baltic coast are the Darss-Zingst-Peninsula, the Vistula Spit and Curonian Spit (Meyer et al. 2008). The present coastal landscape of the southern Baltic coast is characterised by eroding moraine cliffs, alternating with sandy coasts, sandy spits and with large dune complexes, forming a smooth abrasive-accumulative coastline (Borówka 1990).

Coastal dunes form on coastlines with an adequate supply of sand within the size range 0.2–2.0 mm (Doody 1991). Material for coastal dunes of the Southern Baltic originates from marine abrasion of nearby Holocene moraine cliffs. Water-deposited sand, dried out at low tide and blown onto the land by onshore winds, is the initial source for the establishment of dunes (Packham and Willis 1997).

### **Soil development and properties**

Soil patterns in coastal dunes are very complex as vegetation and geomorphic processes are both important soil forming factors (Jungerius 1990). In general, coastal sand dune systems show a regular succession from more active and unstable fore-dunes at the top of the beach to older, more stable vegetated dunes inland (Gerrard 1981) (Figure 1).

Geomorphological processes on the beach, such as sand shift and periodic inundation, prevent a lasting sedimentation. In higher beach zones few pioneer plant species are able to withstand this extreme substrate activity combined with the influx of NaCl from seaspray (Jungerius 1990). They fix the substrate and built up small foredunes and yellow dunes (Figure 1). Erosion processes and sand burial alternate with stabilization of the substrate in this zone (Jungerius 1990). Soils are characterized by primary, often invisible, humus accumulation, alkaline pH-values and high calcium carbonate contents (Piotrowska 1988, Peyrat 2007). Along the Southern Baltic coast from Germany to Lithuania, the mean pH in yellow dunes varies between 6.0 (Darß peninsula), 6.7 (Rügen), 7.0 (Usedom), 7.0 (Leba), 6.9 (Vistula Spit) and 6.9 (Curonian Spit) (own unpublished material). Isermann (2005) and Remke et al. (2009a) report similar pH-values for dune sands along the German Baltic coast from Rostock eastwards and for the Eastern Baltic coast (Poland, Lithuania), respectively.

With increasing distance from the sea, sand incursions decrease and a closer vegetation cover develops. Geomorphologic processes are no longer important and intermediate stages of soil development are initiated (Peyrat 2007). Accumulation of organic matter becomes apparent and translocation of mineral compounds to deeper parts of the soil leads to the formation of an eluvial horizon (Scheffer and Schachtschabel 1998). Weathering processes and precipitation effect a rapid leaching loss of calcium during the dune succession. Decalcification is combined with acidification: the pH decreases from 7.0–6.0 in yellow dunes to 3.5 under pine woods of brown dunes (Piotrowska 1988, Peyrat 2007). This tendency is also described by Giani and Buhmann (2004) for a sand dune chronosequence on the East Frisian Island of Spiekeroog and for dunes along the German Baltic coast by Isermann (2005).

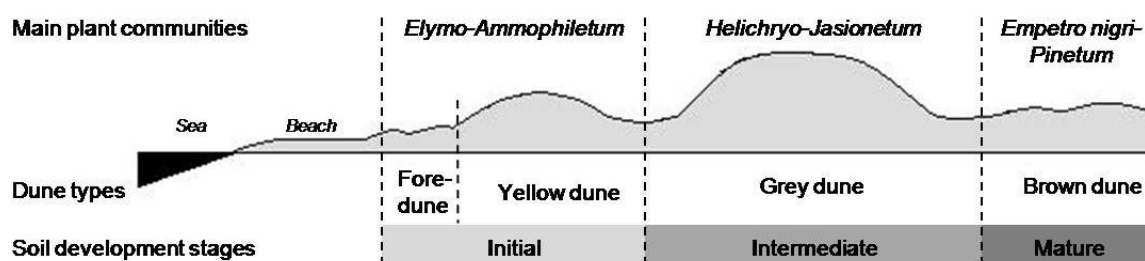
Podzolisation is the predominant trend in the evolution of dune soils, and is most recognisable in the mature stage of soil formation on older and stable surfaces under pine plantations (Sevink 1991). Transformation of mineral and organic compounds,

their vertical transport and relocation to deeper horizons result in the formation of Podzols, which represent the climax stage of soil development (Mücher 1990). The initial podzol stage is reached in 100-year old dune soils (Paul 1953), while mature podzol profiles require 1,100–1,600 years for their formation (Paul 1953).

### Succession of plant communities on dunes

Due to the combined effects of steep environmental gradients, coastal dunes form complex habitat systems for plants (Ranwell 1972, Lichter 2000). Aelion processes, inducing sand burial and salt spray, sedimentation, extreme variations in water regime, nutrient availability and climatic settings are the most important factors in dune development and are influential in the successional trajectories for plant communities (e.g. Rozema et al. 1985, Edmondson et al. 1993, Łabuz 2004).

The dune systems of the Southern Baltic coast comprise of a wide range of embryonic, shifting and fixed dunes. Different spatial sequences of dunes in different stages of vegetation succession and soil development occur along a sea-to-inland gradient and represent a chronological series (Salisbury 1952), which is almost similar on many world coastlines (e.g. Doing 1985, Géhu 1985, Dody 1991, Nordstrom 2000). Vegetation succession on sand dunes occurs in a sequence of plant communities growing on mobile foredunes, backdunes and fixed dunes, the latter defining the inner margin of the Holocene dune field (Doddy 1991, Wiedemann and Pickart 2004). The succession series, which passes from initial forms of the *Elymo-Ammophiletum* through the *Helichryo-Jasionetum* to forest communities, is described in a number of studies for different regions of the southern Baltic coast (e.g. Hueck 1932, Paul 1944, Piotrowska 1988, Wojterski 1993, Dolnik 2003, Stankevičiūtė 2006). Extensive dune ecosystems with the complete range of succession stages exist along prograding coastlines with accumulation of sand such as on the Darß peninsula (Fukarek 1961), Świna Gate Barrier (Łabuz and Grunewald 2007) or Łeba Bar (Wojterski 1964, Piotrowska 1988).



**Figure 1** Zonal distribution of plant communities, dune types and soil development stages on coastal dunes along a sea-to-inland gradient (following Wojterski 1993, Piotrowska and Gos 1995, Peyrat 2007).

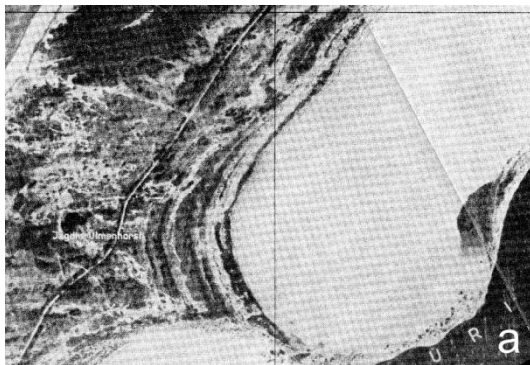
## Human activities and threats to the dune systems

Today's dune landscape along the Southern Baltic coast is the result of a long history of responses to natural forces and human modification. As sedimentary coastal landscapes are relatively unstable, dune formation is characterized by phases of sand drift and geomorphological stability (Provoost et al. 2009). In the past, large parts of Baltic coastal dunes were covered by native dune woodland. Historical records and fossil soils (Paul 1944, Tobolski 1980, Kaiser et al. 2006) testify to the occurrence of a natural dune forest, which existed in most areas until the middle ages. Stand with patches of the original dune forest with *Alnus incana*, *Fagus sylvatica* and *Quercus rubra* still survive on the dunes close to the village of Noer (Eckernförder Bight/Germany), on the Darss-Zingst-Peninsula and on the northern part of the Curonian Spit close to Juodkrantė (Paul 1944, Fukarek 1961, Möller 1975).

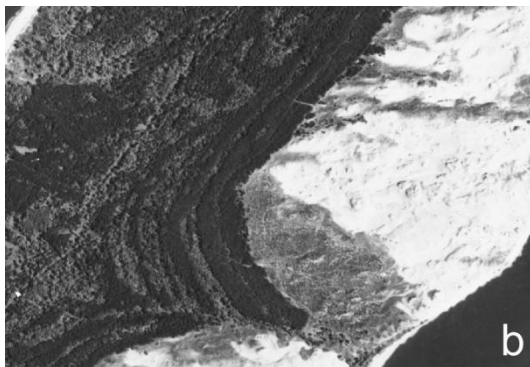
Almost all European dune systems have been affected by human activities (Houston et al. 2001). In many cases, human impact dates back to the very origin of the dunes. During the course of time, human activity in Baltic dunes generally increased. From the Middle Ages onwards, rapid population growth accelerated anthropogenic influences through forest clearings, frequent fires and grazing and shaped the landscape to a greater extent than before. During the period of the 30-year (1618–1648) and 7-year war (1756–1763) the forests of the Curonian Spit were systematically destroyed (Olsauskas 2009). A similar development took place in most dune systems of the Southern Baltic, where the most of the natural plant cover disappeared during the 17<sup>th</sup> and 18<sup>th</sup> century (Fukarek 1961, Piotrowska 1988, Schubert 1996, Baudler 2003). Heavy exploitation of the landscape and degradation of vegetation have exposed the underlying sand to wind erosion. Historical records of the Baltic show that exhaustive destabilization and sand drift lead to the development of huge migrating dunes, as those on the Łeba Bar, Vistula Spit and Curonian Spit, which buried several villages in the 18<sup>th</sup> and 19<sup>th</sup> century (Hueck 1932, Paul 1944). The everlasting mobility of the dune system allowed a continuous establishing and flourishing of life forms that were adapted to a high degree of environmental dynamics. The situation retarded the climax of vegetation stages to develop (e.g. shrubs and dune heaths) but it stimulated all pioneer and transient communities.

During the 18<sup>th</sup> and 19<sup>th</sup> century human activities on a national scale were undertaken to stabilise the drift sand. Large scale measures, such as extensive use of brushwood hurdles as sand fences, reforestation and dune fixation have aided stabilization and prevented further movement of the dunes (Genys 1984). Furthermore, the construction of an artificial fore dune ridge along the beach controlled wind-blown sand. Peyrat (2008) investigated changes in plant communities on the Curonian Spit and showed that dune stabilization and afforestation had a lasting effect on vegetation composition. Dune habitats, which were covered predominantly by varieties of grasslands in 1938, are forested today almost throughout (Figure 2). The policy of dune

forestation, still practised on the Russian part of the Curonian Spit, speeded up degradation, fragmentation, sylvanisation and flattening of the dynamic habitats of active migrating dunes. Ongoing stabilization, wind and missing sand supply stimulate an increasingly closed vegetation cover and shrub development at the expense of pioneer and grassland species. The observed changes in vegetation are very similar to the ones described for the Łeba Bar (Peyrat et al. 2009, chapter 5) and extensive parts of the Polish coast (Piotrowska and Gos 1995). The only larger open migrating dune systems left today are three separate dune fields on the Curonian Spit and a vast area in the middle of the Łeba Bar. These migrating dunes, both stabilised and unstabilised, reach a height of between 40 m (Łeba Bar) and 60 m (Curonian Spit), and form extensive dune ridges, which are among the biggest and most active in Europe.



**Figure 2** Changes of the dune landscape of the Curonian Spit, illustrated by two aerial photographs from 1933 (a) and 2000 (b). Dark colors indicate woodlands, light and dark grey colour grassland vegetation and white colour open dune areas. The decline in aeolian activity and the increase in woodland cover are especially apparent. (Figure 2a: Paul 1944 and Figure 2b: [www.googleearth.com](http://www.googleearth.com)).



From the 20<sup>th</sup> century onwards, human impact on coastal dunes has continued and intensified (Carranza et al. 2008). Coastal protection measures, recreational use, urban development, road construction, reforestation and massive airborne pollution have influenced and changed the dune vegetation drastically (Piotrowska and Stasiak 1982, Westhoff 1985, Herbich and Warzocha 1999, Nordstrom 2000, Łabuz 2004).

Many dune systems along the Southern Baltic coast and worldwide have been modified to increase their role as sea defence structures. In the past, the prime reason for these stabilisation measures was to control large scale destabilisation and sand drift. In the middle of the 19<sup>th</sup> century artificial dune ridges were constructed along the beach shore in parts of the Łeba Bar, on the Vistula Spit and on the Curonian Spit to



prevent further sand supply from the sea reaching the huge migrating dune areas (e.g. Paul 1944, Piotrowska 1988). Today, a major part of the foredunes and yellow dune ridges along the Baltic Sea coast as well as the North Sea coast are regulated to protect the coast from flooding. To stabilize the dunes, to protect them against deflation processes and to create a favourable relief, pioneer grasses were planted, most commonly *Ammophila arenaria*, which resulted in a loss of diversity (Łabuz 2004). The increase in coastal protection measures inhibited the sand transport to the backdunes, and therefore the dune systems are less dynamic. Likewise, reduced sand dynamics, grass encroachment, an increase of tall shrubs and woodlands have been recorded on the island of Anholt (Christensen and Johnsen 2001) and in the dune heathlands on the island of Hiddensee (Schubert 1996, Remke 2009).

Human activity plays an important role in the present day development of coastal dunes (Herbich and Warzocha 1999). Since the changing political affiliation at the beginning of the 1990s, tourism is gaining an increasing importance along the Southern Baltic coast. The new mobility rights and restructuring of a free market economy has led to sudden growth in the number of visitor, especially from Western Europe. In Mecklenburg-Pomerania, for example, the number of overnight stays increased by 200 % from 9.4 million in 1992 to 28.4 million in 2009 (Statistisches Amt Mecklenburg-Vorpommern 2010). In Poland, in Lithuania and in the Kaliningrad region, tourism is one of the few thriving industries, especially after Poland's and Lithuania's joining to the EU. The Russian part of the Curonian Spit is less visited by European tourists than the northern Lithuanian part due to visa-regulation for European visitors. This will change dramatically in the near future as the Curonian Spit designated as one of Russia's tourist development zones (Kavaliauskas 2010).

Vast numbers of holidaymakers concentrate on the seaside, devastating beaches and adjacent dunes (Olšauskas et al. 2009). Remote parts are less frequented and relatively undisturbed, as tourists prefer to accumulate on beach sections with easy and short access (Łabuz and Grunewald 2007). Heavy mechanical damages of the vegetation through trampling physically have affected the dunes and beaches and may lead to a reduction or complete destruction of the plant cover and decrease the species richness. Especially lichen-rich communities in grey dunes are extremely endangered as their regeneration may take decades (Christensen and Johnsen 2001). Rare and endangered species, such as *Eryngium maritimum* and *Linaria loeselli*, which grow on open dry dune areas are also affected by trampling and are on the verge of becoming extinct. Between 1975 and 2006, the population abundance of *Eryngium maritimum* on coastal dunes of the Lithuanian part of the Curonian Spit has decreased by about one third (Aviziene et al. 2008, Olšauskas and Urbonienė 2008). Along the Polish coast the habitats of *Eryngium maritimum* have been lost on dunes neighbouring seaside resorts (Łabuz 2004). Only some habitats are found in the western part of the Słowiński National Park and on a section of the Vistula Spit (Łabuz 2007).

Airborne pollutants are a major threat to Baltic coastal dunes (Remke et al. 2009). Major consequences of elevated atmospheric nitrogen and sulphur depositions are acidification and eutrophication. In central Europe, atmospheric nitrogen deposition has steadily increased during the 20<sup>th</sup> century and has peaked in the 1970 to 1980s (Erisman et al. 2001). Although the depositions have been drastically reduced in Eastern Europe since 1989–1990 (Erisman 2003) a ‘nutrient pool’ in the above ground biomass, the organic matter and soil-bound ammonium have been build up (Houston 2005).

Higher N-loads may stimulate plant growth and accelerate succession rates in acid grasslands, heathlands and dunes (Bobbink et al. 1998). This process may lead to acidification and a loss of buffer capacity increasing the availability of toxic metals ( $\text{Al}^{3+}$ ,  $\text{Fe}^{3+}$ ) within the soils (Heij and Schneider 1991). Nutrient poor and weakly buffered ecosystems, such as dunes systems, are particularly vulnerable. Accelerated acidification and accumulation of organic matter are responsible for a change in vegetation cover and appearance, and a loss of cryptogams as suitable habitats decrease (Remke et al. 2009b). A shift from lichen-rich short grass vegetation towards species-poor vegetation stands dominated by *Ammophila arenaria*, *Carex arenaria* and *Deschampsia flexuosa* is described by Remke et al. (2009b), Christensen and Johnsen (2001) and Berlin et al. (2000) for Baltic dunes. Ketner-Oostra and Sykora (2004), Ten Harkel and van der Meulen (1996) and Veer and Kooijman (1997) report a similar trend for coastal dunes along the North Sea coast.

Critical load for acid to acidic coastal dunes in the Baltic is around 4–6 kg N ha<sup>-1</sup>yr<sup>-1</sup> (Remke 2009b) with a current range of N wet deposition of 3–8 kg N ha<sup>-1</sup>yr<sup>-1</sup> (Fjæran 2006). In a European context these values are low to medium, due to lower intensity of agriculture and industry in the Baltic States (Remke 2009). At the northern Dutch coast, 13–20 kg N ha<sup>-1</sup>yr<sup>-1</sup> wet deposition was measured in open dunes (van Dobben and van Hinsberg 2008). In Great-Britain current levels of nitrogen deposition (7–30 kg N ha<sup>-1</sup>yr<sup>-1</sup>) lie close to the critical load of 10–20 kg N ha<sup>-1</sup>yr<sup>-1</sup> (Jones et al. 2004).

At present, and especially in the future, Baltic coastal dunes will be impacted by climate changes. The man-made increase of energy absorbing gases ( $\text{CO}_2$ ,  $\text{NH}_4$ ,  $\text{NO}_x$ , CFCs) in the atmosphere has intensified the greenhouse effect over the last decades and led to an increase of temperature (Houghton et al. 1996, Braun et al 1999). A rise of temperature in the range of 0.1°C–0.8°C/decade in the twenty-first century is forecast for Poland (Vellinga and Leathermann 1989). Other climate changes could include small increases in precipitation (10–15 %) (Arnell 1999), increases in frequency of extreme events, such as storms or droughts worldwide (Carter 1991), and rising sea-levels (Pruszek and Zawadska 2008).

In coastal dune landscapes of the world’s shoreline, this temperature rise may possibly affect landscape forming processes such as vegetation succession and soil forma-

tion and increased erosion due to accelerated rise in sea levels (van der Meulen et al. 1991, Braun et al. 1999). There is little knowledge about the impact of climatic change on vegetation and the effect of vegetation on soil formation in dune sands (Sevenik 1991). The dune vegetation occupies an extremely stressed environment with numerous factors, restricting the plants productivity. However, it is assumed, that the increase of atmospheric CO<sub>2</sub> will have a direct impact on the growth rate of plants as photosynthesis rates may increase up to 100 % in an enriched CO<sub>2</sub> environment (Pearch and Bjorkman 1983). Most plants show a better growth rate in a CO<sub>2</sub>-enriched environment, reaching photosynthetic optima at different saturations (Carter 1991). *Ammophila* and *Elymus*, the major dune forming grasses, are C<sub>3</sub>-plants that reach optimal production of 60 to 80 mg CO<sub>2</sub>/0.1 m<sup>2</sup>/day, which is about twice as high as current levels (Carter 1991). Vestergaard (1991) studied a dune system of South-East Denmark and concluded that global warming, corresponding to a doubling in CO<sub>2</sub>-level atmosphere, may imply an increase in aridity in coastal dunes due to increased temperatures. It is expected, that mesophytes with superficial root systems such as *Corynephorus canescens* will be disfavored in competition with xerophytes such as *Ammophila arenaria* and *Carex arenaria*, which are able to explore deeper, moister sand layers. Moreover, a rise in temperatures will significantly affect the spatial distribution and amount of snow cover along the southern Baltic Sea: by 2050 snow cover at the end of March will have disappeared (Arnell 1999), which will lead to an extended mean growing season. Under these conditions, southern species and continental xerophytes will be able to immigrate and, reverse, while more northern and Atlantic species will be suppressed (Vestergaard 1991).

These possible vegetation changes, caused by climatic changes, may have a strong impact on dune soils and soil forming processes through changes in litter quality and root distribution (Sevink 1991). Higher temperatures will lead to lower rates of acidification and to a drastic change from leaching to accumulative and a faster turnover of litter in freely drained soils. Consequently, the nutrient economy of the nutrient-poor dune habitats will be improved by these processes (Vestergaard 1991). In areas with greater precipitation effects of surpluses will be less prominent, since the general trend towards acidification and podzolisation will be little affected (Sevink 1991).

Analysis of the southern Baltic coast during the 19<sup>th</sup> and 20<sup>th</sup> revealed an intensification of erosion due to a rise in sea-level at an average rate of 10 cm/100 year (Pruszek and Zawadka 2008). In addition, during the last decades, storm surges affecting the southern Baltic coast have led to increasing dune and cliff erosion. Particularly as the frequency of such storm surges has grown in recent years, changes in atmospheric circulation over the Baltic has resulted in an increase of the intensity and frequency of storms coming from north-west direction (Pruszek and Zawadzka 2005). Heavy storms over the last ten years have been responsible for considerable abrasion and destruction of dune systems (Łabuz 2004, Olšauskas et al. 2009).

Long stretches of the Baltic coast are already devoid of fore dunes, yellow and even grey dunes and the beach directly borders on the forest (Piotrowska 1988). Dune communities along the coastline are heavily fragmented and destroyed. Along the Polish coast 75 % of the dune shores, yellow and grey dunes are being impacted by coastal abrasion processes (Piotrowska 1988). The sea no longer supplies new sand which is essential for the rebuilding of dunes and vegetation (Piotrowska 2002). In a period of 74 years, the width of the beach along the Łeba Bar decreased from approximately 186 m to 50 m, which means a decrease of nearly 300 % (Peyrat et al. 2009, chapter 5). Abrasion was responsible for coastline retreat by a maximum of 80 to 200 m between 1958 and 1984 (Borowka and Rotnicki 1995). Complete succession series with annual communities on primary dunes through grassland on backdunes and dune forest on older stabilized dunes are only visible on few parts of the coast, where long-term feeding of the beach with new sand supplied by the sea occurs, such as on the accumulative coast of the Darss-Zingst peninsula or on the Świna Gate Barrier (Łabuz and Grunewald 2007).

## **Aims and outline of the thesis**

Due to the human exploitation of coastal dunes along the southern Baltic coast, many habitats are irreversible degraded or destroyed. There remain only a few stretches of coastline with pristine or minimally disturbed dune ecosystems containing high biodiversity of native or endemic coastal species. The quality and critical environmental factors for these habitats and species are of vital importance for the future management and nature protection.

A large body of literature about coastal dunes of the Southern Baltic coast already exists. However, most studies are local descriptions. The aim of this work is to compile a comparative study about the vegetation, environmental problems, community dynamics and landscape changes of southern Baltic coastal dunes. The results should stimulate further research for a better understanding of these ecosystems as well as the elaboration of improved conservation and management strategies.

The major objectives of the present study are

- to give a general overview of plant species composition and of main plant communities of dry coastal dunes,
- to outline environmental changes of dunes through natural processes and human activities,
- to describe the annual vegetation on the remnant migrating dune fields in Poland, Russia and Lithuania,
- to describe patterns of plant species diversity,

- to study medium-term vegetation changes in order to understand ecological processes,
- to show the importance of dynamic dune systems for endangered habitats.

The chapters 2–5 are in accordance with the main objectives and are summarized subsequently.

*Chapter 2: Plant communities of the Sundic Baltic Sand Dune Vegetation Complex on dry coastal dunes along the southern Baltic coast.*

Dry coastal dunes along the Southern Baltic have been recognized as an individual geographical vegetation unit within the European Map of Vegetation (Bohn and Golup 2003) called ‘Sundic Baltic Sand Dune Vegetation Complex’. At the present date, undisturbed coastal dune habitats along the Southern Baltic coast are rare and endangered (Łabuz and Grunewald 2007). Effective management measures for the protection of these dune habitats can only be ensured, when there is sufficient knowledge about the ecology and the function of plant communities of coastal dunes (Laime and Tjarve 2009). A wide range of plant communities from Baltic coastal habitats has been described in the past. Since most of these studies have a local perspective, a single framework of occurrence, extend and actual state of dry coastal dune vegetation along the Southern Baltic coast has not yet emerged. For this reason, in this chapter, a general overview of plant species composition, diversity and ecological pattern of main plant communities of the ‘Sundic Baltic Sand Dune Vegetation Complex’ has been given. Furthermore, environmental changes of these dune systems were discussed.

*Chapter 3: Neophytic *Corispermum pallasii* (Stev.) (Chenopodiaceae) invading migrating dunes of the southern coast of the Baltic Sea.*

The southern Baltic endemic plant species *Cakile maritima* subsp. *baltica*, *Corispermum intermedium* and *Linaria loeselii* form annual vegetation, restricted to dynamic sand areas, such as on the migrating dunes of the southern Baltic coast. In this chapter, the annual vegetation on the remnant of migrating dunes fields in Poland, Russia and Lithuania has been described, and a species replacement of the endemic *C. intermedium* by the neophytic *C. pallasii* was documented and discussed in respect of landscape changes and species conservation.

*Chapter 4: Plant species diversity in dry coastal dunes of the Southern Baltic coast.*

Along the Southern Baltic coast increases of human pressure as well as natural and anthropogenic disturbances play a major role in the protection and conservation of coastal ecosystems with results of a substantial loss in regional biodiversity. The measurement of species richness along a sea-to-inland gradient could be an impor-

tant component for ecosystem management. Plant communities which contribute most to the total species richness could be distinguished, highlighting the importance of priority habitats for management planning (Acosta et al. 2009). Based on results obtained from Chapter 2, patterns of diversity of vascular plants, lichens and bryophytes in different dune habitats were described and processes underlying biodiversity were evaluated in this chapter.

*Chapter 5: Vegetation dynamics on the Łeba Bar/Poland: a comparison of the vegetation in 1932 and 2006 with special regard to endangered habitats.*

The migrating dunes of the Łeba Bar are among the largest still active dune areas in Europe. These sandy ecosystems provide suitable habitats for pioneer plant species and vegetation types, which are endangered or almost absent along the southern Baltic coast. Natural dynamics and consistent initiated succession processes form typical vegetation mosaics. However, diminishing sand supply from the sea, natural fixation by succession and sylvanisation threaten these habitats on the Łeba Bar. Therefore, the major aim of this chapter was to reveal medium vegetation changes by comparing current maps with historical ones. The increase, decrease and stability of vegetation types between 1932 and 2006 have been illustrated, and vegetation dynamics were described. The second aim was to demonstrate the importance to enforce the protection of pioneer vegetation types in the still existing extensive drift sand areas.

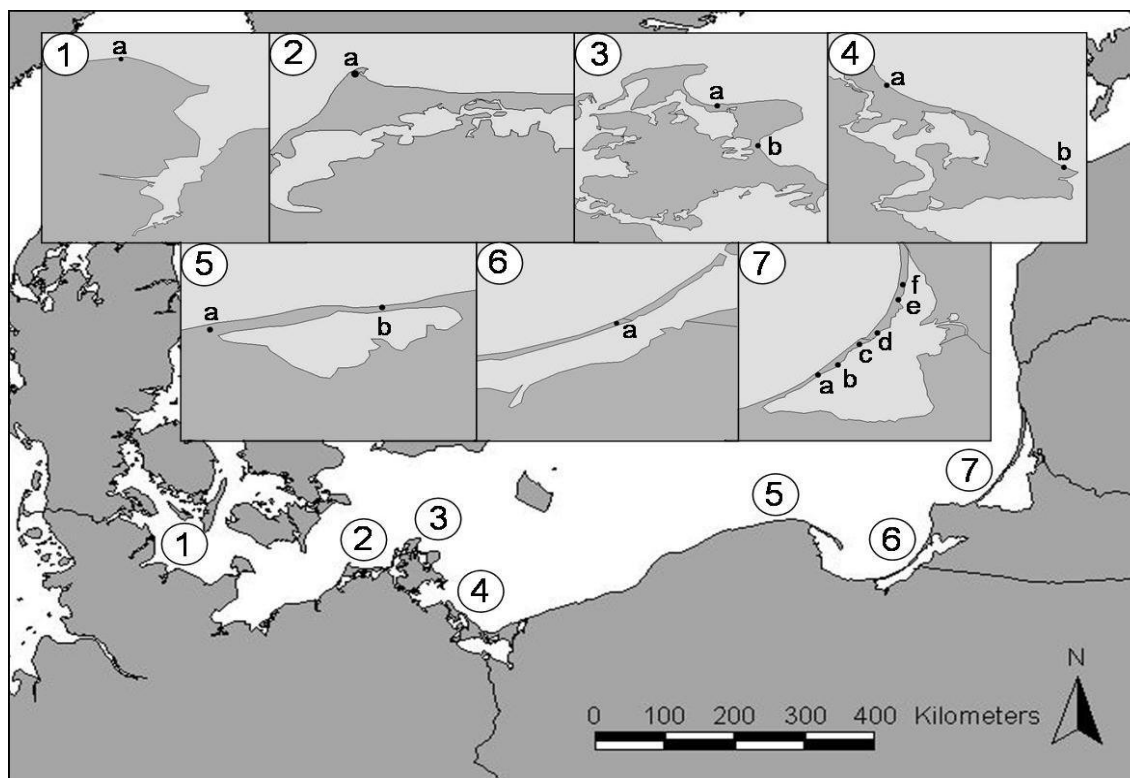
## Study sites

The study sites in this thesis are all dry coastal dune systems in protected areas along the southern Baltic coast. All research has been conducted on 15 coastal sites in four countries (Germany, Poland, Russia and Lithuania) (Figure 3). They are spread over a large geographical gradient from the Eckernförder Bight in the west to the Baltic proper in the east, covering the Central Europe and Baltic terrestrial ecoregion (Olson et al. 2004).

## Habitat conditions

Climatic conditions in the Baltic region are mainly subject to influences of wet air masses from the Atlantic Ocean and dry continental air masses from Eastern Europe. Intensive movement of basic pressure fronts and related frequent changes in wind speed and direction have considerable influence on the climate (Pruszek and Zawadzka 2005). Prevailing winds along the southern Baltic coast are westerly to south westerly, often strong (8–14 m s<sup>-1</sup>) and during winter seasons very strong (>14 m s<sup>-1</sup>) (Piotrowska 1988, Schiewer 2008). They influence coastal currents and alongshore sediment flows (Kharin and Kharin 2006).

The mean annual temperature decreases from 8.5°C in Kiel/Germany to 7°C in Klaipeda/Lithuania as the climate becomes more continental. The precipitation, falling



**Figure 3** Study sites along the Baltic Coast from west to east. Numbers represent the study sites, letters in the above figures represent the different transect locations: 1a) Nature Reserve “Bewaldete Düne von Noer” (DE); 2a) Darsser Ort/National Park “Vorpommersche Boddenlandschaft” (DE); 3a) Schaabe/Island of Rügen (DE); 3b) Nature Reserve “Schmale Heide mit Steinfeldern, Strandseite”/Island of Rügen (DE); 4a) Karlshagen – Trassenheide/Nature Park “Usedom” (DE); 4b) Ahlbeck/Nature Park “Usedom” (DE); 5a) Czołpińska Dune/National Park “Słowiński” (PL); 5b) Łącka Dune/National Park “Słowiński” (P); 6a) Vistula Spit/Landscape Park “Mierzeja Wiślana” (P); 7a) White Dunes/National Park “Kurskaja Kosa” (RU); 7b) Rybachy/National Park “Kurskaja Kosa” (RU); 7c) Morskoje/National Park “Kurskaja Kosa” (RU); 7d) Parnidis Dune/National Park “Kursiu Nerija” (LT); 7e) Nagliu Nature Reserve/National Park “Kursiu Nerija” (LT); 7f) Juodkrantė/National Park “Kursiu Nerija” (LT).

**Table 1** Location of field sites with long-term average temperatures and precipitation. Sources for climate data:

<http://www.klimadiagramme.de>, 1) [-/Deutschland/kiel.html](#) 2) [-/Deutschland/rostock.html](#), 3) [-/Deutschland/arkona.html](#) 4) [-/Deutschland/greifswald.html](#) 5) [-/Europa/hel.html](#) 7) [-/Europa/klaipeda.html](#) 6) <http://www.worldclimate.com/cgi-bin/grid.pl?gr=N54E018>.

Study site	Country	Geographical coordinates	Temperature [°C]	Precipitation [mm yr <sup>-1</sup> ]
1 Noer/Eckernförder Bight	Germany	54° 28'N, 10° 01'E	8.5	755
2 Darss-Zingst-Peninsula	Germany	54°26'N, 12°31'E	8.4	592
3 Island of Rügen	Germany	54°31'N, 13°34'E	7.9	520
4 Island of Usedom	Germany	54°03'N, 13°59'E	8.0	566
5 Łeba Bar	Poland	54°44'N, 17°23'E	7.8	574
6 Vistula Spit	Poland	54°26'N, 19°37'E	7.5	528
7 Curonian Spit	Russia	55°16'N, 20°58'E	7.0	735



usually during autumn and winter (Schiewer 2008), decreases from 755 mm yr<sup>-1</sup> at the westernmost study site (Noer/Eckernförder Bight/Germany) to 520 mm yr<sup>-1</sup> in the middle part of the southern Baltic coast (Island of Rügen/Germany) until the precipitation increases again to 735 mm yr<sup>-1</sup> at the eastern margin of the southern Baltic coast (Curonian Spit/Lithuania) (Table 1).

### ***Noer***

The dunes close to the village of Noer at the Eckernförder Bight (54°28'N, 10°01'E) are a unique feature for the coastal vegetation of the German Baltic coast (Möller 1975). All stages of dune vegetation succession from initial stages on bare soil to close canopy woodland are represented (Möller 1975). The dunes are partly covered with a centuries-old beach and oak forest, which represent the potential-natural climax of vegetation succession on Baltic dune systems (s.f. Bohn et al. 2003). Since 1981, 47 ha of the dune area has been protected as Nature Reserve “Bewaldete Düne bei Noer/Wooded dune of Noer” and the public is prohibited from entering.

### ***Darss***

The Fischland-Darss-Zingst-Peninsula (54°26'N, 12°31'E), in the shape of an obtuse angle of 120°, represents the westernmost element of the West Pomeranian barrier coast (Lampe 2002). The western angle leg (Fischland) is approximately 25 km long, whereas the eastern part of the peninsula (Zingst) has a length of about 29 km. The exposed westerly coast is characterized by strong abrasion of the cliffs and by rapid build up of sand at the Darsser Ort in the north-east caused by predominant westerly winds (Schumacher 2002). The Darss, situated between the two angle legs of the Fischland and Zingst, developed during the Littorina transgression following changes in coastal sedimentation (Schumacher 2000). About 120 well preserved beach ridges have been deposited on a cusped foreland and the shoreline has progressed in a northern direction. Sandy spits, open or vegetated dunes and woodlands are characteristic features of the Darss, where vegetation studies were conducted in the present study. Today a mean accretion of 2m yr<sup>-1</sup>, which constantly leads to the formation of new dunes, is observed at the northern spit (Schumacher 2000). Thus, this dynamic dune ecosystem with all stages of dune development and succession is one of the few primary habitats, remaining in Central Europe (Grunewald 2006). The Darss is part of the National Park “Vorpommersche Boddenlandschaft”, which has been established in 1990 and covers an area of 80,500 ha. Every year, about 3 million tourists are looking for nature experience and recreation inside the national park. Sensible parts of the landscape and nature, such as through the dune areas at the Darsser Ort, have been protected with wooden pathways and observation platforms were created.

### ***Island of Rügen***

The island of Rügen (54°31'N, 13°34'E) is an archipelago with more than a dozen smaller and larger Pleistocene cores connected by Holocene barrier spits (Janke 2002). Two spits, the "Schaabe" and "Schmale Heide", located in the eastern part of Rügen, were taken into consideration for the present study. These coastal areas are characterised by equilibrium between erosion and accumulation. (Schiewer 2008).

The 'Schaabe' is a nearly 12 km long and 0.6–1.5 km wide Holocene spit extending in a south-easterly direction between the Pleistocene plateaus 'Jasmund' and 'Wittow'. The main dune ridge at the Baltic coast is stabilised with *Ammophila arenaria* against erosion and deflation. Landwards, a humpbacked dune landscape with elevations between 1 and 5m and covered with pine plantings, predominates (Ministerium für Bau, Landesentwicklung und Umwelt Mecklenburg-Vorpommern 2000).

The 'Schmale Heide' is a flat, forest-covered sandy barrier spit, 0.8–1.5 km wide and 9.5 km long, stretching from Neu-Mukran in the north to the Granitz hills near Binz in the south (Lampe et al. 2002). Special features of the Schmale Heide are the flint-pebble beach ridges in the central part, protected since 1935 as a nature reserve. In 1994, 13.5 ha of the forested dune belt and open dunes close to the Prorer Wiek were included in the nature reserve to save the almost pristine dune vegetation with its rare and endangered species. Trespassing of this area is prohibited. However, only a small fence encloses the nature reserve, which directly borders the beach and along a landward path and cycling route (own observations).

### ***Island of Usedom***

The island of Usedom (54°03'N, 13°59'E) is the second largest island (after Rügen) along the German Baltic coast. It borders the 'Bodden' in the south and is separated eastwards by the Swine-river from the Polish island of Wolin. Transport of eroded material along the coast from cliff erosion and its redeposition led to the formation of spits and barriers connecting Pleistocene hills (Hoffmann 2002). Today the coastline in the northwest of Usedom is about 42 km long, consisting of dunes in several stages of succession. In 1999, the "Usedom Nature Park" was constituted with an area of 72,000 ha. Altogether 14 nature conservation areas with 4,000 ha form part of the park area today (Siebert et al. 2003). Usedom is a region that offers a large number of short- and long-term activities for tourists (about one million of tourist per year), and tourism is the main source of income (Siebert and Laschewski 2009). Human disturbance from recreational activities and trampling along the coast is considerable, as most tourists accumulate on the seaside (Grunewald 2006).

### ***Łeba Bar***

The Łeba Bar (54°44'N, 17°23'E) between Rowy in the west to Łeba town in the east is about 34 km long and 0.5–2 km wide, enclosing the large Łeba Lake (Mader 1995). Marshy forests, peat bogs, swamps and a large dune belt of open, active sand dunes

form a diversified mosaic of environments (Ostrowski and Symonides 1994). In 1964, 18,618 ha were designated as “Słowinski National Park”. The Łeba Bar is considered to be the favoured destination for at least half a million tourists annually (Ostrowski and Symonides 1994). Two major excursion routes exist, one in the western (Czołpino Dune) and one in the eastern part (Łącka Dune) of the Łeba Bar, crossing the migrating dunes and leading to the beach. The pathways are marked with posts; however they don't prevent trespass into the protected area. These two official paths are the only ones available. As a result the dune fields in the middle of the Leba Bar are more or less unimpaired by tourist pressure (Peyrat et al. 2009, chapter 5). The migrating dunes, which reach heights up to 42 m, are concentrated in the middle part of the Łeba Bar. Dune slopes, gentle on their windward slope and steep to leeward, move eastwards at an average of  $10 \text{ m yr}^{-1}$  (Borowka 1990) driven by the prevailing western winds. They bury forests until the dunes reach the Łebsko Lake. Most other open dune areas have become fixed by plantings during the 19<sup>th</sup> and 20<sup>th</sup> century. Abrasion and marine deposits alternate on the Łeba Bar (Borówka and Rotnicki 1995). The western part of the Łeba Bar, due to its SW–NE-direction is more exposed to the deflating action of the prevailing westerly winds, and wave abrasion is the dominant process here (Borówka and Rotnicki 1995).

### ***Vistula Spit***

The Vistula Spit ( $54^{\circ}26'N$ ,  $19^{\circ}37'E$ ) is a sand tongue with a length of about 55–60 km and a width of 0.5–2.0 km, stretching between Katy Rybackie (Poland) and Baltijsk (Kaliningrad Oblast, Russia) and is divided by the state border between Poland and Russia into two segments (55 % and 45 % of its length) (Chubarenko and Margoński 2008). It separates the large Vistula Lagoon from the open Baltic Sea. Characteristic of the Vistula Spit are an almost continuous beach-adjointing dune ridge, an extensive chain of wood-covered dunes 30–45 m in height, patches of grass-vegetated dunes, mires and active raised bogs (Mader 1995). Until the 19<sup>th</sup> century most of the presently vegetated dunes were open dunes, which were actively migrating towards the Vistula Lagoon. They disappeared completely during the 20<sup>th</sup> century due to afforestation measures. In 1985, 4,000 ha of the Vistula Spit were protected as Landscape Park “Mierzeja Wiślana”.

### ***Curonian Spit***

The Curonian Spit ( $55^{\circ}16'N$ ,  $20^{\circ}58'E$ ) is the largest accumulative barrier sand spit in the Baltic Sea region (Gudelis 1995) and among the five longest in the world (Grönholm and Berghäll 2007). The northern part of the spit belongs to Lithuania, the southern to the Russian Oblast of Kaliningrad. With a length of 98 km and a width between 0.4–4 km it stretches in a gentle curve between Klaipeda and the Sambian Peninsula, separating the Curonian Lagoon from the Baltic Sea. The main morphodynamic trends on the marine side are the increasing erosion on the foot of the spit

(southern part) and increased accretion at the head of the spit (Armaitienė et al. 2007). A sandy beach of up to 80 m borders the mostly artificial protective dune. A deflation area (palve) exists behind the dune ridge, where a small strip of about 50 m is today covered by species rich, dry grassland. However, forests comprise the major part of the deflation area; the most dominant are pine stands, of which half have been planted (Grönholm and Berghäll 2007). Five strips of migrating dunes with dune heights of 60 m remained after large sand-drift stabilisation programmes in the 1800s and 1900s, forming Europe's largest active dune area. The dunes of the Curonian have already been under nature conservation since the 1950s and were turned into a transboundary national park in 1986 (Russia: 6.621 ha) and 1991 (Lithuania: 26.474 ha). The Curonian Spit is a famous destination for thousands of tourists annually (State Department of Tourism Lithuania 2006). In recent years some nature trails have been created to control national park visitors inside sensitive dune habitats (such as through the Nagliai Strict Nature Reserve/Lithuania or through 'Ephas's dune/Russia). Access for visitors to other open dune areas is forbidden (Armaitienė et al. 2007).

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Dune grassland on the Curonian Spit, RU (Photo: Peyrat 2008).

# Plant communities of the Sundic Baltic Sand Dune Vegetation Complex on dry coastal dunes along the southern Baltic coast

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## Abstract

This study describes the vegetation composition of main plant communities of the 'Sundic Baltic Sand Dune Vegetation Complex' on dry coastal dunes in protected areas along the southern Baltic coast. The data comprises 145 relevés of four different countries (DE, PL, RU and LT) distributed among 15 sites. Eleven coastal communities were considered. Pioneer communities were dominated by herbs and had low cover and diversity. Further successional stages had a low cover but moderately higher diversity, with sedges and grasses dominating. Older stages had a greater total mean cover, and shrubs and trees were more abundant. The dune habitats under investigation are important in conservation of threatened species – as 24 vascular species, 17 lichens and two bryophytes, included in National Red List Books, were found. Although the examined coastal habitats contain a highly functional and structurally diverse ecology, this ecology is gradually being degraded by coastal erosion, human impact and nitrogen deposition.



## Introduction

Dune habitats along the southern Baltic coast have been recognised as an individual geographical vegetation unit within the European Map of Vegetation (Bohn and Gollup 2003) called “Sundic Baltic Sand Dune Vegetation Complex”. For instance, the area includes systems with narrow beaches and one or more parallel dune ridges as well as topographically more complex systems with 40–60 m high mobile dunes showing various degrees of stabilisation. The coastal dunes are characterised by a wide range of partly species-rich habitats such as open dunes, grasslands and forests. According to Bohn and Gollup (2003), the “Sundic Baltic Sand Dune Vegetation Complex” is species-poor and less diverse compared to the Atlantic sand-dune vegetation of the North Sea coast. Other studies revealed a high species richness of older dry grassland communities on Baltic dunes, hosting a high number of lichens and bryophytes (Dolnik 2006, Laime and Tjarve 2009). Although some oceanic vascular plant species of the Atlantic coast are missing, other, more continental distributed species, give the “Sundic Baltic Sand Dune Vegetation Complex” its own character.

Since the Middle Age coastal dunes along the southern Baltic coast have been influenced by human intervention. Deforestation of the native woods caused degradation of vegetation and wind erosion led to the formation of huge migrating dune areas. During the 20<sup>th</sup> century – and especially since the 1990s – human activities have been intensified. At present, most natural coastal plant habitats at the southern Baltic coast are threatened (Piotrowska 1988, Łabuz 2004, 2007). Heavy storms over the last ten years have been responsible for considerable abrasion and destruction of coastal dunes and their habitats (Łabuz 2004, Olsauskas et al. 2009). Dune systems are being fragmented by infrastructure and impacted on by coastal defence works and recreation pressure. Missing small-scale disturbances and atmospheric nitrogen deposition led to a decline of dynamic processes and pose serious challenges for the conservation of these ecosystems (Jentsch and Beyschlag 2003). In the future, increasing numbers of visitors are expected in the Baltic region and the pressure on the Baltic coastal zones will increase.

Nevertheless, some coastal regions along the southern Baltic coast are still well preserved with almost natural environments. They host rare and endemic plant species and plant communities, which are restricted to coastal areas and therefore deserve special conservation value. During recent decades, some areas have been turned into protected sites and attention has been drawn to the responsibility of the southern Baltic Sea foreshore countries (DE, PL, RU and LT) concerning the safeguard of these ecosystems. Many of these coastal sites have also been designated under the European Habitats Directive (Council of the European Commission 1992, Council directive 92/43/EEC of 21 May 1992) as protected areas or as Natura 2000 sites, stating that these areas should be preserved in their function as habitats for threatened species.



Previously, several studies on dune vegetation of the southern Baltic coast have been carried out, for instance, in Russia and Lithuania (Paul 1953, Dolnik 2003, Stankevičiūtė 2006), Poland (Piotrowska 1988, 2002, Wojterski 1993, Łabuz 2004) and Germany (Fukarek 1961, Möller 1975, Isermann 1996, Berg et al. 2004). Altogether, a wide range of plant communities from coastal habitats have been described, including several widely distributed and non-area-specific communities. Since most of these studies have a local perspective, the aim of the present study is (i) to describe the species composition, relationships and ecological pattern of main plant communities of the “Sundic Baltic Sand Dune Vegetation Complex” on dry dune habitats in protected areas along the southern Baltic coast with special attention to the occurrence of lichens and bryophytes and (ii) to review the current situation of the coastal dunes along the Southern Baltic coast and to show the causes for this situation by literature research.

## Materials and Methods

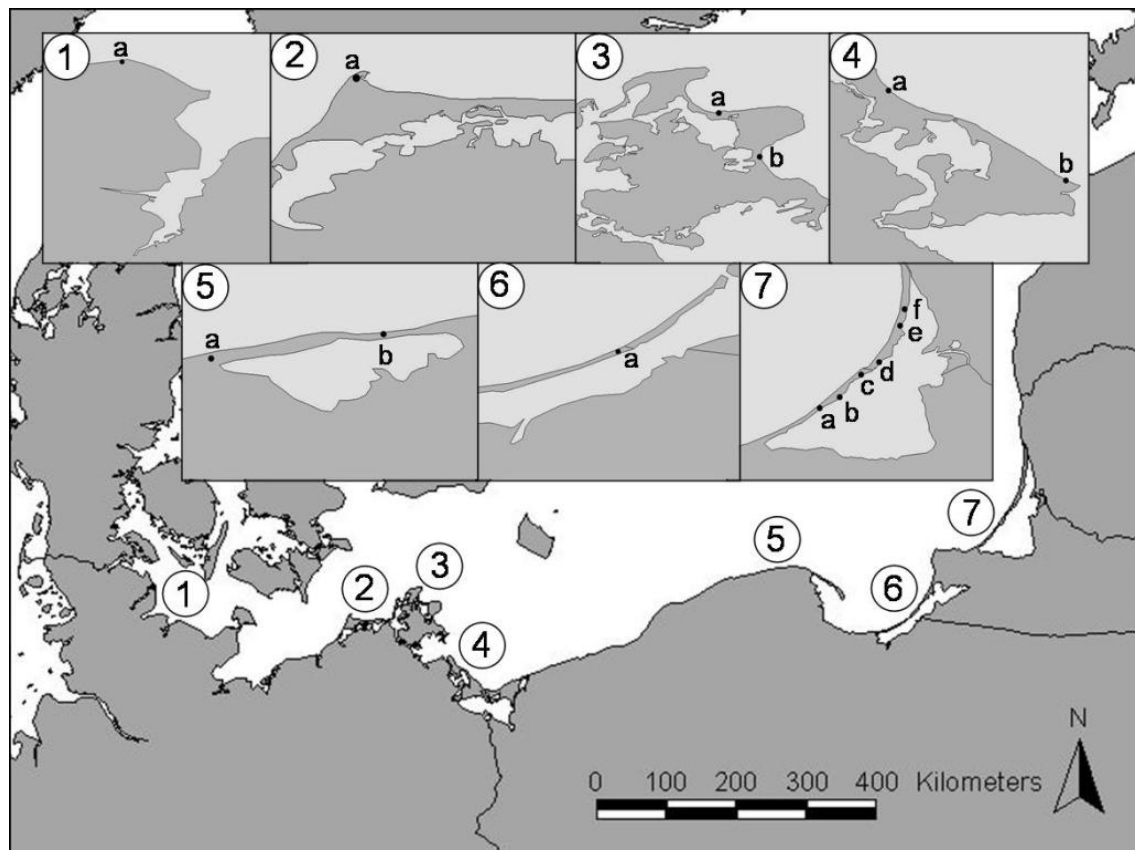
### Study sites

Based on the Map of European Vegetation (Bohn and Gollup 2003), 15 sites, situated within the “Sundic Baltic Sand Dune Vegetation Complex”, were chosen for detailed vegetation analysis. They occurred along a large geographical gradient from the Eckernförder Bight in the west, to the Darß peninsula, and along the islands of Usedom and Rügen towards the Łeba Bar, Vistula Spit and the Curonian Spit in the east (Figure 1). All the investigated dune systems were under some form of conservation, such as national parks or nature reserves (Table 1).

The climate of the southern Baltic has a transitional character with relatively constant temperatures (Schiewer 2008). In the western part it is influenced by the Atlantic Ocean, whereas the effect of the European continent is larger in the eastern part. The mean annual temperature decreases from 8.5 °C in Germany to 7 °C in Lithuania as the climate gets more continental (Table 1). The precipitation, falling usually during autumn and winter (Schiewer 2008), varies between 520 mm yr<sup>-1</sup> on the island of Rügen and 754 mm yr<sup>-1</sup> at Noer (Table 1).

The southern Baltic is a sediment-rich region with ample material for beach barrier and dune formation. The origin of the coast is connected to glaciations history, thus moraine cliffs alternate with sandy coasts, sandy spits and large dune complexes, forming a smooth abrasive-accumulative coastline (Borówka 1990). Sand for coastal dunes originates from marine abrasion of nearby Holocene moraine cliffs. The dune soils (Arenosols, Regosols) are poor in nutrients as well as carbonate and susceptible to acidification (Piotrowska 1988, Peyrat 2007). Soil formation is characterized by fast decalcification (from 26 g kg<sup>-1</sup> CaCO<sub>3</sub> in yellow dunes to 2.1 g kg<sup>-1</sup> in grey dunes),

combined with a rapid decrease of soil pH (from 6.3 in yellow dunes to 3.4 under pine woods) and accumulation of organic matter (from 1.9 g kg<sup>-1</sup> in yellow dunes to 363.9 g kg<sup>-1</sup> under pine woods) with advancing soil age and increasing vegetation cover (Peyrat 2007).



**Figure 1** Study sites along the Baltic Coast from west to east. Numbers represent the study sites, letters in the above figures represent the different transect locations: 1a) Nature Reserve “Bewaldete Düne von Noer” (DE); 2a) Darsser Ort/National Park “Vorpommersche Boddenlandschaft” (DE); 3a) Schaabe/Island of Rügen (DE); 3b) Nature Reserve “Schmale Heide mit Steinfeldern, Strandseite”/Island of Rügen (DE); 4a) Karlshagen – Trassenheide/Nature Park “Usedom” (DE); 4b) Ahlbeck/Nature Park “Usedom” (DE); 5a) Czołpińska Dune/National Park “Słowiński” (PL); 5b) Łącka Dune/National Park “Słowiński” (P); 6a) Vistula Spit/Landscape Park “Mierzeja Wiślana” (P); 7a) White Dunes/National Park “Kurskaja Kosa” (RU); 7b) Rybachy/National Park “Kurskaja Kosa” (RU); 7c) Morskoje/National Park “Kurskaja Kosa” (RU); 7d) Parnidis Dune/National Park “Kursiu Nerija” (LT); 7e) Nagliu Nature Reserve/National Park “Kursiu Nerija” (LT); 7f) Juodkrantė/National Park “Kursiu Nerija” (LT).

### Field methods and data analysis

A total of 145 phytosociological relevés was recorded in 25 m<sup>2</sup> (grassland communities) and 400 m<sup>2</sup> (forest communities), semi-randomly placed plots during summer 2008 and 2009. In every study site, sample plots were subjectively chosen according to homogeneity criteria. An attempt was made to select sample plots, representing the local variation of community types. The plant habitats occurred along a sea-to-inland gradient and were in different stages of succession (after Piotrowska and Gos,

1995), such as pioneer habitats (*Elymo-Ammophiletum*), psammophilous swards (*Helichryso-Jasionetum*) and coastal pine forest (*Empetro nigri-Pinetum*).

**Table 1** Location of field sites with long-term average temperatures and precipitation. Sources for climate data:

<http://www.klimadiagramme.de>: 1) -/Deutschland/kiel.html 2) -/Deutschland/rostock.html, 3) -/Deutschland/arkona.html 4)-/Deutschland/greifswald.html 5) -/Europa/hel.html 7) -/Europa/klaipeda.html 6) <http://www.worldclimate.com/cgi-bin/grid.pl?gr=N54E018>.

	Study site	Country	Geographical coordinates	Temperature [°C]	Precipitation [mm yr <sup>-1</sup> ]
1a	Nature Reserve "Bewaldete Düne von Noer"	Germany	54° 28N, 10° 01E	8.5	755
2a	Darsser Ort/National Park "Vorpommersche Boddenlandschaft"	Germany	54° 28N, 12° 30E	8.4	592
3a	Schaabe/Rügen	Germany	54° 28N, 13° 34E	7.9	520
3b	Nature Reserve "Schmale Heide mit Steinfeldern Strandseite"/Rügen	Germany	54° 34N, 13° 25E	7.9	520
4a	Karlshagen - Trassenheide/Nature Park "Usedom"	Germany	54° 06, 13° 54E	8.0	566
4b	Ahlbeck/Nature Park "Usedom"	Germany	53° 56, 14° 12E	8.0	566
5a	Czołpińska Dune/National Park "Słowiński"	Poland	54° 43N, 17° 15E	7.8	574
5b	Łącka Dune/National Park "Słowiński"	Poland	54° 45N, 17° 27E	7.8	574
6a	Vistula Spit/Landscape Park "Mierzeja Wiślana"	Poland	54° 43N, 19° 36E	7.5	528
7a	White Dunes/National Park "Kurskaja Kosa"	Russia	55° 06N, 20° 45E	7.0	735
7b	Rybachy/National Park "Kurskaja Kosa"	Russia	55° 09N, 20° 50E	7.0	735
7c	Morskoje/National Park "Kurskaja Kosa"	Russia	55° 15N, 20° 56E	7.0	735
7d	Nagliu Nature Reserve/National Park "Kursiu Nerija"	Lithuania	55° 17N, 20° 59E	7.0	735
7e	Nida/National Park "Kursiu Nerija"	Lithuania	55° 26N, 21° 04E	7.0	735
7f	Juodkrantė /National Park "Kursiu Nerija"	Lithuania	55° 33N, 21° 06E	7.0	735

Plot sizes were chosen according to Dierschke (1994). The records included all species of bryophytes, lichens and vascular plants. Plant abundance was assessed using the Londo technique (Londo 1976). Vegetation structure (percentage cover of bryophytes, lichens, herbs, shrubs, trees and bare soil) was determined for each plot. Global Positioning System (GPS) was used for recording the plot coordinates. In general the nomenclature of vascular plants followed the Flora Europaea (Royal Botanic Garden Edinburgh 2009), except for *Corispermum intermedium* and *Corispermum pallasii*, where we relied on the treatment of the genus *Corispermum* by Mosyakin (1995, 2006). Nomenclature of bryophytes followed Hill (1991) and that of lichens followed Santesson (1993). A thin-layer chromatography (acetone extract in eluent A) was made for the determination of some lichens (Culberson and Amman 1979). Plant community nomenclature followed the International Code of Phytosociological Nomenclature (Weber et al. 2000, see Berg et al. 2004) except for the *Corispermum pallasii-Cakile maritima* community, which was named after the dominant species and completed by the suffix '-community'.

The estimated plant abundances were transformed into abundances in percent. All relevés were separated into forested and non-forested relevés and then classified by a TWINSpan analysis (Hill 1979) to distinguish different vegetation groups.

The term “yellow dunes” was used for mobile dunes with initial vegetation development, “grey dunes” were fixed relative stable interior dunes with short herbs, grasses and lichens and “brown dunes” were older stabilized dunes with shrubs and woodland (Doody 2001, 2008). Along a gradient from the sea landwards, changes in vegetation cover (of different vegetation layers) and environmental conditions of plant communities (cover weighted Ellenberg Indicator values of vascular plants; Ellenberg 2001) were estimated using regression analysis. Plant communities of the yellow and grey dunes were used for regression analysis to show general differences in continentality of plant species (Ellenberg Indicator values of vascular plants) along the study sites of Southern Baltic coast from west to east.

## Results

### Vegetation

At the 145 plots along the southern Baltic coast, 230 species were recorded. Altogether, eight associations, two subassociations and two variants from five alliances, five orders and five classes were distinguished.

- C.: *Ammophiletea* Br.-Bl. & Tx. ex Westhoff & al. 1946
  - O.: *Elymetalia arenarii* Br.-Bl. & Tx. ex Fröde 1958
  - All.: *Elymion arenarii* Christiansen 1927a
  - Ass.: *Elymo arenarii-Ammophiletum arenariae* Br.-Bl. & de Leeuw 1936
  - Subass.: *Elymo arenarii-Ammophiletum festucetosum*
  - Corispermum pallasii-Cakile maritima* community
- C.: *Koelerio-Corynephoretea* Klika in Klika & V. Novák 1941
  - O.: *Sedo acris-Festucetalia* Tx. 1951.
  - All.: *Koelerion glaucae* Volk 1931
  - Ass.: *Helichryso arenarii-Jasionetum litoralis* Libbert 1940
  - Subass.: *Helichryso arenarii-Jasionetum cladonietosum*
  - Ass.: *Festucetum polesicae* Regel 1928
- C.: *Calluno-Ulicetea* Br.-Bl. & Tx. ex. Klika & Hadač 1944
  - O.: *Vaccinio-Genistetalia* Schubert ex Passarge 1964
  - All.: *Empetrium nigri* Schubert ex Westhoff & den Held 1969
  - Ass.: *Hieracio umbellati-Empetretum nigri* Libbert ex Passarge 1964
- C.: *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. & al. 1939
  - O.: *Piceetalia excelsae* Pawłowski & al. 1928
  - All.: *Dicrano polyseti-Pinion sylvestris* (Libbert 1933) W. Matuszkiewicz 1962
  - Ass.: *Empetro nigri-Pinetum sylvestris* Libbert & Sissingh in Libbert 1940
  - Var.: young stands of *Empetro nigri-Pinetum sylvestris*
  - Var.: old stands of *Empetro nigri-Pinetum sylvestris*
  - Ass.: *Cladonio-Pinetum sylvestris* Juraszek 1927

C.: *Carpino-Fagetea* Passarge & Hofmann 1968  
 O.: *Fagetalia sylvaticae* Pawłowski & al. ex Tx. 1937  
 All.: *Fagion sylvaticae* Luquet 1926

Ass.: *Asperulo odoratae-Fagetum sylvaticae* Sougnez & Thill 1959

The 145 relevés are combined in a synoptic table (Table 2, appendix). 61 % of the recorded species were vascular plants, 28 % lichens and 11 % bryophytes. 24 vascular plants, 17 lichens and two bryophytes species were included in National Red Books (Berg and Wiehle 1991, Voigtländer and Henker 2005, Mierwald and Romahn 2006, Mirek et al. 2006, Litterski and Schiefelbein 2007, Rašomavičius et al. 2007) or listed as endangered in local studies (Gubareva et al. 1999).

### **Main plant communities on dry coastal dunes along the Southern Baltic coast**

On the seaward slope of the yellow dunes perennial tall grasslands (class *Ammophiletea*: *Elymo arenarii-Ammophiletum arenariae*) developed. They were dominated by *Ammophila arenaria* and accompanied by a number of taxa with *Lathyrus maritima* and *Leymus arenaria* being the most common. On the lee side of the dunes, where sand deposition was lower, the species richness and vegetation cover increased. *Ammophila arenaria* was there associated with *Carex arenaria* and *Festuca rubra* subsp. *arenaria*, forming the *Elymo arenarii-Ammophiletum festucetosum* (class: *Ammophiletea*) and other taxa from the next succession stage, the *Koelerio-Corynephoretea*. Very specific annual vegetation (*Corispermum pallasii-Cakile maritima*-community) grew on bare soils of active migrating dunes and dynamic open sand fields. Typical plants were *Cakile maritima* subsp. *baltica*, *Corispermum pallasii* and *Linaria loeselii*, which formed sparse, species-poor vegetation stands. The Baltic endemic *Corispermum intermedium* also belonged to the typical dune vegetation of active mobile dunes, but nowadays is widely replaced by the neophytic *C. pallasii* (Dolnik et al., in press) and by chance was not covered by the vegetation sampling. *Corispermum pallasii* and *Cakile maritima* subsp. *baltica* were typical for the migrating dunes of the Curonian Spit, whereas the endemic *L. loeselii* occurred on dunes of the Curonian Spit as well as on the Łeba Bar.

Higher sand stability and lower influence of salt spray led to more stable conditions in the interior parts of coastal dunes systems. They were colonised by perennial acidophilous short grasslands of the class *Koelerio-Corynephoretea*. The *Helichryso arenarii-Jasionetum litoralis* (class: *Koelerio-Corynephoretea*) contained in its typical subassociation very few lichens and bryophytes. Herbaceous plants such as *Artemisia campestris*, *Carex arenaria*, *Corynephorus canescens*, *Hieracium umbellatum*, *Jasione montana* and the bryophyte *Ceratodon purpureus* dominated the vegetation. Later succession stages were rich in *Cladonia*-species and other cryptogams and showed a higher coverage with perennial herbs such as *Helichrysum arenarium* and *Thymus*

*serpyllum*. Such vegetation was best summarized under the plant community *Helichryso arenarii-Jasionetum cladonietosum* (class: *Koelerio-Corynepherea*), although other plant communities with similar vegetation composition but varying species dominance have been described (c.f. Dengler 2004). Additionally, the perennial tussock grass *Festuca polesica* occurred in places in the herb layer of stable secondary dune areas as well as in dynamic coastal grey dunes. Such stands could be classified in the association *Festucetum polesicae* (class: *Koelerio-Corynepherea*).

Low shrublands with *Empetrum nigrum* (class *Calluno-Ulicetea: Hieracio umbellati-Empetretum nigri*) occupied older, stabilised dunes. Species such as *Carex arenaria*, *Corynephorus canescens* and *Dicranum scoparium* reflected a close interaction with the nearby *Helichryso arenarii-Jasionetum litoralis*. Under natural conditions, seedlings of *Pinus sylvestris* growing under the protection of *Empetrum nigrum* initiated the development of a coastal pine forest (class *Vaccinio-Piceetea: Empetro nigri-Pinetum sylvestris*). The *Empetro nigri-Pinetum sylvestris* preferred young, relatively low acid sands. *Deschampsia flexuosa*, *Melampyrum pratense*, *Pleurozium schreberi* and *Polypodium vulgare* were the most frequent species. It was possible to distinguish between a variant with young and one with old pine stands. The vegetation in the younger variant was mainly composed of relicts from the *Helichryso arenarii-Jasionetum litoralis*. *Carex arenaria*, *Corynephorus canescens*, *Hypericum perforatum*, *Jasione montana* and *Trifolium pratense*, but also basiphilous species such as *Listera cordata*, *Pyrola chlorantha* and *Pyrola media* occurred. In contrast, older coastal forests were composed of denser dwarf shrub vegetation in the understory, such as *Empetrum nigrum* and *Vaccinium vitis-idaea*. In some areas, *Pinus mugo*-plantations on dry and acidic sand of migrating dunes have led to the formation of the sparse, species-poor *Cladonio-Pinetum sylvestris* (class: *Vaccinio-Piceetea*). Apart from some scattered individuals of *Deschampsia flexuosa* and *Melampyrum pratense*, a dense ground layer with *Cladonia*-species, *Dicranum polysetum*, *Hypnum jutlandicum* and *Pleurozium schreberi* has developed.

A completely different vegetation composition was found on the brown dunes of the Nature Reserve of Noer/Eckernförder Bight. The preliminary final stage of succession was represented by a beech-forest (class *Carpino-Fagetea: Asperulo odoratae-Fagetum sylvaticae*), growing on fresh basiphilous soils. *Fagus sylvatica* was the predominant species in the tree-layer, accompanied by young stands of *Quercus robur*. *Festuca altissima*, *Melica nutans*, *Oxalis acetosella* and *Pteridium aquilinum* dominated the ground layer. This association was, from a floristic point of view, poorly defined, because characteristic species were missing.

### **Zonation and environmental conditions**

There was a distinct zonation of plant communities related to distance from the sea. Along this zonation, a change in cover of the different vegetation layers occurred. The

total vegetation cover increases linearly as pioneer plant communities on yellow dunes give way to the more complex grey and brown dune communities (Table 3). This pattern was strongly related to a decrease in bare soil. Bryophyte species occurred mainly in the transition zone between mobile yellow dunes and stable grey dunes. Cover of shrubs and trees was only remarkable in brown dunes. The environmental conditions based on Ellenberg Indicator values (Ellenberg 2001) show a linear decline in light, temperature and reaction with distance from the sea (Table 3). The highest light availability, temperature, pH-values and nitrogen were measured in yellow dunes. In contrast, grey and brown dune habitats were characterised by higher moisture and less light availability.

**Table 3** Relationships between plant communities along the Southern Baltic coast, which occurred in a gradient related to distance from the sea, and indicator values and vegetation cover. Shown are best fitting linear or quadratic regressions. Coefficients of determination ( $R^2$ ) and probability ( $p$ ) are given. The number of observations was  $n = 144$ . Only significant relations are shown, ns = not significant. Best fitting relation in bold.

	Linear regression		Quadratic regression	
	$R^2$	$p$	$R^2$	$p$
Cover (%)				
total	0.5878	<0.0001	<b>0.0501</b>	<b>&lt;0.0001</b>
bare soil	<b>0.5807</b>	<b>&lt;0.0001</b>	0.0570	<0.0001
lichens	0.0788	0.0007	ns	
bryophytes	<b>0.4786</b>	<b>&lt;0.0001</b>	0.0144	0.0476
herbaceous plants	0.0598	0.0031	<b>0.0568</b>	<b>0.0031</b>
shrubs	<b>0.1243</b>	<b>&lt;0.0001</b>	0.0480	0.0049
trees	<b>0.6089</b>	<b>&lt;0.0001</b>	0.0380	0.0002
Indicator value				
Nitrogen N	0.1614	<0.0001	ns	
Light L	<b>0.6042</b>	<b>&lt;0.0001</b>	ns	
Temperature T	<b>0.2188</b>	<b>&lt;0.0001</b>	0.0300	0.0199
Continentality C	ns			
Moisture M	0.1372	<0.0001	<b>0.0244</b>	<b>0.0454</b>
Reaction pH	<b>0.1632</b>	<b>&lt;0.0001</b>	0.0496	0.0035

Along a gradient from the western study sites along the southern Baltic coast to the Curonian Spit, species indicating continentality (based on Ellenberg indicator values) slightly increased ( $R^2_{\text{adj}} = 0,061$ ,  $p = 0.005$ ). Species with a continental distribution, such as *Astragalus arenarius*, *Festuca polesica*, *Petasites spurius* and *Helichrysum arenarium* were recorded in the eastern study sites on Usedom, the Vistula Spit and on the Curonian Spit, but it is rare on the Łeba Bar. In contrast, *Galium saxatile*, which was recorded on Rügen and the Darß peninsula, is a species with an oceanic distribution. Some species, such as *Carex arenaria* and *Jasione montana*, which indicate oceanic conditions, were found in mostly all study sites along the Southern Baltic coast.

## Discussion

### Floristic composition of the “Sundic Baltic-Sand Dune Vegetation Complex”

The distinguished syntaxa of plant communities are typical for dry coastal dunes along the southern and western Baltic coast (Möller 1975, Wojterski 1993, Isermann 1996, Piotrowska 2002, Bohn and Gollup 2003, Berg et al. 2004, Stankevičiūtė 2006). They appear on coastal dunes with a zonal distribution related to distance from the sea. The observed shifts in Ellenberg indicator values mark a succession in vegetation. The accumulation of organic matter, resulting in higher soil moisture, and a decline in light conditions, lead to the encroachment of grasses and woody plants (Kuiters et al. 2009). The zonation from initial plant communities on yellow dunes towards coarse grassland on grey dunes and woodland communities on brown dunes is consistent with studies of other European dunes (Doing 1985, van Til et al. 2002, Provoost et al. 2004, Isermann in press).

However, some characteristic plant communities for dry coastal dunes along the Southern Baltic coast were not covered by the present vegetation records. Several reports (Wojterski 1993, Isermann 2004) describe the *Elymo arenarii-Agropyretum juncei* (class: *Ammophiletea*) which forms embryonic dunes and occurs on the seaward foot of yellow dunes. This association is restricted to the German Baltic coast and the western part of the Polish coast (Piotrowska 2002) as the distribution of the dominant species, *Elymus farctus* subsp. *boreali-atlanticus*, is decreasing eastwards (Isermann 2004). Furthermore, dominant stands of *Petasites spurius* form the *Petasitetum spurii* (class: *Artemisietea vulgaris*) on yellow dunes (Dengler and Wollert 2004). This continental association is distributed along the southern Baltic coast (Steffen 1931) and reaches its western distribution area in Mecklenburg-Pomerania. Due to intensive tourism and coastal protection measurements combined with long-term erosion along the southern Baltic coast, foredunes and yellow dune habitats are steadily destroyed and the *Elymo arenarii-Agropyretum juncei* and the *Petasitetum spurii* appear fragmentized (Piotrowska 1988, Dengler and Wollert 2004).

Further associations, which are not described in the present study, are the *Festucetum arenariae* on yellow dunes (class: *Ammophiletea*) with dominant stands of *Festuca rubra* subsp. *arenaria* and the *Caricetum arenariae* on grey dunes (class: *Koelerio-Corynephoretea*). The latter is forming extremely species poor heterogeneous vegetation stands with *Carex arenaria* (Dengler 2004). This association was already described by Paul (1953) for the Curonian Spit, where it still occurs on deflation areas in close neighbourhood to the *Helichryso arenarii-Jasionetum litoralis* (Stankevičiūtė 2006). Hueck (1932) observed a *Caricetum arenariae* on some parts of the trailing arms of the parabolic dunes on the Łeba Bar. In addition to the *Hieracio umbellati-*



*Empetretum nigri* on brown dunes, Berg (2004) describes coastal heaths with dense *Calluna vulgaris*-stands (class *Calluno-Ulocetea: Salici repentis-Empetretum nigri*).

### **Conservation of coastal dune plant communities**

The conservation of coastal dunes is important for the protection of littoral species (Laime and Tjarve 2009), as we recorded 24 vascular plants, 17 lichens and two bryophytes which are included in National Red List Books (Berg and Wiehle 1991, Voigtländer and Henker 2005, Mierwald and Romahn 2006, Mirek et al. 2006, Litterski and Schiefelbein 2007, Rašomavičius et al. 2007) and local studies (Gubareva et al. 1999). Some of these species, such as *Eryngium maritimum* and *Pulsatilla vulgaris* have a very high conservation value because they occur in protected dunes in higher quantities than on most other non-protected dunes (Łabuz 2007). Several lichens, recorded in the present study, are vulnerable or have decreasing populations along the German Baltic coast, such as *Cladonia cervicornis*, *Cladonia coccifera*, *Cladonia cornuta*, *Cladonia gracilis*, *Lecanora symnicata* or *Peltigera rufescens* (Litterski and Schiefelbein 2007). *Astragalus arenarius*, *Cakile maritima* subsp. *baltica* and *Tragopogon heterospermus* are species with distribution ranges limited to the Baltic region. Along the Baltic from Germany eastwards continental species such as *Helichrysum arenarium* and *Festuca polesica* become more important because of a change from more atlantic to more continental macroclimate (Houston 2008).

Two plant communities are exclusive to the Southern Baltic coast and underline the separation of the “Sundic-Baltic Sand Dune Vegetation Complex” from a northern ‘Baltic-Bottnian Sand Dune Complex’ and from the ‘Atlantic Sand Dune Vegetation’ of the North Sea area (Bohn and Gollup 2003). First, the *Corispermum pallasii-Cakile maritima*-community is specific to open sandy areas along the southern Baltic Area (Dolnik et al. in press). The annual pioneer vegetation with *Corispermum pallasii*, *Cakile maritima* subsp. *baltica* and the endemic *Linaria loeselli* is only found on the Łeba Bar and on the Curonian Spit. The syntaxonomical position of the *Corispermum pallasii-Cakile maritima*-community is problematic as the community shows a mixture of elements from the classes *Cakiletea maritimae*, *Stellarietea mediae* and *Ammophiletea*. The dominance of annuals clearly differentiates the open dunes of the *Corispermum pallasii-Cakile maritima*-community from the perennial dune vegetation of the *Ammophiletea*. It is obvious that in the succession series perennial species of the *Ammophiletea* follow the annual vegetation, and therefore transitional zones with a mosaic of places where both vegetation types occur. On the Curonian Spit the neophytic *Corispermum pallasii* is widely replacing the local endemic *Corispermum intermedium* (Dolnik et al. in press). Due to coastal protection programs such as *Ammophila arenaria*-plantations on yellow dunes and the stabilisation of migrating dunes by forest plantings, the habitat of the *Corispermum pallasii-Cakile maritima*-community has decreased by more than approximately 95 % within 150 years (Dol-

nik et al. in press). Second, coastal pine forests of the syntaxon *Empetro nigri-Pinetum sylvestris* are restricted to the southern Baltic. They are limited to a small coastal strip and show a subatlantic-boreal distribution. Their main distribution area is found along the Polish Baltic coast up to the Curonian Spit (Heinken 2008). The *Empetro nigri-Pinetum sylvestris* can be considered as the stage of the dune succession that follows yellow and grey dunes and develops into deciduous forests (Heinken 2008).

### **Threats to dry coastal dunes vegetation along the Southern Baltic coast**

Despite the concern for natural conservation, the coastal dunes along the southern Baltic are being fragmented by infrastructure and impacted on by coast defence measures, recreation pressure and climate changes. Hence, the protection of coastal dunes, their management and restoration are in the focus of attention for the countries bordering the southern Baltic.

Heavy storms over the last ten years have been responsible for considerable abrasion and destruction of many fore dunes and yellow dunes and their habitats and the beach directly borders on the forest (Łabuz 2004, Olšauskas et al. 2009). During the last decades, storm surges and hurricanes, affecting the southern Baltic coast, led to increasing dune and cliff erosion and caused extensive destruction on the relief and vegetation coverage of the protective dune ridge. Along the Polish Baltic coast, the smallest land losses are observed along the Łeba Bar and Vistula Bar. However, the western part of the Łeba Bar is due to its SW–NE-direction more exposed to the deflation action of the prevailing westerly winds and abrasion is the dominant process (Borówka and Rotnicki 1995). Abrasion was responsible for coastline retreat by a maximum of 10 to 200m and a shoreline retreat between 10 to 65 m between 1958 and 1984 (Borówka and Rotnicki 1995). The Curonian Spit seashore and protective dunes also suffered from five strong storms and the hurricane “Anatoly” during the last decades (Olšauskas 2009). Due to extensive abrasion, the vegetation cover of the windward slope of the protective dune decreased from 50 % to 39 % between 1982 and 2009 (Olšauskas 2009). Consequently, the sea no longer supplies new sand essential for the rebuilding of dunes and vegetation (Piotrowska 2002). Only a few parts of the coast denote positive accretion of sand, where long-term feeding of the beach with new sand, supplied by the sea, occurs, such as on the accumulative coast of the Darß peninsula or the Świna Gate Barrier.

To the present day, the relief of the yellow dunes on the Baltic Sea, North Sea and Atlantic Ocean coast is regulated and planted with *Ammophila arenaria* to prevent deflation and to create a favourable relief. As a result, a small-scaled relief with different habitats and small-scaled vegetation mosaics is often missing. Especially on the Łeba Bar and on the Curonian Spit the creation of an artificial yellow dune ridge had a lasting influence on the vegetation composition, as it prevented further sand supply from the sea, reaching the open migrating dunes. The dynamic sandy habitats were over-

grown by grasslands and furthermore stabilised by pine monocultures e.g. with *Pinus mugo* (Piotrowska 1988).

On the Russian part of the Curonian Spit pine planting is still being used for dune consolidation. Since 1938, the area of bare sands and grasslands were reduced by more than half and were replaced by woodlands (Peyrat 2008). Likewise, open sandy areas at the Vistula Spit disappeared completely due to afforestations during the 20<sup>th</sup> century. Today, inland transportation of sand along with the translocation of psamphytic vegetation only occurs in extensive drift sand areas on the Łeba Bar. However, the area of dynamic sandy habitats diminished by 27 % during the last 74 years (Peyrat et al. 2009).

Tourism is a major threat to the examined coastal habitats, as most of the protected areas are popular destinations for tourists and visitors. Since the changing political affiliation at the beginning of the 1990s, tourism is gaining an increasing importance along the Southern Baltic coast. National tourism was already well established on the Lithuanian part of the Curonian Spit, the Łeba Bar and the East-German islands of Usedom and Rügen before 1990. Since then, the new mobility rights and the restructuring to the free market economy led to an explosion of the number of visitor, especially from Western Europe. In the German federal state Mecklenburg-Vorpommern, for example, the number of overnight stays increased by 200 % from 9.4 million in 1992 to 28.4 million in 2009 (Statistisches Amt Mecklenburg-Vorpommern 2010). Enormous masses of holidaymakers concentrate on the seaside devastating beaches and adjacent dunes (Olsauskas et al. 2009). In fact, the number of tourists and overnight stays at the east European Baltic coast is almost not that high compared to the West European Baltic coast. On the Lithuanian part of the Curonian Spit around 28.000 tourists and 66.000 overnight stays were registered in 2006 (State Department of Tourism 2007), but a growing number of visitors is expected in the future. In Poland, Lithuania and Kaliningrad region, tourism is one of the few thriving industries, especially after the Poland's and Lithuania's joining to the EU. The Russian part of the Curonian Spit National Park, which is, due to visa-regulation for European visitors, less visited by tourists than the northern, Lithuanian part, is planed as one of Russians tourist development zones (Kavaliauskas 2010). Four project zones for tourism infrastructure development in Rybachy, Morskoje and Lesnoje are included in the plan for development of recreational-tourism infrastructure. The total project area of these zones amounts to 382 ha and has already been allotted for construction of hotel complexes, leisure centres, culture complexes, swimming pools, marinas and parking sites. The start of construction works is expected for 2010 (Kavaliauskas 2010).

Most of the study areas of the present survey are located close to seaside resorts (Curonian Spit), camping sites (Noer, Darss-Zingst-Peninsula) and settlements

(Rügen, Usedom, Łeba). National parks, such as on the Darss-Zingst-Peninsula, Łeba Bar and Curonian Spit attract numerous visitors and are popular destinations for millions of tourists. Especially the beach and adjacent dunes are favoured locations for recreation and are physically affected by beach management, non-official paths and trampling (Isermann and Krisch 1995, Łabuz 2004, Grunewald 2006). Heavy mechanical damages of the vegetation may lead to a reduction or complete destruction of the plant cover as well as a decrease in species richness. Especially lichen-rich communities in grey dunes, which are highly protected, are heavily endangered and their regeneration may take decades (Christensen and Johnsen 2001). Rare and vulnerable species such as *Eryngium maritimum* and *Linaria loeselli*, growing on open dry dune areas, are on the verge of becoming extinct (Stasiak 1987, Łabuz 2007). Between 1975 and 2006, the population abundance of *Eryngium maritimum* on coastal dunes of the Lithuanian part of the Curonian Spit has decreased by about one third (Olšauskas and Urbonienė 2008, Aviziene et al. 2008). Along the Polish coast the habitats of *Eryngium maritimum* are no longer present on dunes neighbouring seaside resorts (Łabuz 2007). Only some habitats are found in the western part of the Słowiński National Park and on a section of the Vistula Spit. Furthermore, constant deterioration of environmental conditions and reduction in habitat areas decreased the abundance of *Lathyrus maritimum* and *Gypsophila maritima* significantly between 1982 and 2007 (Olšauskas and Olšauskaitė-Urbonienė 2001, Olšauskas et al. 2009).

Increasing nutrient levels due to human defecation, deposition of rubbish and particularly atmospheric deposition of nitrogen heavily influence the nutrient poor dune systems. Based on EMEP-data, the wet N-deposition for the examined study sites is the lowest at Preila/Curonian Spit with  $4.6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  and rise to  $5.98 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  at Łeba and  $6.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  at Zingst/Darss-Zingst-Peninsula (Remke et al. 2009). In comparison to other European environments, these values are low to medium (Remke et al. 2009). At the northern Dutch coast,  $13\text{--}20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  wet deposition was measured in open dunes. In Great-Britain current levels of nitrogen deposition ( $7\text{--}30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) lie close to the critical load of  $10\text{--}20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Jones et al. 2004). The lower concentrations at the Baltic coast, especially in the eastern coastal sites, are caused by the lower intensity of agriculture and industry in the Baltic States (Remke et al. 2009). Nevertheless, the critical load for acidic, dry coastal Baltic dunes is around  $4\text{--}6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Remke et al. 2009) with a current range of N wet deposition of  $3\text{--}8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Plants growing in dune ecosystems are adapted to low nutrient conditions and get under higher competitive capacity with increasing eutrophic conditions. As a result, a shift from lichen-rich short grass vegetation towards species-poor vegetation stands dominated by *Carex arenaria*, *Deschampsia flexuosa* and *Ammophila arenaria* can be observed for Baltic dunes (Christensen and Johnsen 2001, Grunewald 2006, Houston 2008, Remke et al. 2009). Grass encroachment and loss of

herbaceous species was also found in grasslands of Dutch dry coastal dunes (Veer and Kooijman 1997).

## Conclusion

This study highlights the importance of natural or almost natural dune environments along the southern Baltic coast from Lithuania to Germany for documenting and surveying undisturbed plant communities and dune dynamics. The conservation of these dry coastal dunes is of international importance due to the limited range of its characteristic flora and vegetation. Programmes for the preservation and restoration of endangered species, such as *Eryngium maritimum* and *Linaria loeselli*, have to be worked out to ensure their population stability. Further studies are needed to compare undisturbed sites with sites disturbed by recreational activities, as already performed for the Świna Gate Barrier (Grunewald 2006). Changes and especially negative effects from recreational activities can be monitored and management measures can be taken.

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## Appendix

**Table 2** Synoptic table of dry coastal dune communities of the ‘Sundic Baltic Sand Dune Vegetation Complex’ along the southern Baltic coast. The plant layers are abbreviated as t = tree layer, s = shrub layer, h = herb layer, b = moss layer, e = epiphytic cryptogams and dw = cryptogams colonizing on deadwood and plant debris. Character and differential species are marked: CC: character taxon of a class, CD: differential taxon of a class; AC: character taxon of an alliance, AD: differential taxon of an alliance; AsC: character taxon of an association, AsD: differential taxon of an association. Associations are indicated by dark shading, subassociations by light shading and species of variants by frames. Columns based on less than 10 relevés (and therefore less reliable) are printed in italics. The first figure in the columns indicates the percentage constancy values, the second superscript the range of plant abundance (LONDO, 1976). Species, which are not character or differential species and which occur in less than 5 relevés, are shown at the end of the table. Red Book Species are marked: MV= federal state Mecklenburg-Vorpommern/Germany, LT = Lithuania, P = Poland, RU = Russia (Kaliningrad Oblast), SH= federal state Schleswig-Holstein/Germany. Countries, where the species was not found, but where it is included in National Red Data Books, are put in brackets.

	1	2	3	4	5	6	7	8	9	10	11
number of relevés	4	40	16	36	11	5	3	10	16	2	1
<b>mean cover (%)</b>											
total	3	20	45	64	77	90	95	100	100	93	100
trees	0	0	0	1	3	0	0	39	35	55	80
shrubs	0	1	1	6	2	7	10	7	12	5	2
herbaceous plants	3	19	38	37	25	42	45	30	39	8	40
bryophytes	0	0	1	15	20	23	30	45	43	38	5
lichens	0	0	4	14	30	30	33	18	5	38	2
bare soil	97	79	57	36	23	10	5	0	0	8	0
<b>number of species</b>											
total	1	4	8	15	16	22	20	20	17	14	28
vascular plants	1	3	7	9	5	14	9	15	12	7	24
bryophytes	0	0	0	2	3	3	3	3	2	2	2
lichens	0	0	0	3	8	5	8	3	3	6	2

	sociological value	layer	Red List								
<b><i>Cakile maritima-Corispermum pallasii-community</i></b>											
<i>Cakile maritima</i> subsp. <i>baltica</i>	AD	h	MV, RU	50 <sup>1a-2m</sup>	45 <sup>1p-4a</sup>	6 <sup>1a</sup>					
<i>Linaria loeselii</i>		h	LT, P, RU	50 <sup>1a-4m</sup>	30 <sup>1p-1a</sup>	13 <sup>1a</sup>					
<i>Corispermum pallasii</i>		h	RU	25 <sup>1a</sup>	30 <sup>1p-1a</sup>	6 <sup>4a</sup>					
<i>Tragopogon heterospermus</i>		h	RU		8 <sup>1r-1p</sup>	13 <sup>1r-1p</sup>					
<b><i>Ammophiletea, Elymo arenarii-Ammophiletum arenariae</i></b>											
<i>Ammophila arenaria</i>	CC	h		95 <sup>1p-5</sup>	69 <sup>1p-3</sup>						
<i>Lathyrus maritimus</i>	CC	h	(SH)	15 <sup>1p-6</sup>	56 <sup>1p-3</sup>						
<i>Leymus arenarius</i>	CD	h		15 <sup>1p-4m</sup>	31 <sup>1m-2</sup>	3 <sup>1a</sup>					
<b><i>Ammophiletea, Elymo-arenarii-Ammophiletum arenariae festucetosum</i></b>											
<i>Festuca rubra</i> subsp. <i>arenaria</i>	AsC	h		20 <sup>1p-1</sup>	69 <sup>1a-3</sup>	25 <sup>1p-2</sup>	8 <sup>4m</sup>	40 <sup>2a-2m</sup>	30 <sup>1a-1</sup>		
<b><i>Koelerio-Coryneporetea, Helichryso arenarii-Jasionetum litoralis</i></b>											
<i>Corynephorus canescens</i>	AC	h		8 <sup>1a-1</sup>	31 <sup>1r-1</sup>	83 <sup>1a-3</sup>	83 <sup>2m-5</sup>	40 <sup>1m-4a</sup>	67 <sup>4m</sup>	10 <sup>1a</sup>	6 <sup>2a</sup>
<i>Carex arenaria</i>	CD	h		5 <sup>1m-2m</sup>	38 <sup>1a-6</sup>	69 <sup>1a-2</sup>	58 <sup>1m-2</sup>	100 <sup>1a-4a</sup>	100 <sup>1m-4m</sup>	60 <sup>1a-4m</sup>	31 <sup>1a-1</sup> 50 <sup>1m</sup>
<i>Hieracium umbellatum</i>	CC	h		13 <sup>1p-2m</sup>	63 <sup>1p-4a</sup>	78 <sup>1p-1</sup>	42 <sup>1p-2a</sup>	18 <sup>1p-1</sup>		60 <sup>1r-4a</sup>	13 <sup>1a</sup> 50 <sup>1r</sup>
<i>Jasione montana</i>	CC	h	(SH)		31 <sup>1r-1</sup>	69 <sup>1p-1</sup>	50 <sup>1a-1</sup>	80 <sup>1p-2a</sup>	67 <sup>1a-2m</sup>	10 <sup>1p</sup>	
<i>Artemisia campestris</i>	CD	h	(SH)	8 <sup>1p-2m</sup>	50 <sup>1r-4m</sup>	67 <sup>1r-1</sup>	8 <sup>1</sup>	60 <sup>2a-1</sup>			
<i>Cladonia rangiformis</i>	AD	b	MV		6 <sup>4m</sup>	42 <sup>1m-2</sup>		60 <sup>1m-2</sup>		20 <sup>1-3</sup>	
<i>Rumex acetosella</i>	CC	h			25 <sup>1r-2a</sup>	50 <sup>1p-2m</sup>	17 <sup>1p-1</sup>	20 <sup>1a</sup>	33 <sup>1a</sup>	60 <sup>1p-1m</sup>	

Plant communities on dry coastal dunes

<i>Helichrysum arenarium</i>	CC	h	(SH)	5 <sup>1a-1</sup>	13 <sup>1a</sup>	56 <sup>1p-2m</sup>	17 <sup>1p-1a</sup>	100 <sup>1a-2a</sup>	33 <sup>1m</sup>	20 <sup>2a</sup>		
<i>Brachythecium albicans</i>	CC	b			6 <sup>4m</sup>	36 <sup>1m-4</sup>	8 <sup>1a</sup>	40 <sup>2m-1</sup>				
<i>Thymus serpyllum</i>	CC	h	MV, SH		13 <sup>1p-1</sup>	31 <sup>1m-3</sup>		40 <sup>2m-1</sup>				
<i>Dicranum scoparium</i>	CD	b			6 <sup>8</sup>	19 <sup>1m-1</sup>	25 <sup>1m-3</sup>	40 <sup>1</sup>	100 <sup>1-4</sup>	50 <sup>4m-2</sup>	50 <sup>4m-8</sup>	.2m
<i>Cladonia scabriuscula</i>	AC	b	MV		6 <sup>2m</sup>	22 <sup>1p-1</sup>	8 <sup>4m</sup>	40 <sup>1a-4m</sup>		20 <sup>1m-2m</sup>		
<i>Cephaloziella divaricata</i>	CD	b			6 <sup>2m</sup>	19 <sup>2a-4m</sup>	58 <sup>1a-1</sup>	40 <sup>4m-2</sup>	67 <sup>1</sup>	10 <sup>2m</sup>		
<i>Viola tricolor</i> subsp. <i>tricolor</i>	CC	h	MV		25 <sup>1a-2a</sup>	19 <sup>1r-2a</sup>	8 <sup>1p</sup>					
<i>Galium verum</i>	CD	h			6 <sup>1r</sup>	19 <sup>1p-1m</sup>		40 <sup>1a-4m</sup>		10 <sup>1p</sup>		
<i>Sedum acre</i>	CC	h			6 <sup>1m</sup>	39 <sup>1p-4m</sup>		80 <sup>1p-1</sup>		20 <sup>2a-2m</sup>		
<i>Tortula ruraliformis</i>	CD	b				22 <sup>4m-3</sup>		20 <sup>2a</sup>				
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	CD	b				25 <sup>1m-1</sup>	8 <sup>2m</sup>	40 <sup>2m-2</sup>		20 <sup>1m-2</sup>	6 <sup>2</sup>	.2m
<i>Peltigera rufescens</i>	CC	b	MV			14 <sup>1m-1</sup>		20 <sup>1p</sup>		10 <sup>2a</sup>		
<i>Cladonia pyxidata</i>	CD	b				17 <sup>2a-4m</sup>	19 <sup>1m</sup>	60 <sup>1m-1</sup>	67 <sup>2m-1</sup>			
<i>Cladonia fimbriata</i>	CD	b				17 <sup>1a-4m</sup>	8 <sup>1a</sup>	20 <sup>1a</sup>				
<i>Cladonia furcata</i>	CC	b				28 <sup>1a-3</sup>	8 <sup>1a-1</sup>	60 <sup>1a-4m</sup>	100 <sup>2m-4m</sup>		50 <sup>2m</sup>	
<i>Cetraria aculeata</i>	CC	b	(MV)			8 <sup>1m-2m</sup>	58 <sup>1m-2</sup>		67 <sup>2a-2m</sup>			
<i>Cladonia foliacea</i>	CC	b	MV			6 <sup>2m-4m</sup>	17 <sup>1m-2a</sup>		100 <sup>2m-4m</sup>	10 <sup>1</sup>		

**Koelerio-Coryneporetea, Helichryso arenarii-Jasionetum litoralis cladonietosum**

<i>Cladonia ramulosa</i>	b	MV			3 <sup>1m</sup>	58 <sup>1a-4m</sup>		20 <sup>1m</sup>	67 <sup>2m</sup>	10 <sup>1</sup>		
<i>Calluna vulgaris</i>	h					42 <sup>1p-1</sup>					50 <sup>1a-4</sup>	
<i>Cladonia glauca</i>	b				3 <sup>2m</sup>	42 <sup>2m-4m</sup>		20 <sup>4</sup>				
<i>Cladonia chlorophaea</i> var. <i>novochlorophea</i>	b					50 <sup>1r-4m</sup>				10 <sup>2</sup>		
<i>Cladonia floerkeana</i>	b					50 <sup>1r-2m</sup>						
<i>Campylopus introflexus</i>	b					25 <sup>1-4</sup>			67 <sup>1</sup>			
<i>Cladonia mitis</i>	b				8 <sup>1p-2m</sup>	25 <sup>1a-2</sup>					6 <sup>4m</sup>	
<i>Cladonia subulata</i>	AD	b			6 <sup>1m-2m</sup>	33 <sup>1a-4m</sup>		20 <sup>2m</sup>				
<i>Hypogymnia physodes</i>	b				11 <sup>1p-2m</sup>	33 <sup>1p-4m</sup>						

**Koelerio-Coryneporetea, Festucetum polesicae**

<i>Festuca polesica</i>	AsC	h	MV, RU						100 <sup>2m-2</sup>			
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**Calluno-Ulicetea, Hieracio umbellati-Empetretum nigri**

<i>Empetrum nigrum</i>	AC	h				3 <sup>1p</sup>				100 <sup>1-4</sup>		38 <sup>1a-1</sup>
<i>Galium saxatile</i>	CC	h			6 <sup>1m</sup>	3 <sup>1a</sup>				67 <sup>1a</sup>	10 <sup>1a</sup>	
<i>Cladonia portentosa</i>	CC	b	MV			3 <sup>1p</sup>	17 <sup>2m-2</sup>			100 <sup>2m-1</sup>		6 <sup>4m</sup> 50 <sup>4m</sup>
<i>Cladonia cornuta</i>	CC	b	MV			17 <sup>1a-4m</sup>	17 <sup>2a-4m</sup>	20 <sup>1a</sup>		33 <sup>2m</sup>		
<i>Hypnum jutlandicum</i>	CC	b								33 <sup>1m</sup>	20 <sup>1m-4m</sup>	13 <sup>1</sup> 50 <sup>4m</sup>

**Vaccinio-Piceetea, Empetro nigri-Pinetum sylvestris**

<i>Pinus sylvestris</i>	CD	t				8 <sup>4p-1</sup>	8 <sup>4r</sup>				100 <sup>1-6</sup>	100 <sup>3-5</sup>	
<i>Deschampsia flexuosa</i>	CD	h				3 <sup>4m</sup>			100 <sup>1m-4m</sup>		90 <sup>2m-6</sup>	100 <sup>2m-5</sup>	50 <sup>2m</sup>
<i>Melampyrum pratense</i>	CD	h				6 <sup>1p-2m</sup>		20 <sup>1p</sup>			100 <sup>1r-2m</sup>	75 <sup>1a-3</sup>	25 <sup>1a</sup> .4m
<i>Pleurozium schreberi</i>	CD	b					17 <sup>2</sup>	20 <sup>2</sup>			70 <sup>4m-6</sup>	63 <sup>1-7</sup>	50 <sup>8</sup>
<i>Pinus sylvestris</i>	CD	s				33 <sup>1r-1</sup>	17 <sup>1</sup>	60 <sup>1p-1</sup>	3 <sup>2r</sup>		60 <sup>1p-4a</sup>	38 <sup>1p-1</sup>	
<i>Sorbus aucuparia</i>	AD	h									40 <sup>1r-4m</sup>	50 <sup>1p-2r</sup>	
<i>Sorbus aucuparia</i>	AD	s				3 <sup>4r</sup>					50 <sup>1p-4a</sup>	44 <sup>1p-3</sup>	.2r
<i>Betula pendula</i>	AD	s									50 <sup>1r-2a</sup>	13 <sup>2p-1</sup>	
<i>Polypodium vulgare</i>	AC	h				6 <sup>1r-1p</sup>		20 <sup>2r</sup>			40 <sup>1r-2r</sup>	19 <sup>1p-2a</sup>	
<i>Trientalis europaea</i>	CD	h									40 <sup>1m</sup>	25 <sup>1a-2m</sup>	
<i>Scleropodium purum</i>	AC	b							67 <sup>2m-4m</sup>		20 <sup>2-6</sup>	31 <sup>4m-4</sup>	
<i>Betula pendula</i>	AD	t									20 <sup>1r-1</sup>	25 <sup>1r-4p</sup>	
<i>Quercus robur</i>	AD	h				3 <sup>2a</sup>		20 <sup>1a</sup>			30 <sup>1a-4r</sup>	69 <sup>1p-1</sup>	.4r
<i>Melampyrum pratense</i>	CD	h									30 <sup>1a-2m</sup>	19 <sup>1a</sup>	
<i>Galium album</i>	AsD	h				8 <sup>1a-2a</sup>		60 <sup>1p-4m</sup>			30 <sup>1r-2a</sup>	13 <sup>2a-2p</sup>	
<i>Pinus sylvestris</i>	CD	h				33 <sup>1r-2a</sup>	17 <sup>1p-2p</sup>	80 <sup>1a-2r</sup>	33 <sup>1r</sup>		20 <sup>1m-2r</sup>	13 <sup>1p-1m</sup>	
<i>Quercus robur</i>	AD	s									30 <sup>1r-1p</sup>	50 <sup>1r-2m</sup>	

**Vaccinio-Piceetea, Empetro nigri-Pinetum sylvestrum, variant of young pine stands**

<i>Hypericum perforatum</i>	h				6 <sup>1p</sup>	11 <sup>1p-1a</sup>		40 <sup>1a</sup>			50 <sup>1r-1a</sup>	
<i>Galium x pomeranicum</i>	h					6 <sup>1a-2a</sup>		20 <sup>1a-2</sup>			20 <sup>1r-1p</sup>	
<i>Ceratodon purpureus</i>	CD	b			13 <sup>2m</sup>	56 <sup>2m-4</sup>	42 <sup>1m-1</sup>	60 <sup>2m-3</sup>			10 <sup>2m</sup>	
<i>Cladonia rei</i>	b					22 <sup>1a-1</sup>		40 <sup>1m-1</sup>			10 <sup>1</sup>	

<i>Listera cordata</i>	AsC	h	(MV), (LT), (P), (SH), RU						10 <sup>1m</sup>
<i>Lotus corniculatus</i>		h							10 <sup>1p</sup>
<i>Medicago lupulina</i>		h			6 <sup>1p-1a</sup>				10 <sup>1m</sup>
<i>Pyrola chlorantha</i>	AsC	h	(MV), (SH), RU						10 <sup>1p</sup>
<i>Pyrola media</i>	AsC	h	(MV), (P), RU						10 <sup>1a</sup>
<b>Vaccinio-Piceetea, Empetro nigri-Pinetum sylvestrum, variant of old pine stands</b>									
<i>Vaccinium vitis-idaea</i>	CD	h							38 <sup>1a-3</sup>
<i>Luzula pilosa</i>	AD	h			8 <sup>1p</sup>		33 <sup>1p</sup>		25 <sup>1a-1m</sup>
<i>Lepraria incana</i>		b							25 <sup>1p-2a</sup>
<i>Agropyron repens</i>		h			3 <sup>1a</sup>				13 <sup>1a</sup>
<i>Anthoxanthum odoratum</i>	CC	h		3 <sup>1m</sup>					13 <sup>1p-1a</sup>
<i>Lophocolea heterophylla</i>		b					33 <sup>1m</sup>		6 <sup>1</sup>
<i>Luzula multiflora</i>		h							6 <sup>1p</sup>
<i>Betula pubescens</i>		s							6 <sup>1p</sup>
<i>Prunus padus</i>		h			3 <sup>2r</sup>				6 <sup>1r</sup>
<i>Rubus idaeus</i>		s							6 <sup>4p</sup>
<b>Vaccinio-Piceetea, Cladonio-Pinetum sylvestris</b>									
<i>Pinus mugo</i>	CD	t			3 <sup>4p</sup>	8 <sup>3</sup>			100 <sup>5-6</sup>
<i>Cladonia gracilis</i>	CC	b	MV			42 <sup>1a-1</sup>	33 <sup>2a</sup>		50 <sup>1</sup>
<i>Pinus mugo</i>	CD	h		6 <sup>1r</sup>					50 <sup>4p</sup>
<i>Cladonia uncialis</i>	CC	b	MV				33 <sup>2a</sup>		50 <sup>2m</sup>
<i>Cardaminopsis arenosa</i>		h			8 <sup>1r-1p</sup>			11 <sup>1p</sup>	50 <sup>1r</sup>
<b>Carpino-Fagetea, Asperulo odoratae-Fagetum sylvaticae</b>									
<i>Fagus sylvatica</i>	CC	t							7
<i>Geranium robertianum</i>		h		6 <sup>1r</sup>				30 <sup>1r-1p</sup>	1
<i>Quercus robur</i>	CC	t						10 <sup>1</sup>	6 <sup>1a</sup>
<i>Stellaria holostea</i>		h						10 <sup>1a</sup>	1
<i>Arrhenatherum elatius</i>		h			3 <sup>1a</sup>				.1m
<i>Festuca altissima</i>		h	(LT)						.1m
<i>Melica nutans</i>		h							.1m
<i>Oxalis acetosella</i>		h						20 <sup>1p-1m</sup>	6 <sup>1p</sup>
<i>Galium mollugo</i>		h		6 <sup>1r</sup>					.1a
<i>Pteridium aquilinum</i>		h							.2m
<i>Sambucus nigra</i>		s							13 <sup>1p-4m</sup>
<i>Sambucus nigra</i>		s							.2p
<i>Sambucus nigra</i>		s							.2r
<b>others</b>									
<i>Hypochoeris radicata</i>	CD	h	MV, RU	6 <sup>1m</sup>	6 <sup>1p</sup>	17 <sup>1r-1p</sup>	20 <sup>2p</sup>		
<i>Astragalus arenarius</i>		h	(MV)		6 <sup>1p-1a</sup>	8 <sup>1p</sup>	40 <sup>1p-2m</sup>		
<i>Potentilla argentea</i>		h			8 <sup>1p-1a</sup>		20 <sup>1a</sup>		50 <sup>1p</sup>
<i>Cerastium semidecandrum</i>	CC	h		6 <sup>2m</sup>	8 <sup>1p-1a</sup>			10 <sup>1a</sup>	
<i>Trifolium arvense</i>	CC	h			8 <sup>1p-1a</sup>			10 <sup>2m</sup>	
<i>Polytrichum piliferum</i>	CD	b			3 <sup>4m</sup>	33 <sup>1-4</sup>			
<i>Calamagrostis epigejos</i>		h						10 <sup>1m</sup>	13 <sup>1a-4m</sup>
<i>Placynthiella icmala</i>		b			6 <sup>1a-2m</sup>	8 <sup>1r</sup>	33 <sup>1m</sup>	10 <sup>1a</sup>	6 <sup>1r</sup>
<i>Lonicera periclymenum</i>	AD	h							31 <sup>1p-4a</sup>
									.1p

Additional plants differentiated by layers:

**Tree layer:** *Betula pubescens* (10) 3<sup>2r</sup>; *Picea abies* (8) 10<sup>1r-1p</sup> (9) 13<sup>1p-4r</sup>; *Populus tremula* (8) 6<sup>1p</sup>; **Shrub layer:** *Acer platanoides* (9) 13<sup>2r-2p</sup>; *Crataegus monogyna* (11) .4r; *Frangula alnus* (9) 13<sup>1r-2p</sup>; *Juniperus communis* (9) 13<sup>1a-2p</sup>; *Lonicera periclymenum* (9) 6<sup>4p</sup>; *Picea abies* (9) 6<sup>1p</sup>; *Populus tremula* (9) 10<sup>4r</sup>; *Prunus padus* (9) 6<sup>1r</sup>; *Ribes nigrum* (11) .2r; *Rosa rubiginosa* (4) 3<sup>1</sup> (7) 6<sup>7.4a</sup>; *Rosa rugosa* (9) 6<sup>2r</sup>; *Rubus caesius* (4) 3<sup>1r</sup> (9) 6<sup>4p</sup>; *Rubus fruticosus* (11) .2r; *Salix daphnoides* (2) 5<sup>1r-1a</sup>; *Salix repens* (MV), (SH), RU (2) 5<sup>1</sup> (8) 10<sup>1p</sup>; **Herb layer:** *Acer campestre* (8) 10<sup>1r</sup>; *Acer platanoides* (9) 6<sup>2r</sup> (11) 2<sup>r</sup>; *Achillea millefolium* (6) 20<sup>1p</sup>; *Agrostis capillaris* (8) 10<sup>1a</sup> (9) 6<sup>1p</sup>; *Aira praecox* (LT) (9) 13<sup>1m-2a</sup>; *Anthyllis vulneraria subsp. maritima* MV, RU (4) 6<sup>2a</sup>; *Arabidopsis thaliana* RU (3) 6<sup>1r</sup> (4) 14<sup>1p-1a</sup> (5) 8<sup>1p</sup> (6) 20<sup>1p</sup> (8) 10<sup>1a</sup>; *Armeria maritima* (MV) (4) 3<sup>1p</sup>; *Artemisia maritima* MV (2) 3<sup>1p</sup> (3) 13<sup>1p</sup> (4) 8<sup>1a-2a</sup> (6) 20<sup>1a</sup> (8) 10<sup>2a</sup>; *Betula pendula* (19) 50<sup>1p</sup>; *Briza media* MV, (SH) (7) 33<sup>1a</sup>; *Cynoglossum officinale* RU (2) 3<sup>1p</sup>; *Dactylis glomerata* (4) 3<sup>1m</sup> (9) 6<sup>1m</sup>; *Epilobium angustifolium* (4) 3<sup>2p</sup>; *Epipactis atrorubens* (LT), (MV),

**RU** (4) 3<sup>1p</sup> (5) 8<sup>1p</sup>; *Eryngium maritimum* (**LT**), **MV**, **RU**, (**SH**) (3) 13<sup>1r-1p</sup> (4) 3<sup>1p</sup> (6) 20<sup>1r</sup>; *Euphrasia stricta* (6) 20<sup>1p</sup>; *Fagus sylvatica* (11) .1p; *Fragaria vesca* (3) 6<sup>1r</sup> (4) 3<sup>1a</sup> (6) 20<sup>2a</sup> (8) 30<sup>1p-1m</sup>; *Galium odoratum* (11) .2m; *Glechoma hederacea* (11) .1a; *Gypsophila paniculata* (3) 6<sup>1p</sup> (4) 3<sup>1p</sup>; *Hieracium pilosella* (4) 3<sup>1a</sup> (6) 40<sup>1a-1</sup>; *Hippophae rhamnoides* (4) 3<sup>1</sup> (9) 6<sup>2r</sup>; *Holcus lanatus* (8) 20<sup>1a-1</sup> (9) 25<sup>1p</sup>; *Honkenya peploides* (2) 3<sup>1r</sup> (3) 19<sup>1r-1m</sup>; *Impatiens noli-tangere* (11) .4m; *Juncus articulatus* (2) 5<sup>2p</sup>; *Juniperus communis* (9) 13<sup>2p</sup>; *Lactuca tatarica* (2) 3<sup>1p</sup> (4) 3<sup>1p</sup>; *Larix decidua* (9) 6<sup>1r</sup>; *Elymus giganteus* (10) 3<sup>1a</sup>; *Leymus racemosus* (3) 6<sup>4a</sup>; *Linaria vulgaris* (4) 3<sup>1r</sup>; *Lolium perenne* (8) 10<sup>1m</sup>; *Luzula campestris* (7) 33<sup>1a</sup>; *Moehringia trinervia* (8) 10<sup>1p</sup>; *Oenothera biennis* (3) 13<sup>1p-1a</sup> (4) 8<sup>1p</sup>; *Petasites spurius* (**SH**) (2) 15<sup>1m-1</sup> (3) 30<sup>1p-4m</sup> (4) 3<sup>4a</sup>; *Picea abies* (10) 6<sup>1r</sup>; *Pimpinella saxifraga* (4) 3<sup>1a</sup>; *Plantago lanceolata* (4) 14<sup>1p-1a</sup>; *Plantago media* (**MV**), **SH** (4) 6<sup>1p-1a</sup>; *Poa angustifolia* (7) 33<sup>1m</sup>; *Poa pratensis* (4) 3<sup>2m</sup> (8) 20<sup>2a-2m</sup> (9) 6<sup>1p</sup>; *Populus tremula* (8) 20<sup>1r-1a</sup>; *Pulsatilla pratensis* **MV** (4) 3<sup>1p</sup>; *Pyrola secunda* (8) 10<sup>1r</sup> (9) 6<sup>2a-2p</sup>; *Ranunculus acris* (8) 10<sup>1r</sup>; *Rosa rugosa* (2) 3<sup>1p</sup> (3) 6<sup>1p</sup> (4) 11<sup>1p-2p</sup>; *Rhinanthus serotinus* (4) 3<sup>2r</sup> (6) 20<sup>2p</sup> (8) 10<sup>2p</sup>; *Ribes rubrum* (3) 6<sup>1r</sup>; *Rosa rubiginosa* (7) 33<sup>4a</sup>; *Rubus caesius* (8) 10<sup>1p</sup> (9) 6<sup>2a</sup>; *Salix daphnoides* (3) 6<sup>1p</sup> (4) 3<sup>1p</sup>; *Salix repens* (**MV**), (**SH**), **RU** (8) 10<sup>1r</sup>; *Salsola kali* (**LT**), **MV** (**P**) (2) 3<sup>1m</sup>; *Sanguisorba minor* **MV** (8) 10<sup>2m</sup>; *Senecio vernalis* (3) 13<sup>1r-1p</sup> (4) 3<sup>1r</sup> (9) 6<sup>1r</sup>; *Setaria pumila* **RU** (8) 10<sup>1a</sup>; *Silene nutans* (4) 6<sup>1a-2m</sup>; *Solanum dulcamara* (3) 6<sup>1r</sup>; *Sorbus aria* (7) 33<sup>1r</sup>; *Stellaria graminea* (8) 10<sup>1p</sup>; *Taraxacum spec.* (8) 10<sup>1p</sup>; *Tortula ruralis* (4) 8<sup>4m</sup>; *Trifolium campestre* (8) 20<sup>1r-1p</sup>; *Urtica dioica* (11) .2m; *Veronica chamaedrys* (6) 20<sup>1p</sup> (8) 20<sup>1p-1m</sup>; *Veronica officinalis* (4) 3<sup>1a</sup>; *Vicia hirsuta* (5) 8<sup>1r</sup>; *Ammophila x baltica* (4) 3<sup>1</sup>; Moss Layer: *Aulacomnium androgynum* (4) 3<sup>2a</sup>; *Brachythecium oedipodium* (9) 6<sup>1</sup>; *Bryum argenteum* 6<sup>2m-4m</sup>; *Bryum caespiticium* (4) 3<sup>4m</sup> (6) 20<sup>1m</sup>; *Bryum elegans* (4) 3<sup>4a</sup>; *Bryum moravicum* (3) 6<sup>4m</sup> (4) 14<sup>2a-2m</sup> (5) 17<sup>4</sup>; *Cladonia arbuscula* (**MV**) (4) 6<sup>2m-1</sup> (5) 17<sup>1</sup>; *Cladonia arbuscula ssp. mitis* (4) 3<sup>2m</sup> (5) 8<sup>4m</sup>; *Cladonia arbuscula subsp. squarrosa* (4) 3<sup>1</sup>; *Cladonia cervicornis* **MV** (4) 3<sup>1a</sup> (5) 25<sup>2a-2m</sup> (7) 67<sup>1m-2m</sup>; *Cladonia ciliata* **MV** (11) .1m; *Cladonia chlorophaea* (4) 14<sup>1a-1</sup> (5) 8<sup>4m</sup> (6) 60<sup>1a-4m</sup>; *Cladonia coccifera* **MV** (5) 58<sup>1r-2m</sup> (7) 33<sup>1p</sup>; *Cladonia coniocraea* (9) 10<sup>2m</sup> (10) 6<sup>1m</sup>; *Cladonia gracilis ssp. turbinata* (4) 3<sup>2m</sup>; *Cladonia humilis* **MV** (4) 8<sup>4m</sup>; *Cladonia macilenta* (5) 8<sup>4m</sup> (8) 33<sup>1p</sup> (9) 20<sup>2a-2m</sup>; *Cladonia merochlorophaea* (5) 8<sup>1p</sup>; *Cladonia phyllophora* (4) 3<sup>1m</sup>; *Cladonia rangiferina* (**MV**) (10) 50<sup>4m</sup>; *Cladonia squamosa* **MV** (5) 8<sup>4m</sup>; *Cladonia stellaris* (**MV**), (**P**) 20<sup>3</sup>; *Cladonia sulphurina* (**MV**), (**P**) (5) 8<sup>1a</sup>; *Cladonia uncialis subsp. biuncialis* (5) 17<sup>1a-1</sup> (9) 6<sup>1</sup>; *Dicranum polysetum* (6) 20<sup>1</sup> (8) 20<sup>2m-4</sup> (9) 13<sup>1m-1</sup>; *Eurhynchium praelongum* (7) 33<sup>1m</sup>; *Lecanora persimilis* (**P**) (4) 3<sup>1p</sup>; *Lecanora saligna* (4) 3<sup>1a</sup>; *Lepraria jackii* (9) 6<sup>2a</sup>; *Leucobryum glaucum* (8) 30<sup>2a-1</sup> (9) 13<sup>1m</sup> (10) 50<sup>2</sup>; *Lophozia excisa* **MV** (4) 3<sup>1m</sup>; *Micarea denigrata* (4) 3<sup>1a</sup> (5) 8<sup>1a</sup>; *Parmelia sulcata* (4) 6<sup>1p-2m</sup>; *Peltigera didactyla* (4) 14<sup>2m-4m</sup>; *Peltigera hymenina* (**MV**), (**P**) (5) 8<sup>1r</sup>; *Pohlia nutans* (5) 25<sup>1a-4m</sup> (8) 10<sup>4a</sup> (9) 6<sup>1a</sup>; *Pseudevernia furfuracea var. furfuarcea* (4) 3<sup>1p</sup>; *Racomitrium canescens* **MV** (4) 3<sup>5</sup> (6) 20<sup>2m</sup>; *Racomitrium elongatum* (**MV**) (3) 3<sup>2m</sup> (5) 20<sup>2</sup>; *Trapeliopsis granulosa* (4) 3<sup>1p</sup> (5) 17<sup>1a-2p</sup>; *Xanthoria parietina* (4) 3<sup>1p</sup>; *Xanthoria polycarpa* (4) 3<sup>1p</sup>; Cryptogams growing on dead wood: *Bryoria fuscescens* (**MV**), **P** (9) 6<sup>2r</sup>; *Chrysothrix flavovirens* (9) 13<sup>2r-2a</sup>; *Cladonia chlorophea* (10) 6<sup>1m</sup>; *Hymnum cupressiforme subsp. lacunosum* (9) 6<sup>1m</sup>; *Hypogymnia physodes* (5) 17<sup>2p</sup>; *Hypogymnia tubulosa* (**P**) (4) 3<sup>2m</sup>; *Lecanora conizaeoides* (8) 10<sup>1a</sup>; *Lophocolea heterophylla* (9) 6<sup>1m</sup>; *Pleurozium schreberi* (9) 6<sup>1m</sup>; *Pseudevernia furfuracea var. furfuarcea* (8) 10<sup>1r</sup>; *Trapeliopsis granulosa* (8) 8<sup>2p</sup>; Epiphytic cryptogams: *Chaenotheca ferruginea* (8) 10<sup>1r</sup> (9) 6<sup>4m</sup>; *Chaenothecopsis pusilla* (**MV**) (9) 6<sup>1r</sup>; *Cladonia coniocrea* (9) 10<sup>2p</sup> (10) 6<sup>1r</sup> (11) 50<sup>1</sup>; *Cladonia digitata* 6<sup>2m</sup>; *Cladonia portentosa* **MV** (3) 6<sup>1p</sup> (8) 6<sup>1p</sup> (9) 50<sup>1a</sup>; *Hypocenomyce scalaris* (8) 10<sup>1r</sup> (9) 19<sup>1p-2a</sup>; *Hypogymnia physodes* (5) 17<sup>1m-2p</sup> (8) 70<sup>1p-2m</sup> (9) 19<sup>1p-2m</sup> (10) 100<sup>2a-1</sup>; *Lecanora conizaeoides* (8) 20<sup>1p</sup> (9) 13<sup>1p</sup>; *Lecanora symnicata* **MV** (7) 33<sup>1p</sup>; *Lepraria incana* (5) 8<sup>2p</sup> (8) 20<sup>1p-4m</sup> (9) 38<sup>1p-4m</sup> (11) .1m; *Placynthiella icmalea* (8) 10<sup>1r</sup>; *Platismatia glauca* (**MV**) (8) 10<sup>1p</sup> (10) 50<sup>1</sup>; *Pseudevernia furfuracea var. furfuarcea* (5) 3<sup>2p</sup> (8) 10<sup>1a</sup> (9) 6<sup>2</sup> (10) 50<sup>1</sup>; *Scoliosporum chlorococcum* (8) 10<sup>1p</sup> (9) 13<sup>1r-1p</sup>; *Usnea hirta* (**MV**), **P** (8) 10<sup>1a</sup> (9) 6<sup>1p</sup> (10) 50<sup>1</sup>; *Xanthoria polycarpa* (7) 33<sup>1p</sup>



Dune grassland and woodland in different stages of development on the migrating dunes “Caspalege Berg” and “Lepas Kalns” close to Morskoje with view to the Curonian Lagoon, Curonian Spit, RU (Photo: Peyrat 2008).

# Neophytic *Corispermum pallasii* (Stev.) (*Chenopodiaceae*) invading migrating dunes of the southern coast of the Baltic Sea

Christian Dolnik, Jann Peyrat, Alexandra Volodina and Alexey Sokolov. 2011. *Polish Journal of Ecology*. 59 (2): 17-25.

## Abstract

Actively migrating dunes along the southern coast of the Baltic Sea have a very specific vegetation of annual pioneer plants, some of which are endemic to that area. This vegetation type was studied on the migrating dunes of the Łeba Bar (Poland) and the Curonian Spit (Russia and Lithuania) and is for the first time represented by 18 vegetation relevés according to the Braun-Blanquet approach. Typical plants on bare soil of active migrating dunes and sand fields in Baltic dunes are the endemics *Corispermum intermedium* (Chenopodiaceae), *Cakile maritima* subsp. *baltica* (Brassicaceae), and *Linaria loeselii* (Scrophulariaceae). A comparison of our field investigations with literature records revealed a gradual replacement of *C. intermedium* by the neophytic Siberian bugseed *Corispermum pallasii* (Syn. *C. leptopterum*). *C. intermedium* suffered from severe habitat loss by dune afforestation, while the ruderal weed *C. pallasii* expanded its distribution range in the 20<sup>th</sup> century to various open gravel and sand fields in Europe, including dunes of the Baltic coast. New concepts of coastal conservation management, including aspects of coastal dynamics and nature conservation of endemic species, should be applied to conserve the remaining populations of *C. intermedium*.

## Introduction

The coastal dune vegetation of the southern Baltic coast is dominated by rhizomatous grasses and sedges representing the Atlantic coastal dune communities of the class Ammophiletea. Although this perennial dune vegetation was investigated repeatedly (Regel 1928, Steffen 1931, Paul 1953, Piotrowska 1988, Stankevičiūtė 2006), the specific annual vegetation on migrating dunes has been neglected so far. The extremely sparse dune vegetation of *Cakile maritima* ssp. *baltica* (Jord. ex Rouy and Foucaud) Hyl. Ex P.W. Ball, *Corispermum intermedium* Schweigg. and *Linaria loeselii* Schweigg. is unique in the southern Baltic area. Though mentioned as ephemeral pioneer vegetation by Preuss (1912), studies of plant communities have never focused on it.

The endemic species are the specific heritages that are related to the Eurasian steppe flora, such as *Corispermum intermedium*, a member of the Eurasian *Corispermum marshallii* group (Sukhorukov 2007), and *Linaria loeselii*, a relative of the Caspian *Linaria odora* agg. *Linaria loeselii* was included in the European Habitats Directive Annex IV as protected species of community interest in the European Union (Directive 92/43/EEC, Treaty of Accession 2003, Council of the European Commission 1992). *C. intermedium* is treated as spreading outside its native range in the Handbook of Alien Species in Europe (DAISIE 2009).

Another species in coastal dunes is the neophytic Siberian bugseed *Corispermum pallasii* Stev. 1817 (Syn. *C. leptopterum* Iljin 1929), which has attained a holarctic distribution (Mosyakin 1995, 1997). In Europe it was most probably released from horticultural collections in the early 19<sup>th</sup> century in southwestern Germany (Aellen 1961). Later, it spread as a ruderal weed along railroads, and in urban, industrial and other anthropogenically disturbed sites (Iljin 1929, Guzikowa 1975, Krisch 1987). The first records from ruderal sites of the Baltic coast date back to 1894 (leg. Ruthe, Świnoujście/Poland, according to Iljin 1929). Further coastal locations in Poland and Germany are cited in Krisch (1987). A specimen from the Latvian coast near Riga, collected by Kupffer in 1896 (Kupffer 1927) and named *C. hyssopifolium* L., corresponds to *C. pallasii*, according to his detailed description. The invasion of *C. pallasii* along the southern Baltic coast is noteworthy because it affects the distribution range of the Baltic endemic *Corispermum intermedium* occupying the same coastal dune habitats. During the 20<sup>th</sup> century, the distribution of *C. intermedium* and the increase of *C. pallasii* did not raise much attention. In particular, the separation of species within the genus *Corispermum* was counted as extremely difficult, even by leading botanists. Botanists such as Preuss (1912) and Steffen (1931) mentioned *C. intermedium* and the neophytic *C. marshallii* Stev. as characteristic plants of open dune areas. In contrast, Paul (1953) summerised all *Corispermum* species under the name *C. hyssopifolium*. In the second half of the 20<sup>th</sup> century, doubts arose concerning the endemism of *C. intermedium*, resulting in the synonymy of *C. leptopterum* with *C. intermedium* in



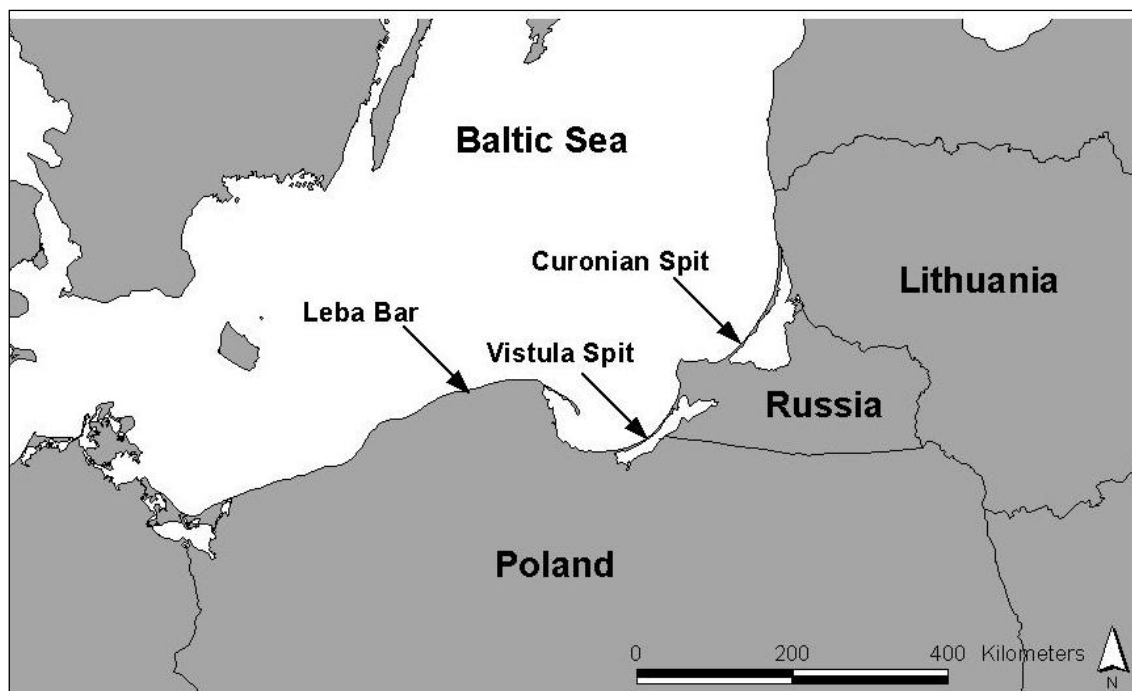
the Flora Europaea (Jalas & Suominen 1980, Akeroyed 1993). *C. intermedium* then became the accepted reference name for *C. pallasii* (Syn. *C. leptopterum*) in several Floras and was recorded throughout Europe. The recent monographic treatment of the genus *Corispermum* by Mosyakin (1995, 2006), however, discovered closer relationships within the genus. *C. intermedium* and *C. pallasii* were then separated by seed morphology into distinct groups (Mosyakin 1997, Sukhorukov 2007). Based on this historical taxonomical confusion, in publications from the second half of the 20<sup>th</sup> century that cover southern Baltic coast dune vegetation and that do not differentiate between *C. intermedium* and *C. pallasii*, it is difficult to correctly assess species. The spread of *C. pallasii* on drifting dunes of the Baltic coast in Lithuania has since been discovered by Gudžinskas (2000).

The aims of the present study are (i) to describe the annual vegetation on the remnant migrating dune fields in Poland, Russia and Lithuania, (ii) to document a species replacement of the endemic *C. intermedium* by the neophytic *C. pallasii*, and (iii) to discuss this fact in the light of landscape changes and species conservation.

## Study sites

The migration of southern Baltic Sea coastal dunes has likely been exacerbated by the influence of man, who settled the area during the late stone age about 5000 years ago (Rimantienė 1999). Forest-protected fragile vegetation on grey dunes and brown dunes was disturbed by fires, stock grazing, wood cutting and coal mining activities. Exposure of the underlying sand to wind resulted in erosion and migration of the dunes.

In the 19<sup>th</sup> century, several afforestation programs were initiated to stabilise the migrating dunes with willow and pine plantings. Today, most of the dune areas along the Baltic sea- coast are covered by forest, dry grassland and perennial dune vegetation. The only larger open migrating dune systems left are three separate dune fields on the Curonian Spit and a large area in the middle of the Łeba Bar (Figure 1). These mobile sand fields are now isolated from the coastal beach by artificially created dune ridges preventing sand transport to the migrating dunes. This has led to a flattening of the migrating dunes on the Curonian Spit and reduced the mean speed of the dune migration to 2–3 m yr<sup>-1</sup> (Povilanskas *et al.* 2006), and in some parts, to less than 1 m yr<sup>-1</sup> (Peyrat 2008). At present, migrating dunes reach heights of 54 m on the Curonian Spit and 42 m on the Łeba Bar. The open dune areas of the southern Baltic coastal area are parts of strict nature reserve areas of national parks (Curonian Spit National Park, Slowinski National Park). The coastal dune vegetation is furthermore protected by international agreements (HELCOM) and the Habitats Directive of the European Union (for Poland, Latvia and Lithuania).



**Figure 1** Southern Baltic seacoast with annual dune vegetation on active, migrating dunes on the Łeba Bar, on the Curonian Spit and the afforested migrating dunes without annual vegetation on the Vistula Spit.

## Methods

The annual vegetation of the migrating dunes was studied between 2005 and 2008 on the Lithuanian and Russian part of the Curonian Spit (55°15'N, 17°22'E) and the Łeba Bar (54°44'N, 17°23'E) in Poland (Figure 1). Vegetation records (relevés) were made according to Braun-Blanquet (1964) with a modified abundance-cover estimation scale of Reichelt and Wilmanns (1973) and are shown in APPENDIX. In order to be representative, they were located in the centres of small homogeneous vegetation stands or along transects. A uniform plot size of 25 m<sup>2</sup> (5 m × 5 m) was used. This plot size is recommended by Dierschke (1994) for coastal dune communities. Nomenclature of vascular plants is used according to the Flora Europaea (Royal Botanic Garden Edinburgh 2009) except for *Corispermum intermedium* and *C. pallasii*, where we rely on the treatment of the genus *Corispermum* by Mosyakin (1995, 2006). A reliable key for the determination of *Corispermum* species is given in Aellen (1961, including pictures of seeds) and Mosyakin (2006).

## Results

The annual pioneer vegetation on migrating dunes of the southeastern Baltic seacoast is today restricted to the remaining open dune fields on the Łeba Bar and on the Curonian Spit, where it is absent on the Vistula Spit (Figure 1). The pioneer vegetation is

dominated by *Corispermum pallasii*, *Cakile maritima* subsp. *baltica*, and *Linaria loeselii* (Table 1). *Corispermum pallasii* and *Cakile maritima* subsp. *baltica* are found only on the dunes of the Curonian Spit, whereas the endemic *Linaria loeselii* grows on the Curonian Spit as well as on the Łeba Bar. The endemic *Corispermum intermedium* has not yet been found and seems to be widely replaced by the neophytic *C. pallasii*. Two vegetation types of annual dune vegetation can be separated by species dominance: one with *Cakile maritima* and *Corispermum pallasii*, provisionally named the *Cakile-Corispermum*-community, and another one with *Linaria loeselii*.

*Corispermum pallasii* and *Cakile maritima* subsp. *baltica* form extended vegetation stands on drifting sand fields with low sand turnover during the vegetation season (Figure 2). The dominance of the annual life form clearly differentiates such vegetation stands from the perennial dune vegetation of the Ammophiletea, which is dominated by *Ammophila arenaria* (L.) Link and *Festuca rubra* ssp. *arenaria* (Osbeck) F. Aresch. Nevertheless, single juveniles of these perennial grasses and *Lathyrus maritimus* Bigelow, barely surviving the sand turnover during winter time, can also be found. Furthermore, some dry grassland species of the class Koelerio-Corynephoretea, such as *Anthyllis vulneraria* ssp. *maritima* (Schweigg. ex K.G.Hagen) Corb., *Artemisia campestris* L. or *Tragopogon floccosus* ssp. *heterospermus* (Schweigg.) C.Regel occur in shifting sand fields of eroded grey dunes. Presently, the *Cakile-Corispermum*-community is restricted to the Curonian Spit but historically is mentioned from the Vistula Spit as well.

It is noteworthy that neither the circum-Baltic distributed *Cakile maritima* ssp. *baltica*, nor *C. pallasii* are part of the annual vegetation of the migrating dunes of the Łeba Bar, which is located in the west of the native range of *C. intermedium*. *Cakile maritima* ssp. *baltica* is normally distributed in drift lines along the shore of the entire Baltic Sea coast, but in the southeastern region is found as well growing on drifting dune tops higher than 30 m (Figure 2).

*L. loeselii* is distributed along the southern Baltic seacoast from Pomerania in Poland to the Baltic States (Preuss 1912). It is an erect-to-ascending, annual-to-perennial plant which can cope with sand accumulation by producing stolone-like shoots towards the soil surface. It inhabits patches of a few square meters, mainly on slopes of eroded dunes and dune valleys. In this extreme environment, *L. loeselii* is often the only species and forms its own plant community (Table 1). It also occurs associated with species of the perennial dune communities Ammophiletea, such as *Ammophila arenaria* and *Festuca rubra* subsp. *arenaria*.

The *Linaria loeselii* community was found on the migrating dunes of the Polish Słowiński National Park as well as on the Russian and Lithuanian part of the Curonian Spit. The species also spread on the Vistula Spit (Stasiak 1987, Gubareva 1994). Due

to afforestation during the 20<sup>th</sup> century, the actual occurrence of stands which could be described as *L. loeselii* communities on the Vistula Spit remains ambiguous.



**Figure 2** Annual pioneer vegetation with *Corispermum pallasii* and *Cakile maritima* ssp. *baltica* on shifting sand of migrating dunes of the Curonian Spit, Russia (Photo: Dolnik 2005).

## Discussion

### **Decrease of *Corispermum intermedium* and replacement with *Corispermum pallasii***

The species replacement of the Baltic endemic *C. intermedium* by the neophytic Siberian bugseed (*C. pallasii*) is one of the most surprising results of our study. It raises several research questions and demands for habitat management and species conservation of coastal dunes of the southern Baltic coast. The new assessment of species delimitation in the genus *Corispermum* by Mosyakin (1995, 2006) also allows a critical reflection of older literature and a revision of herbarium specimens to follow the process of species replacement.

An extended herbaria revision will be part of a separate research project, but a first revision of herbarium specimens revealed that several specimens determined as *C. intermedium* actually belong to *C. pallasii*, especially those sampled from Central European mainland areas. “Real” specimens of *C. intermedium* were restricted to the coastal area of Poland, Russia, Lithuania and Latvia as the historically known range of that plant (Aellen 1961).

The current treatment of *C. intermedium* as a species, which became alien outside its

native range in Europe (van Grunsven 2008, DAISIE 2009), was based on wrong amplification of the name *C. intermedium* and refers to *C. pallasii*.

Those specimens, sampled in the last decades in dune areas of the Vistula and Curonian Spit in Russia and revised by us, belong to *C. pallasii*. The youngest specimen of *C. intermedium* dates back to 1967 (leg. Razumow, Curonian Spit, herb. Kaliningrad). Nevertheless, some relict populations still exist. As for the Lithuanian part of the Curonian Spit, Gudžinskas (2000) states that *C. pallasii* is much more frequent on dunes of the Baltic Sea coast than the native *C. intermedium* and Kabucis (2003) presents a map for the distribution of *C. intermedium* in Latvia. It becomes obvious that the few remaining populations of *C. intermedium* should be mapped and protected before the species becomes extinct.

Jalas and Suominen (1980) hypothesized that the extending Central European population of *C. leptopterum* (= *C. pallasii*) and the coastal *C. intermedium* intermingled and now form one population, however, this has never been proven and meanwhile seems not likely. Instead, collections of *C. pallasii* from the native area of *C. intermedium* and other places have been repeatedly misidentified for the latter, as in the *Atlas of Seeds and Fruits of Central and East-European Flora* (Bojňanský and Fargašová 2007), for example. Nevertheless, both species are wind-pollinated and each may react differently to pollen of the other. In this respect, molecular studies are necessary to clarify the hybridisation hypothesis and the relationship of *C. intermedium* with other, more closely related species, such as *C. gallicum* Iljin and *C. marshallii*.

### **Annual dune vegetation**

The annual dune vegetation on migrating dunes is species-poor but very specific. None of the three most characteristic species is restricted to annual vegetation stands on open dunes, as is *C. intermedium*. A community approach for the annual dune vegetation of the southern Baltic coast is attractive for nature conservation policy. However, it should be linked to vegetation stands with *C. intermedium* to fulfill phytosociological criteria, such as a characteristic species with a clear preference for single plant communities (Braun-Blanquet 1964). This is not the case with *C. pallasii*. This species is distributed mainly in ruderal places on gravelly and sandy soils in inland habitats, occurring in several annual and perennial plant communities (c.f. Korneck 1974, Krisch 1987). These communities differ considerably in their species composition and species richness from the vegetation stands on migrating dunes. Nevertheless, *C. pallasii* was reported in disturbed sites of coastal dunes in Belgium (Duvigneaud and Lambinon 1963), the Netherlands (Sissingh 1950 and Boerboom 1969 cit. in Hülbusch 1977), and other ruderal coastal places in Poland (Misiewicz 1976 cit. in Krisch 1987) and Germany (Hülbusch 1977, Krisch 1987). Such stands were described as the distinct plant association, Bromo-Corispermetum leptopteri (Sissingh 1950 cit. in Weeda and Schaminee 1998).

*L. loeselii* is fairly common also in the perennial plant community *Festucetum arenariae* Regel 1928 and related communities described from the Curonian Spit (Regel 1928, Steffen 1931, Paul 1953, Balevičienė and Stankevičiūtė 2000). Therefore, it is difficult to separate a distinct phyto-sociological association with *L. loeselii* as diagnostic species. Typical, dominant *Linaria loeselii* stands on open dune slopes can be understood to be pioneer phases of *Festucetum arenariae*. In the original table by Regel (1928), the *Festucetum arenariae* is characterised by species-poor dominant stands of *Festuca arenaria*, in which *Linaria loeselii* can occur. Thus, a distinct *Linaria loeselii* community, where *Festuca rubra* ssp. *arenaria* may occur, represents a shift in species dominance from one extreme to another. As there exist only a few relevés to support a *Linaria loeselii* community as separate vegetation type, we treat it in this study as rankles community connected with the *Festucetum arenariae*, belonging to the *Ammophiletea*.

### **Conservation of annual dune vegetation**

Taking into account that recent mobility of dunes is caused by anthropogenic destruction of vegetation, it is remarkable that *Linaria loeselii* and *Corispermum intermedium*, two endemic species, restricted generally to open sand fields in dune areas, occur along the southeastern Baltic coast. This indicates that there have always been enough suitable habitats for these species on sand fields of yellow dunes, on eroded grey dunes, or probably on small migrating dunes in the post-glacial period. It must have been a “pioneer and gap” vegetation extending its range only temporarily, when areas of bare sand developed after strong storms and major flood events. From the 16<sup>th</sup> century onward, increasing areas of migrating dunes provided more stable conditions to annual dune vegetation. Presently, the undisturbed migrating dunes of the southern Baltic coast form an important secondary habitat for these plant communities.

According to the NATURA 2000 habitat directive of the European Community and the Helsinki Convention (HELCOM), these coastal dunes are under strict protection. Nevertheless, it is still under discussion in Russia and Lithuania as to whether the migrating dunes should be kept as an open, dynamic system, where erosion processes are allowed to devastate the dunes, or whether it is worth stabilising the dunes with forest plantations in order to prevent erosion and keep geomorphologic forms intact. The protection of the Baltic endemic dune species *Corispermum intermedium* and *Linaria loeselii* give a clear priority to the first. Both species became rare due to coastal protection programs such as *Ammophila arenaria* plantations on white dunes and stabilisation of the migrating dunes by forest plantings. As a result the habitat of *Corispermum intermedium* and *L. loeselii* has decreased by more than approximately 95 % within 150 years.

It is beyond the scope of this article to deny the need for coastal protection, but new

concepts for coastal protection have to be developed in time, which include aspects of coastal dynamics and nature conservation of endemic species.

## Conclusion

The decline of the population of the Baltic endemic *Corispermum intermedium* corresponds with a severe loss of high-dynamic open dune areas along the southern Baltic coast. At the same time, the spreading of the invasive *Corispermum pallasii* in coastal dune areas along the Baltic coast has caused considerable confusion in the species delimitation of the genus *Corispermum*, clarified by Mosyakin (1995, 2006). As the current distribution of *C. intermedium* along the Baltic coast is insufficiently known, a mapping of the remnant populations and conservation measures are necessary. The impact of the neophytic *C. pallasii* on the population of the endemic *C. intermedium* needs further attention.

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## Locations of relevés of **Table 1:**

### *Corispermum pallasii-Cakile maritima*-community

1) on shifting dune near Biological field station Fringilla, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'12"N, 20°44'26"E, eastern slope of a shifting dune towards the Curonian lagoon, 20 m, 14. 07. 2005. 2) on shifting dune near Biological field station Fringilla, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'11"N, 20°44'28"E, transect line along the eastern slope of a shifting dune towards the Curonian lagoon, 17 m, 14. 07. 2005. 3) on shifting dune near Biological field station Fringilla, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'10"N, 20°44'30.3"E, eastern slope of a shifting dune towards the Curonian lagoon, 14 m, 14. 07. 2005. 4) on shifting dune near Biological field station Fringilla, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'08.5"N, 20°44'33"E, eastern slope of a shifting dune towards the Curonian lagoon, 8 m, 14. 07. 2005. 5) on stabilised shifting dune, deflation hollow at Curonian lagoon, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'01.6"N, 20°44'25"E, 3 m, 14. 07. 2005. 6) on stabilised shifting dune, deflation hollow at Curonian lagoon, forest management unit 14 Zelenogradsk, Curonian Spit, Russia; approx. 55°05'00"N, 20°44'21.4"E, 5 m, 14. 07. 2005. 7) open sand field between stabilised migrating dune, deflation area close to Curonian lagoon, forest management unit 15 Zelenogradsk, Curonian Spit, Russia; approx. 55°04'55"N, 20°44'13"E, 5 m, 14. 07. 2005. 8) open sand field between stabilised migrating dune, eastern slope, deflation area close to Curonian lagoon, forest management unit 15 Zelenogradsk, Curonian Spit, Russia; approx. 55°04'54"N, 20°44'09"E, 10 m, 14. 07. 2005. 9) open sand field dune top between stabilised migrating dune, deflation area close to Curonian lagoon, forest management unit 15 Zelenogradsk, Curonian Spit, Russia; approx. 55°04'55"N, 20°44'13"E, 14 m, 14. 07. 2005. 10) open sand field field in gray dunes, deflation zone with path, migrating dunes north of Morskoje, forest management unit 9 Rybachy, Curonian Spit, Russia; approx. 55°14'45.38"N, 20°56'20.2"E, 35 m, 22. 08. 2007. 11) on shifting dune Parnidas, Nida, Curonian Spit, Lithuania, approx. 55°17'30"N, 20°59'54"E, 21 m above sea level, 18. 07. 2008. 12) on shifting dune Parnidas, Nida, Curonian Spit, Lithuania, approx. 55°17'25"N, 20°59'58"E, 17m above sea level, 18. 07. 2008. 15) on shifting dune Parnidas, Nida, Curonian Spit, Lithuania, approx. 55°17'30"N, 20°59'52"E, 20 m above sea level, 18. 07. 2008.

### *Linaria loeselii*-community

14) inshifting dune valley in large open dune field north of Morskoje, north of Hirschbudenberg, forest management unit 9 Rybachy, Curonian Spit, Russia; 55°14'59"N, 20°56'35"E, 32 m above sea level, 22. 08. 2007. 15) on shifting dune Naglia, north of Pervalka, Curonian Spit, Lithuania, approx. 55°26'45"N, 21°05'23"E, 30 m above sea level, 18. 07. 2008. 16) on shifting dune Naglia, north of Pervalka, Curonian Spit, Lithuania, approx. 55°26'45"N, 21°05'17"E, 33 m above sea level, 18. 07. 2008. 17) on shifting dune Czolpinska dune, Slowinski National Park, Poland, 54°43'33"N, 17°15'40"E, 15 m above sea level, 18. 08. 2008. 18) on shifting dune, deflation zone, Czolpinska dune, Slowinski National Park, Poland, 54°43'36"N, 17°15'39"E, 17 m above sea level, 18. 08. 2008.



*Eryngium maritimum* on coastal dunes of the Curonian Spit, RU (Photo: Peyrat 2008).

# Plant species diversity in dry coastal dunes of the Southern Baltic coast

Jann Peyrat and Andreas Fichtner. *Community Ecology* (submitted)

## **Abstract**

This study describes patterns of plant species diversity in well preserved dry coastal dune systems along the southern Baltic coast. Variations in diversity and in distributional character of plant species and plant communities throughout the study areas result mainly because of the interplay between plant succession, exposure, disturbance and resource availability. Environmental indicator values, used to describe dynamics in dune habitats, show a decline of light and temperature with increased distance to the sea, accompanied by higher soil moisture due to accumulation of organic matter. Species richness, Shannon Index and Simpson Index of Dominance showed a humped-shaped curve along a sea-to-inland gradient. The highest species richness of vascular plants and cryptogamic species were found in grey dunes at intermediate levels of environmental and disturbance gradients, which confirms the intermediate disturbance theory.

## Introduction

Dune habitats are among the most important ecosystems in Europe, containing a high ecological diversity in terms of environmental heterogeneity and variability of species composition. Despite the narrow widths of coastal ecosystems, there is a complex sea-to-inland environmental gradient with spatial sequences of dune ridges, representing chronological series. This dune chronosequence with yellow dune, grey dune and brown dune habitats has been described for many coastal dune formations worldwide (Doing 1985, Lichter 1998, 2000, Łabuz and Grunewald 2007, Miller et al. 2010). A complex gradient of changing environmental conditions as well as the interplay among plant succession, exposure, disturbance and resource availability lead to different patterns and rates of succession (Lichter 1998).

Soil development, nutrient accumulation, plant height and habitat compartmentation produce the majority of changes in species during dune succession. Along the dune chronosequence, there is an increase in species richness and species diversity from species poor yellow dunes to young grey dunes after surface stabilisation (Isermann in press). In many cases, species richness decreases towards the mature stage of succession in brown dunes, possibly caused by less fluctuations and increasing stability (Margalef 1963, Stankevičiūtė 2001).

Dune heterogeneity is often initiated by disturbances at different scale (Hobbs and Huenneke 1992). Variations in disturbance regime can affect ecosystem and community structure and functioning (Hobbs and Huenneke 1992). In general, disturbance creates open patches for plant establishment and increases the amount of available ecological niches. Large scale disturbances, such as severe storms, waves, wind action and heavy rainfall lead to high sand dynamics within yellow and grey dune habitats (Miller et al. 2010). On a smaller scale animal digging, grazing, trampling and anthropogenic transformation (e.g. afforestation and coastal conservation measures) disturb the dune habitats with varying frequency and intensity (Jentsch and Beyschlag 2003).

Several hypotheses with contrasting views try to explain diversity patterns. The intermediate disturbance model (Connell 1978, Grime 1979) suggests that species diversity of a system is maximised and should be highest at moderate levels of disturbance (Whittaker 1977, Hobbs and Huenneke 1992). Recent investigations have proved that species richness reaches highest values at intermediate disturbance levels in dune grasslands (Stankevičiūtė 2001, Isermann in press), tropical rain forests (Molino and Sabatier 2001) and wetlands (Pollock et al. 1998). Apart from this, the resource-ratio hypothesis (Tilman 1982, 1985) provided evidence that species diversity within grassland communities contributes to soil heterogeneity (Reynolds et al. 1997). In coastal dunes from the North Sea and Baltic Sea the variability in soil pH

increases with greater species diversity and also with scale (Isermann 2005, Löbel and Dengler 2008). According to Jackson and Caldwell (1993), there is a positive correlation between environmental variability and species richness. Thus, along a sea-to-inland gradient with changing environmental conditions (soil, microclimate) the establishment of various species is favoured and species richness and diversity is varying.

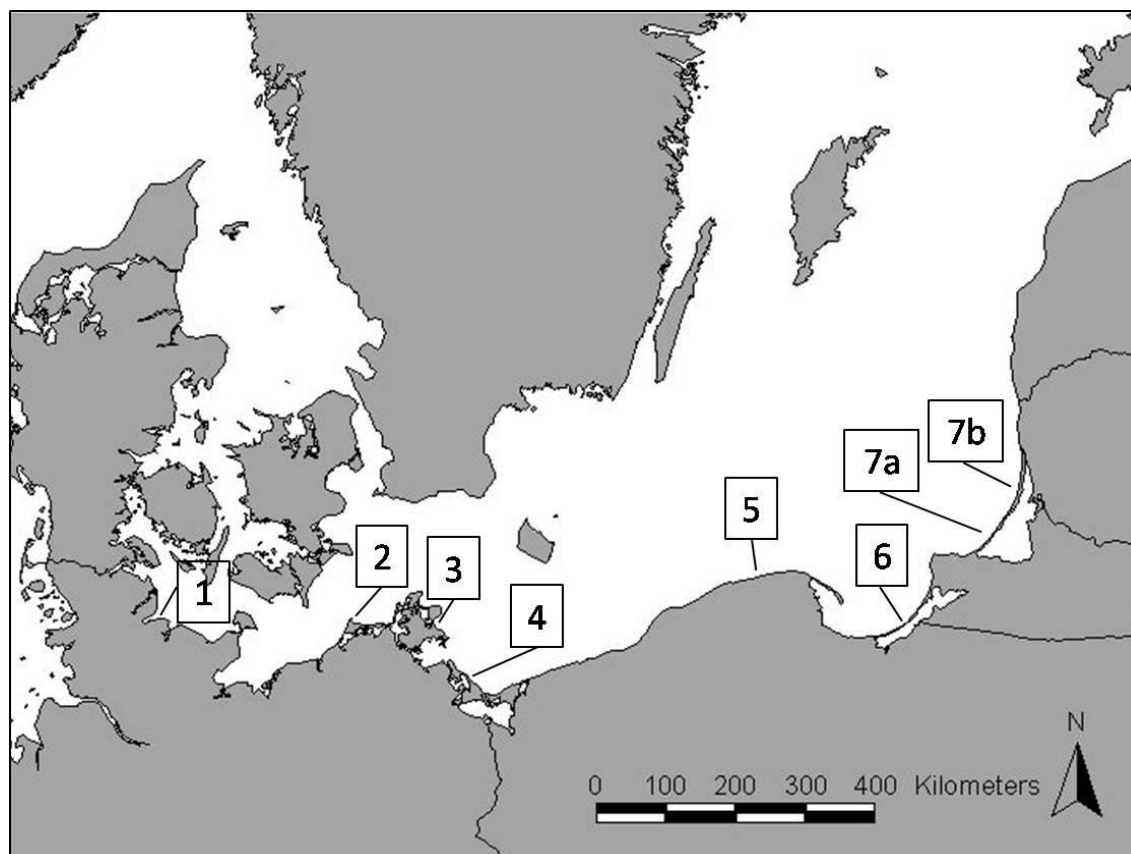
Today, most European coastal dune ecosystems are threatened by human pressure, natural and anthropogenic disturbance resulting in a substantial loss of regional biodiversity (e.g. Piotrowska 1988, Łabuz 2004). The measurement of species richness along the coastal dune gradient could be an important component for ecosystem management. Plant communities which best contribute to total species richness could be identified, underlining the importance of priority habitats for management planning (Acosta et al. 2009). Hence, it is essential to understand baseline diversity patterns of community mosaic, especially in areas, remaining relatively undisturbed and containing relatively intact dune systems (Łabuz 2004). To comprehend processes underlying biodiversity of coastal dunes the study describes (i) patterns of diversity of vascular plants, lichens and bryophytes across different habitats in well preserved dune systems along the southern Baltic coast and evaluate (ii) how each habitat contributes best to the total species richness.

## Materials and Methods

### Study area

This study was conducted in dry coastal dunes along the southern Baltic coast. Most of these coastal dunes were protected areas and designated as priority habitats in the European Fauna Flora Habitats Directive 92/43/EEC (Council of the European Commission 1992).

Based on the Map of European Vegetation (Bohn and Gollup 2003), 15 sites, situated within the “Sundic Baltic Sand Dune Vegetation Complex”, were selected for detailed vegetation analysis (Figure 1). The study sites covered a large geographical gradient from the Eckernförder Bight in the west, along the islands of Usedom and Rügen towards the Darß peninsula, Łeba Bar, Vistula Spit and the Curonian Spit in the east (Figure 1). The coastal dune systems were heterogeneous, consisting of distinct plant communities that occurred along a sea-to-inland ecological gradient but usually in a complex mosaic pattern. The climate of the southern Baltic is influenced by both the Atlantic Ocean and the European continent and has a transitional character with relatively constant temperatures (Schiewer 2008). The continental influence increases in eastern direction (Schiewer 2008).



**Figure 1** Study sites: 1) Nature Reserve “Bewaldete Düne von Noer” (DE); 2a) National Park “Vorpommersche Boddenlandschaft” (DE); 3) Island of Rügen (DE); 4) Nature Park “Usedom” (DE); 5) National Park “Słowiński (PL); 6) Landscape Park “Mierzeja Wiślana” (PL); 7a) National Park “Kurskaja Kosa” (RU); 7b) National Park “Kursiu Nerija” (LT).

## Field methods

A total of 144 phytosociological relevés was collected in pioneer vegetation of yellow dunes (*Ammophiletea*), dune grassland of grey dunes (*Koelerio-Corynephorotea*) or in shrub/woodland of brown dunes (*Calluno-Ulicetea*, *Vaccinio-Piceetea* and *Carpino-Fagetea*). Vegetation relevés were carried out in 5 m × 5 m-plots. Plant abundance/cover of all species of bryophytes, lichens and vascular plants was estimated using the Londo scale (Londo 1976). The nomenclature of vascular plants followed the Flora Europaea (Royal Botanic Garden Edinburgh 2009), except for *Corispermum pallasii*, where we relied on the treatment of the genus *Corispermum* by Mosyakin (1995, 2006). Bryophytes were determined according to Hill (1991) and lichens to Santesson (1993). Plant community nomenclature followed the International Code of Phytosociological Nomenclature (Weber et al. 2000, see Berg et al. 2004). Unweighted averages of indicator values according to Ellenberg (2001) were used as a proxy for ecological site factors. Mean indicator values for light (mL), temperature (mT), moisture (mF), soil pH (mR), continentality (mK) and nitrogen (mN) were calculated for each relevé.



## Data analysis

The estimated plant abundances were transformed from abundances in percent. All relevés were separated into forested and non-forested relevés and then classified by a TWINSpan analysis (Hill 1979) to distinguish different vegetation groups. The relevés were then rearranged manually to describe typical plant communities of the “Sundic Baltic Sand Dune Vegetation Complex”.

Due to missing values of some covariates we omitted 7 relevés (95 % of the data remained) for statistical analysis to ensure comparable inference. To characterise the main coastal dune habitats, plant communities were pooled to three dune types: yellow dunes, grey dunes and brown dunes. Differences in species richness and diversity of vegetation structure between plant communities and dune habitats, respectively, were evaluated by mixed-effects models with islands as random factor. Species richness was modelled as a function of vegetation type using the log link function and a Poisson distribution followed by pairwise Tukey comparisons. The generalised linear mixed models (GLMM) were scaled to correct for over-dispersion and fitted to the data with the *glmmPQL* function. Variations in structural species diversity (Simpson Index of Dominance and Shannon Index) were analysed by mixed-model ANOVA with a post hoc performance test (Tukey HSD test) (Zuur et al. 2009).

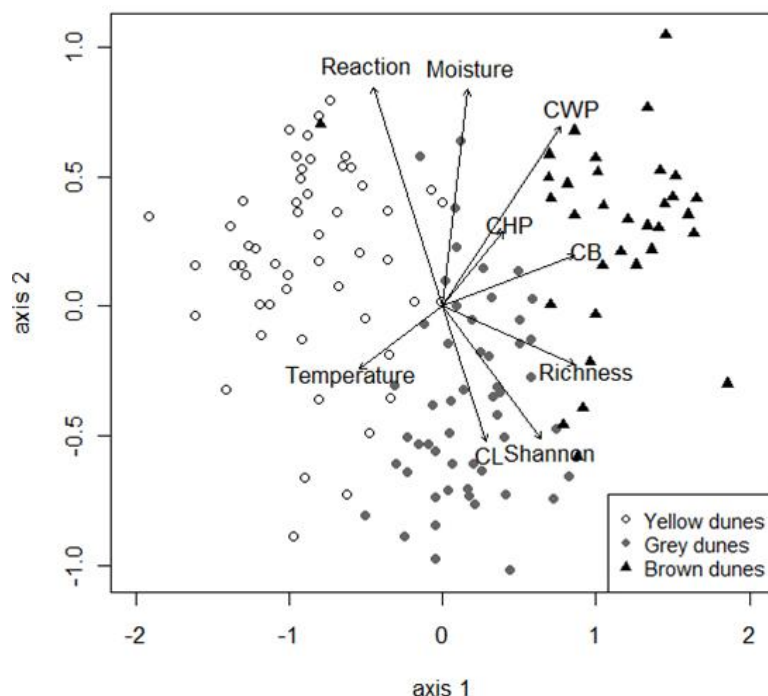
Non-metric multi-dimensional scaling (NMDS), using the *metaMDS* function, was performed to determine the main environmental gradients for species assemblages of dune habitats (Oksanen et al. 2009). We used the Bray-Curtis index based on abundance to examine changes in species composition related to dune succession. To reduce the effect of dominant species, abundance data were square-root transformed prior to analysis. Variations in species composition between dune types were tested with multivariate ANOVA (ADONIS) (Bray-Curtis dissimilarities, 1000 permutations). Collinearity between covariates was assessed by variance inflation factors (VIF). Only variables with VIF values < 3 were considered for further analysis. For this reason Simpson Index of Dominance and Ellenberg indicator values for light and nitrogen were not considered in the ordination. Pearson’s correlations between environmental variables and NMDS-axes scores were calculated using the function *envfit*. The effects of biotic and abiotic vectors on species composition of dune habitats were evaluated by Monte Carlo tests (1000 permutations). Significant variables were passively projected in the resulting ordination space. Furthermore, Wilcoxon-Mann-Whitney *U*-tests with a Bonferroni adjustment were used to analyse differences in vegetation structure (coverage of vascular plants and cryptogams) between dune types, since these observations could not be considered normally distributed. Differences of the vegetation composition of the different plant communities were tested with a Kolmogorov-Smirnov-test, and as these observations were not normally distributed, a Kruskal-Wallis test was performed. All statistical analyses were performed using R (R Development Core Team 2009, version 2.10.1). The regression models were fitted

using the *lme* and *MASS* R library. We used the *vegan* R library for multivariate analysis.

## Results

### Species composition and habitat patterns

A total number of 230 species was recorded at the 144 plots along the Baltic coast representing 11 plant communities. Dune succession revealed a significant effect on assemblages of bryophytes, lichens and vascular plants (ADONIS:  $F = 21.59$ ,  $p < 0.001$ ). The ordination resulted in a two-dimensional solution with a stress of 19.5. Dune habitats are clearly separated along the first NMDS-axis (Figure 2) and represent different succession stages.



**Figure 2** Non-metric multi-dimensional scaling (NMDS) ordination diagram of 137 vegetation plots from dry coastal dunes along the southern Baltic coast. Yellow dune plots are open circles, grey dune plots are filled circles and brown dune plots open triangles. Only variables with VIF values  $< 3$  were considered for further analysis. For this reason Simpson Index of Dominance and Ellenberg indicator values for light and nitrogen were not included in the ordination. Arrows indicate significant correlations of NMDS axis with vegetation structure (cover woody plants = CWP, cover herbaceous plants = CHP, cover bryophytes = CB, cover lichens = CL), average Ellenberg indicator values for temperature, moisture and reaction (soil acidity), species richness (Richness = total number of vascular plants, bryophytes and lichens) and species diversity (Shannon = Shannon Index).

Three groups of plots were distinguished: group 1 (plant communities A1–A3, for abbreviations see table 3) represented early succession stages of yellow dunes with species restricted to sandy and unstable soils such as *Ammophila arenaria*, *Cakile*

*maritima*, *Corispermum pallasii* or *Leymus arenarius*. Plant communities of group 2 belonged to grey dunes and were characterised by herbaceous rich short *Corynephorus canescens* swards (A4), *Cladonia*-rich grasslands (A5) and grasslands with dominance of *Festuca polesica* (A6). Group 3 consisted of heathlands (A7), pinewoods (A8–A10) and deciduous forest (A11), occurring on brown dunes. Cover of woody plants and soil acidity were the most important gradients, followed by total species richness, bryophytes cover, soil moisture and species diversity. Cover of lichens, herbaceous plants and temperature values had a weak impact in dune habitat differentiation (Table 1). Brown dunes were linked to a high cover of trees, shrubs (*U*-test:  $p_{adj.} < 0.001$ , for all comparisons), bryophytes (*U*-test:  $p_{adj.} < 0.001$ , for all comparisons) and a high occurrence of moist sites (*U*-test:  $p_{adj.} < 0.001$ , for all comparisons), while yellow dunes were characterised by less acidophytic conditions than grey and brown dunes (*U*-test:  $p_{adj.} < 0.001$ ). In contrast, grey dune communities were associated with high lichen cover (*U*-test  $p_{adj.} < 0.05$ , for all comparisons). An increase of herbaceous plant cover (*U*-test: yellow dunes vs. grey & brown dunes:  $P_{adj.} < 0.05$ ; grey vs. brown dunes:  $p_{adj.} 0.74$ ) and a decrease of mean temperature values (*U*-test:  $p_{adj.} < 0.05$ , for all comparisons) could be observed during dune succession.

**Table 1** Correlations of NMDS axis with environmental variables, species richness, species diversity and vegetation cover. Coefficients of determination ( $R^2$ ) and probability  $p$  ( $>|R^2|$ ) are given. Only significant relationships are shown (ns = not significant). Number of observations was  $n=137$ .

	NMDS 1	NMDS 2	$R^2$	$p$ -value
<b>Ellenberg values</b>				
Reaction	-0.4736	0.8807	0.60	<0.001
Moisture	0.1915	0.9815	0.47	<0.001
Temperature	-0.9148	-0.4040	0.23	<0.001
Continentality	0.8492	-0.5282	ns	
<b>Species richness (total)</b>	0.9677	-0.2521	0.51	<0.001
<b>Species diversity (Shannon Index)</b>	0.7837	-0.6212	0.44	<0.001
<b>Vegetation cover</b>				
Woody plants	0.7409	0.6716	0.70	<0.001
Herbaceous plants	0.8085	0.5885	0.16	<0.001
Bryophytes	0.9742	0.2259	0.50	<0.001
Lichens	0.4801	-0.8772	0.23	<0.001

## Vegetation zonation and succession

Along the chronosequence and during succession a significant negative change in light indication, temperature and pH could be observed (Table 2), with lowest values reached in *Festucetum polesicae* and *Hieracio umbellati-Empetro nigri*. Moisture showed a U-shaped relation with lowest values in grey dunes. Total species richness and number of bryophytes showed humped-back relationships with highest species numbers in the transition zone between mobile yellow dunes and stable brown dunes. Number of vascular plants and lichens increased significantly during the dune

succession. This development was in accordance with the species diversity (Simpson's Index of Dominance and Shannon Index), which reached highest values in grey dune communities. Moreover a change in cover of the different vegetation layers could be observed. The total vegetation cover increased linearly along a sea-to-inland gradient. The cover of shrubs and trees was only remarkable in brown dunes.

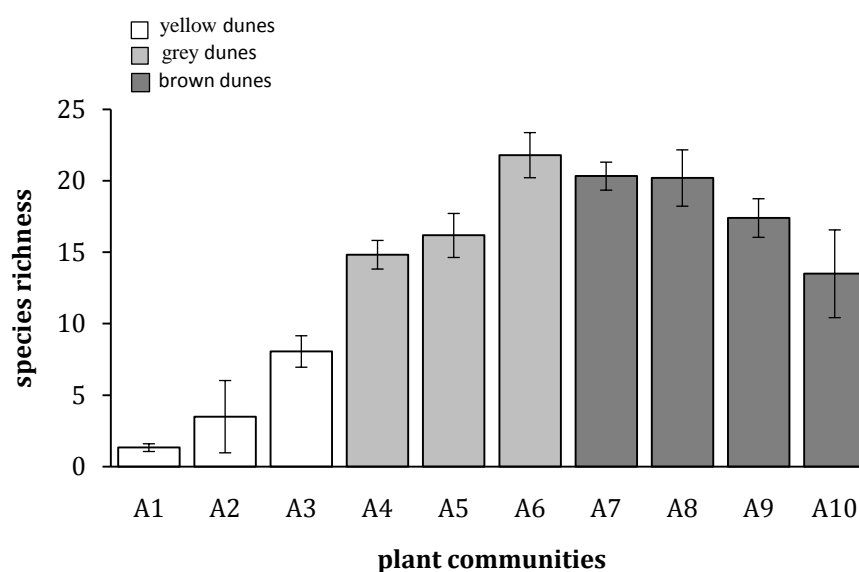
**Table 2** Regression results between plant communities and indicator values, species richness, species diversity and vegetation cover. The plant communities occur along a sea-to-inland gradient. Slope of the linear relation, form of the quadratic relation (U or  $\cap$ ), coefficients of determination ( $R^2$ ) and probability  $p$  ( $>|R^2|$ ) are given. Regression results with a higher  $R^2$  are marked in bold. Only significant relationships are shown (ns = not significant). The number of observations was  $n = 137$ .

	Linear regression			Quadratic regression		
	slope	$R^2$	$p$	form	$R^2$	$p$
<b>Indicator values</b>						
Nitrogen	-0.401	0.30	< 0.001	U	<b>0.65</b>	< 0.001
Light	-0.282	<b>0.61</b>	< 0.001	U	0.61	< 0.001
Temperature	-0.089	<b>0.19</b>	< 0.001	$\cap$	0.22	< 0.001
Continentality		ns			ns	
Moisture	+0.132	0.12	< 0.001	U	<b>0.44</b>	< 0.001
Reaction	-0.183	0.17	< 0.001	U	<b>0.43</b>	< 0.001
<b>Species richness</b>						
Total	+2.019	0.41	< 0.001	$\cap$	<b>0.54</b>	< 0.001
Vascular plants	+1.294	<b>0.37</b>	< 0.001	$\cap$	0.04	< 0.001
Bryophytes	+0.319	0.20	< 0.001	$\cap$	<b>0.40</b>	< 0.001
Lichens	+0.507	0.16	< 0.001	$\cap$	<b>0.11</b>	< 0.001
<b>Species diversity</b>						
Simpson's Index of Dominance		ns		$\cap$	<b>0.09</b>	< 0.001
Shannon Index	+0.141	0.25	< 0.001	$\cap$	<b>0.30</b>	< 0.001
<b>Cover</b>						
Total	+11.18	<b>0.59</b>	<b>0.0007</b>	$\cap$	0.05	< 0.001
Trees	+5.436	<b>0.63</b>	< 0.001	U	0.04	< 0.001
Shrubs	+1.175	<b>0.13</b>	< 0.001	$\cap$	0.045	< 0.001
Herbaceous plants	+1.684	<b>0.06</b>	<b>0.0424</b>	$\cap$	0.04	0.0028
Bryophytes	+5.935	<b>0.49</b>	< 0.001	$\cap$	0.01	< 0.001
Lichens	+1.925	<b>0.08</b>	< 0.001	$\cap$	0.01	0.0015
Bare soil	-11.08	<b>0.59</b>	< 0.001	U	0.08	< 0.001

### Species richness and diversity

Species richness and species abundance patterns differed with habitat. Considering the mean total number of species per dune type, grey dune associations accounted for 65 % higher species richness than yellow dune communities (Tukey HSD-test,  $p < 0.001$ ) (Figure 3). By contrast differences between grey dune communities and brown dune communities were statistically not significant. The mean number of spe-

cies increased following the sea-to-inland gradient and ranges from 3.5 in yellow dune communities with initial vegetation development (A2) up to 21.8 in *Festucetum polesicae* (A6) on grey dunes (Figure 3). Differences in total species richness and species richness of vascular plants, bryophytes and lichens between each of the plant communities were significant (Kruskal-Wallis-test,  $p < 0.001$ ). Cryptogams started to prevail in the *Elymo-Ammophiletum festucetosum* (A3) with a mean contribution to the total species number of 7 % and increased to 36 % (*Festucetum polesicae* A6) and 55 % (*Hieracio umbellati-Empetro nigri* A7) (Table 3). Mean species richness of cryptogams in woodlands reached its maximum in the *Cladonio-Pinetum sylvestris* (A10), where cryptogams represent around 50 % of the total species.

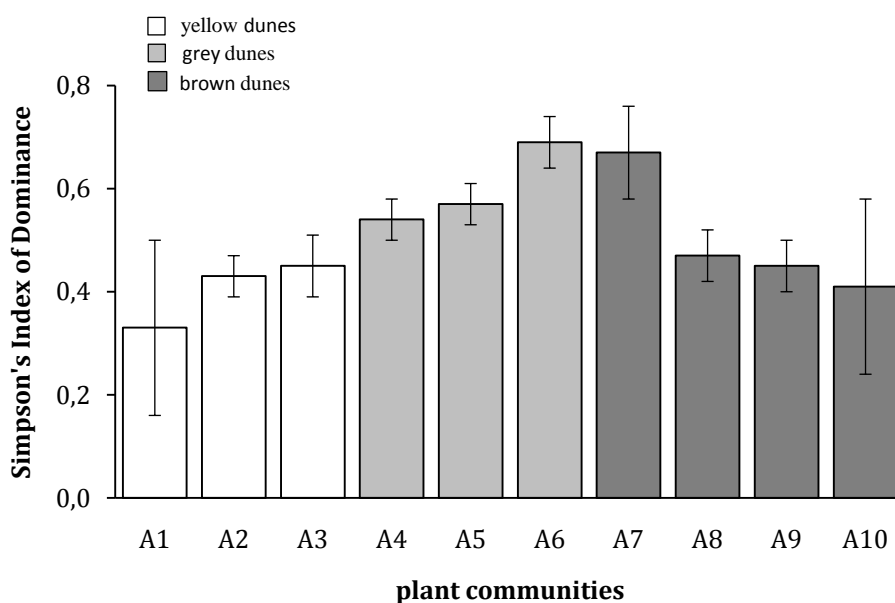


**Figure 3** Variation in the total number of species richness (mean  $\pm$  SE) for 25 m<sup>2</sup>-plots along the dune xeroserie from yellow dunes to brown dunes. The vegetation zonation from the beach across the dune system is reflected by an increasing community number (see table 3). Plant community A11 is not included in the figure, because it consists of only one plot.

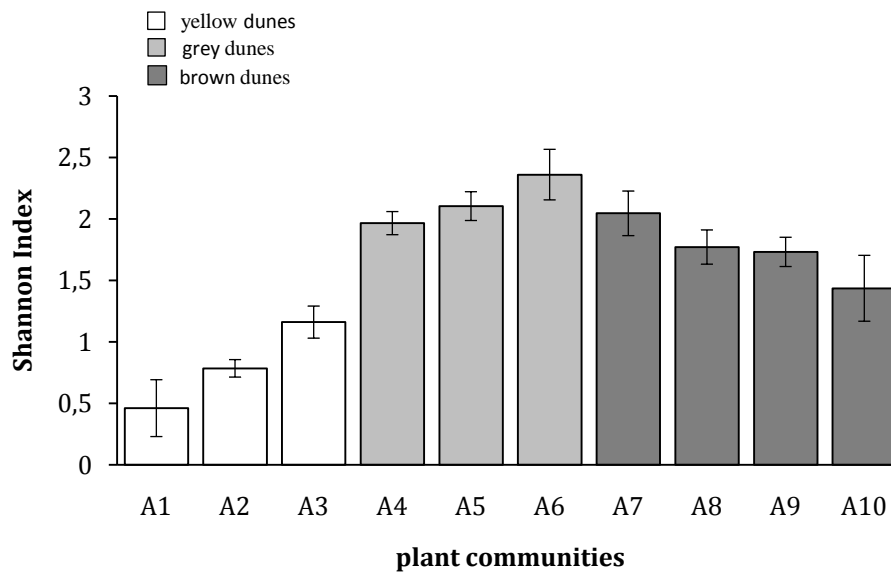
A similar trend could be observed for species diversity (Figure 4 and 5). Mean Simpson Index of Dominance increased with dune succession in open grassland communities. Simpson Index of Dominance was lower in yellow dunes than in grey dune habitats (Tukey HSD test,  $p < 0.05$ ), but did not significantly differ from values found in brown dune associations (Tukey HSD test,  $p = 0.18$ ). Differences among grey dune and brown dune communities were statistically not significant (Tukey HSD test,  $p = 0.57$ ). Diversity values derived from the Shannon Index indicated a similar successional trend with highest diversity in grey dunes. The results of Shannon's diversity index were intermediate to species richness and Simpson Index of dominance as could be expected from the formula structure. Variations among dune types were all statistically significant (Tukey HSD test,  $p < 0.05$ ) (Figure 5).

**Table 3** Mean species number (M), Standard Error of Mean(SEM) of vascular plants, bryophytes and lichens and the percentage of vascular plants, bryophytes and lichens on the total species number of 11 different plant communities on dry coastal dunes along the southern Baltic coast (y = yellow dunes, g = grey dunes, b = brown dunes). n = number of relevés. There were significant differences of the species number between the 11 plant communities tested with Kruskal-Wallis (total species number:  $p < 0.001$ ; vascular plants:  $p < 0.001$ , SEM; bryophytes:  $p < 0.001$ , SEM; lichens:  $p < 0.001$ , SEM).

plant community	dune type	n	vascular plants			bryophytes			lichens		
			M	SEM	%	M	SEM	%	M	SEM	%
A1 <i>Cakile maritima-Corisperrum pallasii</i> -community	y	3	1,3	0,3	100	0,0	0,0	0	0,0	0,0	0
A2 <i>Elymo-Ammophiletum typicum</i>	y	35	3,5	0,3	100	0,0	0,0	0	0,0	0,0	0
A3 <i>Elymo-Ammophiletum festucetosum</i>	y	16	7,4	1,0	92	0,4	0,3	5	0,2	0,1	2
A4 <i>Helichrysum arenariae-Jasionetum typicum</i>	g	36	9,4	0,7	63	2,3	0,3	16	3,1	0,5	21
A5 <i>Helichrysum arenariae-Jasionetum cladonietosum</i>	g	11	4,9	0,7	30	3,3	0,4	20	8,0	1,0	49
A6 <i>Festucetum polesicae</i>	g	5	14,0	2,2	64	3,2	0,6	15	4,6	1,2	21
A7 <i>Hieracio umbellati-Empetretum nigri</i>	b	3	9,0	1,7	44	3,3	0,7	16	8,0	0,0	39
A8 <i>Empetro nigri-Pinetum sylvestrum</i> (variant of young pine stands)	b	10	14,5	1,7	72	2,5	0,4	12	3,2	0,8	16
A9 <i>Empetro nigri-Pinetum sylvestrum</i> (variant of old pine stands)	b	15	12,7	1,3	73	2,1	0,3	12	2,6	0,6	15
A10 <i>Cladonio-Pinetum sylvestris</i>	b	2	6,5	1,2	48	1,5	0,5	11	5,5	2,2	41
A11 <i>Asperulo odoratae-Fagetum sylvatica</i>	b	1	24,0		86	2,0		7	2,0		7



**Figure 4** Variation in vascular plant species diversity expressed by Simpson's Index of Dominance (mean  $\pm$  SE) for 25 m<sup>2</sup> plots during dune succession. The vegetation zonation from the beach across the dune system is reflected by an increasing community number (see table 3). Plant community A11 is not included in the figure, because it consists of only one plot.



**Figure 5** Variation in vascular plant species diversity expressed by the Shannon Index (mean  $\pm$  SE) for 25 m<sup>2</sup> plots during dune succession. The vegetation zonation from the beach across the dune system is reflected by an increasing community number (see table 3). Plant community A11 is not included in the figure, because it consists of only one plot.

### Total plant species richness in relation to Ellenberg indicator values

Species richness showed a humped back relationship to nitrogen, light, temperature and reaction (pH) with highest values reached on sites with intermediate Ellenberg indicator values. In single regression, temperature only explained 6 % whereas nitrogen explained 35 % and light 38 % of the data variation (Table 4). Multiple linear regression analysis of total plant species and environmental parameters was significant ( $p < 0.001$ ) and accounted for 50 % of the total variation. The major and significant contributions to this regression were nitrogen and light ( $p < 0.001$ ).

**Table 4** Single regression results between total plant species richness and Ellenberg indicator values. Shown are best fitting linear and quadratic regressions, tested stepwise backwards and forwards. Slope of the linear relation, form of the quadratic relation (U or  $\cap$ ), coefficients of determination ( $R^2$ ) and probability  $p$  ( $> |R^2|$ ) are given. Only significant relationships are shown (ns = not significant). Regression results with a higher  $R^2$  are marked in bold. The number of observations was  $n = 137$ .

	Linear Regression			Quadratic regression		
	slope	$R^2$	$p$	form	$R^2$	$p$
<b>Indicator values</b>						
Nitrogen	-2.257	0.35	< 0.001	U	<b>0.36</b>	<b>&lt; 0.001</b>
Light	-5.613	0.38	< 0.001	$\cap$	<b>0.42</b>	<b>&lt; 0.001</b>
Temperature	-4.082	0.06	0.0040	$\cap$	<b>0.13</b>	<b>&lt; 0.001</b>
Continentality	+1.978	0.03	0.0404		ns	
Moisture		ns			ns	
Reaction	-3.182	0.21	< 0.001**	$\cap$	<b>0.33</b>	<b>&lt; 0.001</b>

## Discussion

The zonation across major coastal dune habitats with distinct plant communities (yellow, grey and brown dunes) as well as the increase in plant cover and species number is in line with other studies of sandy coasts and typical for the dune xerosere at a global scale (e.g. Doing 1985, Piotrowska 1988, Isermann 1996, 2005, Łabuz 2004, Stankevičiūtė 2006). The examined dune chronosequence shows a complex gradient of changing environmental factors that influence the survival, growth and reproduction of plant species (Lichter 1998). The general trend indicates a decrease in physical severity of habitat conditions, such as a reduction in salt spray, sand movement, protection from wind as well as an increase in species diversity, life form, aerial cover and abundance of woody cover, which was also noted for coastal sand dunes in South Africa (Avis and Lubke 1996). Shifts in Ellenberg indicator values highlight this vegetation succession. Along the southern Baltic Coast, vegetation patterns are correlated with light and temperature; they decline with distance to the sea due to encroachment of dense grasses and cover increase of woody species. Accumulation of organic matter results in higher soil moisture. This is important for the vegetation productivity and the species composition, especially for typical grassland species adapted to low nutrient levels, also observed in Dutch coastal dunes (Kuiters et al. 2009). Weathering processes and precipitation cause a rapid leaching of calcium combined with an acidification, which can be seen in a decline of pH-value, represented as Ellenberg R indicator value, during the dune succession. Most typical dry dune plant species are adapted to fluctuating, extreme temperatures, drought and frequent soil moisture changes (Remke et al. 2009).

During dune succession, the vegetation structure changes. Initial succession stages are often homogenous with generally uniform environmental conditions (Morrison and Yarranton 1974). Only a few highly specialised dune builder plants, supporting sand burial, colonise and stabilise the sediments. Further succession stages of back dune areas, e.g. communities of the grey dunes, are characterised by initial dune stabilisers that occur next to burial intolerant species. Sedges and grasses dominate the vegetation and an increase in cover and abundance of cryptogamic species is noted. Older stabilised dune habitats on brown dunes have a greater total mean cover and woody shrubs and trees are more abundant. This is consistent with studies on sand dunes in the Netherlands (van der Maarel 1978), in Lithuania (Stankevičiūtė 2001), in Germany (Isermann 2005) and Florida/US (Miller et al. 2010).

Species richness differs among dune habitats along the southern Baltic Coast. The changes in total species richness across various environmental gradients are caused by variations in availability of resources such as light, soil moisture and nutrients that may influence succession and species richness (Lichter 1998, Stankevičiūtė 2001, Isermann in press). Total species richness increases from yellow dunes to grey dunes



along the dune chronosequence. Morrison and Yarranton (1974) reported that species richness attains a constant level or decreases during later stages of sand dune succession, which is in line with our observations. Old stabilised brown dune communities with low frequency and intensity of disturbance and environmental conditions show much lower species richness than grey dunes, where the highest total species richness occurred. Grey dune habitats lie in a transition zone between mobile dunes and interior dunes with higher sand stability and species from both habitats may be present. These habitats are characterised by intermediate levels of environmental and disturbance gradients, confirming the intermediate disturbance theory (Connell 1978). Like Schuster and Diekmann (2003) and Isermann (2005) our researches showed a humped-back relationship between species richness and soil pH, with highest values at intermediate levels of soil pH (Ellenberg value R). Nitrogen and light (Ellenberg indicator values) proved to be the most important environmental factors determining species richness in our study area, whereas the effects of other environmental were rather low.

Species richness as well as cover abundance of bryophytes and lichens showed a humped-back relation along the dune chronosequence, reaching highest values in the *Hieracio umbellati-Empetretum* of brown dunes. In contrast to the grey dune communities, bryophytes and lichens play a more important role in heathland-communities and contribute to the total species richness. In contrast to grey dune communities with intermediate values of sand dynamic, nutrients and soil reaction, habitats of brown dune are characterised by intermediate values of soil moisture and light.

Lowest total species richness is observed on active migrating dunes. Annual dune vegetation with the endemics *Corispermum pallasii*, *Cakile maritima* ssp. *baltica* and *Linaria loeselii* colonise these habitats with harsh environmental conditions such as drought, high solar radiation, salt spray, variation in temperature and sand burial. Species-poor vegetation stands are formed which are exclusive to migrating dunes of the southern Baltic coast and endangered by coastal defense measures, reforestation and tourism (Dolnik et al. in press). Although these habitats are dominated by only a few species, they contribute to the overall biodiversity. Therefore we agree with Mills and Schwartz (2005) and Acosta (2009) who emphasized not only to conserve species richness but also to focus on species-poor habitats.

## Conclusion

This study emphasises the relationships between biodiversity and environment in dunes of the southern Baltic coast. Our research confirmed that plant species richness along the coastal dune gradient is definitely dependent on permanent interaction of abiotic and biotic environmental factors, with include changes of characteristics dur-

ing the processes of dune succession. Understanding and monitoring dune vegetation dynamics is the key for the conservation and protection of species as well as the support of a sustainable development of biodiversity at different scales.

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Czołpino dune, Łeba Bar, PL (Photo: Peyrat 2008).

# Vegetation dynamics on the Łeba Bar/Poland: a comparison of the vegetation in 1932 and 2006 with special regard to endangered habitats

Jann Peyrat, Małgorzata Braun, Christian Dolnik, Maike Isermann and Hartmut Roweck. 2009. *Journal of Coastal Conservation* 13 (4): 235–246.

## Abstract

Coastal dune ecosystems are among the most dynamic habitats with high conservation value in Europe but are also under strong anthropogenic pressure regarding coastal protection and recreation. Hence, it is of high importance to know about long-term natural and anthropogenic changes and development of protected dune habitats for nature conservation, as well as for coastal management.

This paper aims to identify the vegetation dynamics on the Łeba Bar/Poland over a period of 74 years by cartometric comparison using modern Geographical Information System (GIS). To quantify the rate of vegetation dynamics two aerial photographs dating from 1932 and 2006 were digitalized and analyzed with GIS to produce digital vegetation maps. Information about decrease, increase, stability of vegetation types of this area are discussed. The results show that there has been a clear reduction in the total area of bare sand and a considerable increase of woodlands and dense grass communities. Nevertheless, the remaining extensive drift sand areas and deflation hollows on the Łeba Bar offer one of the most important habitats for pioneer vegetation on bare sand of migrating dunes and dunes at the Southern Baltic coast.

The present work proved the need to observe the future development of the vegetation communities and to implement management measures to maintain the dynamic of this unique dune landscape.

## Introduction

Many dunes at the coast of the North Sea and Baltic Sea originally developed as active mobile dunes and shifted across and along islands, spits and mainland bands, before becoming overgrown by plants and being stabilized by natural or anthropogenic dune fixation (Mader 1995). Meanwhile anthropogenic dune fixation in the frame of coastal protection prevents such dynamic processes in most dune systems. Therefore, most of the European dunes are nowadays more or less covered by vegetation. Up until now only a few dune-systems have preserved their large-scale mobility for a long time: Råbjerg Mile/Denmark, Dune du Pyla/France, Coto de Doñana/Spain, dunes of Listland on Sylt/Germany, Łeba Bar/Poland and Curonian Spit/Lithuania and Russia (Mader 1995).

The migrating dune fields on the Łeba Bar at the southern Baltic coast are one of the most significant still active mobile dune areas in Europe. The open dune areas and sandy ecosystems are very endangered habitats (Ssymank et al. 1998). Pioneer species form a typical vegetation mosaic when disturbances are present (Jentsch 2001) and succession processes are consistently initiated (Jentsch and Beyschlag 2003).

In parts of the Baltic Coast this very dynamic landscape disappeared during the last decades by afforestation and stabilisation (Volkova 1998, Dolnik 2003). Sandy ecosystems, which were kept open by land use and human impact became increasingly rare and are currently more endangered than bogs or calcareous grasslands. Open, dynamic sand ecosystems lose much of their nature value once the dynamic is decreasing (Schwabe et al. 2002). Peyrat (2008) revealed that the Curonian Spit, which was dominated by natural developed grass communities and huge migrating dunes at the end of the 19th century (Preuss 1912, Tomuschat and Ziegenspeck 1930, Paul 1944, 1953) is today almost entirely afforested. Piotrowska and Gos (1998), Tastet and Pontee (1998) and Christensen and Johnsen (2001) describe a similar development for coastal dunes at the Polish, southwestern French and Danish Baltic Sea coast.

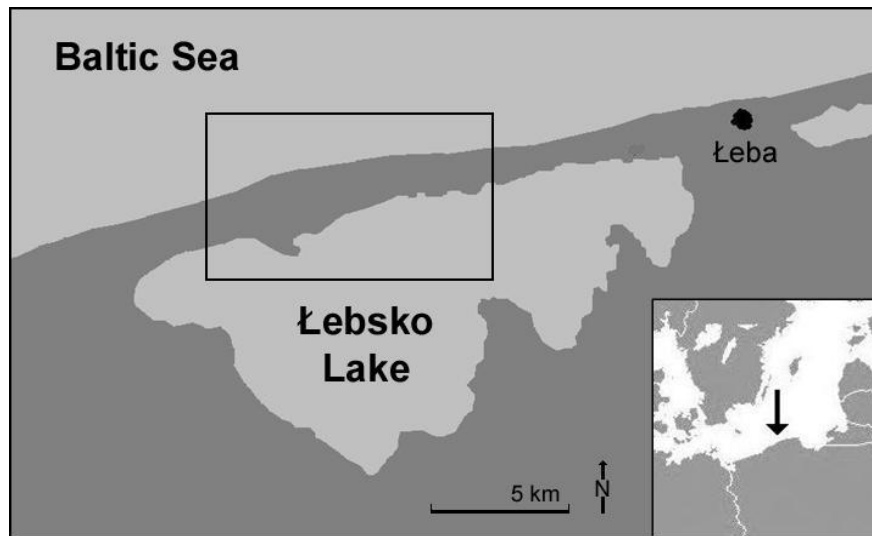
The present paper has two main objectives: The first is to provide a comparative image analysis of historical and current charts of vegetation. GIS tools are used to produce corresponding maps of different vegetation types. This study of medium-term vegetation changes is important for understanding ecological processes, notably succession (Bakker et al. 1996). The second objective is to show the importance of dynamic dune systems for endangered habitats like dune slacks and pioneer vegetation on bare dune sand which are threatened by coastal management measures. The study is essential to monitor vegetation succession and to plan and establish effective conservation and management programs on the Łeba Bar.



## Study area

### Geomorphology

The study area, with a surface of 1,050 ha, is part of the 16 km long Łeba Bar at the Baltic coast of Poland, west of the town of Łeba (Figure 1). The Łeba Bar was originally covered by oak woods, which were destroyed around 2,000 B.P. by fires. Acidophilic beechwoods took over the habitat (Piotrowska and Gos 1995). Tree cutting as well as overgrazing and trampling by cattle and in the 17<sup>th</sup> century destroyed the natural plant cover and led to the development of large open sand areas, which build up huge mobile dunes. They migrated on the bar and destroyed what remained of the forest and vegetation. In the 19<sup>th</sup> and early 20<sup>th</sup> century plantings of psammophytes followed by pine nurseries fixed parts of the migrating dunes to prevent large sand drift areas. Brushwood fencing, willow palings and psammophytes created a regular yellow dunes rampart along the beach (Piotrowska and Gos 1995). One part in the middle of the Łeba Bar was never afforested and is today representing the famous migrating dunes (Piotrowska and Gos 1995).



**Figure 1** Łeba Bar with study area (rectangle).

The topography of the Łeba Bar is characterized by a 50 to 100 m wide beach, which is bordered by primary and secondary dunes reaching heights between 10 and 12 m. The unvegetated migrating dunes, with up to 42 m height and several hundreds of meter width and length, represent the dominant landscape features (Mader 1995). They are slowly migrating eastwards towards the Łebsko Lake at a rate of 2 to 10 m per year (Miszalski 1973), burying the forest on the plain in front of their steep slip face. A few rotten trees emerge at the top of the open windward slope of the dunes testifying to the migrating rate of the mobile dunes (Mader 1995). Deflation fields appear on the western foot of the retreating migrating dunes (Piotrowska and Gos 1995), reaching up to one km<sup>2</sup> of the study area and laying 4.5 m above sea level. A

very specific micro relief with dry ridges and moist slacks is built up on the windward side of the migrating dunes, laying transversally to their long axis (Zoladeski 1991). As the dune moves on easterly winds blow sand to the west building up small, residual dunes. A similar process is described for the migrating dunes on Sylt (Neuhaus 1994) and on the Curonian Spit, where these ridges are named 'Gegenwälle' (Paul 1953).

## Vegetation

The sparsely vegetated beach is bordered by embryonic dunes dominated by *Cakile maritima* and accompanied by *Ammophila arenaria*, *Honckenya peploides* and *Salsola kali*. *Eryngium maritimum* and *Tragopogon heterospermus* are very rare (Wojterski 1978). Next inland, the neighbouring yellow dunes are covered by a relatively species-poor *Elymo-Ammophiletum*. *Ammophila arenaria*, *Calammophila x baltica*, *Festuca rubra* ssp. *arenaria* and *Leymus arenarius* are characteristic species. *Hieracium umbellatum*, *Lathyrus maritimus*, *Linaria loeselii*, as well as *Viola tricolor* are less frequent (Wojterski 1978). *Ammophila arenaria* also occurs on the foot of the migrating dunes' slip face.

The succession of the *Elymo-Ammophiletum* changes to short grass-communities with *Corynephorus canescens* and *Festuca polesica*, which start to develop on the lee side of the yellow dunes and in sheltered spots at the Łebsko Lake (Hueck 1932). In earlier stages this *Helichryso-Jasionetum litoralis* (Table 1) is almost composed of vascular plants such as *Artemisia campestris*, *Carex arenaria*, *Corynephorus canescens* and *Viola tricolor* (Piotrowska and Gos 1995). Lichens are prevailing in later stages attaining high cover values. Hueck (1932) observed a *Carex arenaria* dominated association (*Caricetum arenariae* Steffen 1931) on some parts of the trailing arms of the parabolic dunes. The *Helichryso-Jasionetum litoralis* directly develops into a coastal pine forest (*Empetro nigri-Pinetum*). Unlike in other areas, brown dunes dominated by dwarf shrubs like *Calluna vulgaris* and *Empetrum nigrum* only occur fragmented, together with pioneer pine trees, on the Łeba Bar. Therefore, in past mappings (Hueck 1932, Wojterski 1993, last mapping) they were included in the forest community of the *Empetro nigri-Pinetum*. Wojterski (1993) distinguishes four subassociations, of which three can be found in the study area (Table 1): On extremely dry and poor habitats such as on parabolic arms numerous lichen species characterise the *Empetro-Pinetum cladonietosum*. Wojterski (1993) terms the second association as *Empetro-Pinetum typicum*, which is at its optimum on fresh and fertile habitats on the deflation fields of the retreating migrating dunes. In front of these dunes, where the ground water level is close to the surface, a wet coastal pine forest occurs (*Empetro-Pinetum ericetosum*).

A special succession series with various plant communities can be observed in the deflation slacks and ridges on the windward side of the migrating dunes. *Agrostis stolonifera* establishes in moist slacks in between ridges which are built up by *Ammo-*

*phila arenaria*. Further succession of the vegetation on wet sand leads to a *Polytrichum-Lycopodium inundatum*-association (similar to the *Polytrichum commune* var. *perigoniale*-*Pohlia nutans*-*Drosera rotundifolia* community (Zoladeski 1991)) and a *Ranunculus reptans*-*Radiola linoides* community (Table 1) (Hueck 1932).

**Table 1** Main plant communities in the study area used by Hueck (1932), Fałtynowicz (2003) and Jackowiak (2003) modified according to Matuszkiewicz (1980).

Location on the Łeba Bar	plant communities according to	
	Hueck (1932)	Fałtynowicz (2003), Jackowiak (2003)
Beach	Vegetation free beach	Vegetation free beach
Primary dune and yellow dune	<i>Ammophiletum arenariae</i>	<i>Elymo-Ammophiletum</i>
Lee side of yellow dunes, dry ridge of the deflation fields, sheltered spots on the Łebsko Lake	<i>Corynephorum</i>	<i>Helichryso-Jasionetum litoralis</i>
Lower dry parabolic dunes	pine wood with lichens	<i>Empetro nigri-Pinetum cladonietosum</i>
Deflation fields	pine wood <i>Myrtyllus</i> -type	<i>Empetro nigri-Pinetum typicum</i>
Plain in front of the migrating dunes	wet pine wood	<i>Empetro nigri-Pinetum ericetosum</i>
Migrating dunes	migrating dunes	migrating dunes
Wetland at the Łebsko Lake	alder wood	<i>Carici elongatae-Alnetum</i>
Dune slacks, deflation field and wet troughs	Dune slack communities: <i>Calluna</i> -heath <i>Polytrichum-Lycopodium inundatum</i> -association, <i>Ranunculus reptans-Radiola linoides</i> -community	Dune slack communities: <i>Nardo-Callunetea</i> , <i>Polytrichum commune</i> var. <i>perigoniale</i> - <i>Pohlia nutans</i> - <i>Drosera rotundifolia</i> -community
Łebsko Lake	Reed zone	<i>Phragmitetum communis</i>

The communities of the wet slacks are taken over by dwarf shrubs like *Calluna vulgaris* and *Empetrum nigrum* and change into a heathland of the class *Nardo-Callunetea* (Table 1) (Hueck 1932). This society, dominated by *Calluna vulgaris*, is very species-poor in vascular plants, but contains often high numbers of lichens. Pines and birches penetrate into the older supplies, converting the open heathlands into a heath-dominated pinewood. These pinewoods (*Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum*) dominate the groundwater-influenced deflation fields between the migrating dunes (Hueck 1932).

The migrating dunes are without vegetation, except some patches of *Ammophila arenaria*, *Festuca arenaria* and *Linaria loeselii*, which are growing in less exposed dry sites. Extensive areas on the north bank of the Łebsko Lake are aggregated by the sand of the migrating dunes, emerging into the lagoon. In this area a 20 to 150 m wide reed zone establishes (*Phragmitetum communis*, Table 1). In a few parts of this swampy zone young alder carrs (*Carici-elongatae-Alnetum*, Table 1) develop. Thus, the Łeba Bar is one of the few larger areas in the southern Baltic, where primary succession series with their full range of plant communities occur (Piotrowska 1988).

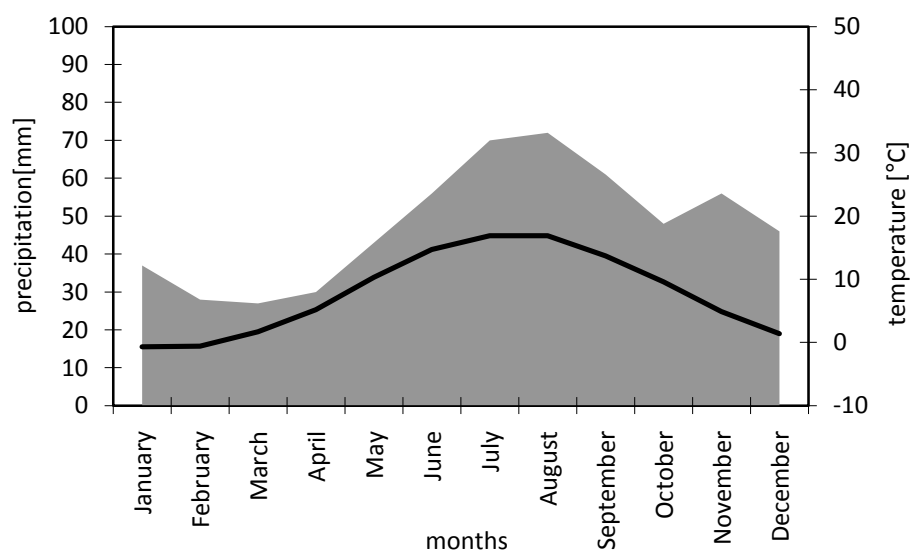
## Recreation

Despite its mostly undisturbed nature the Łeba Bar is a popular destination for at least half a million tourists annually (Ostrowski and Symonides 1995). Two major excursion routes exist in the western (Czołpino Dune) and eastern part (Łącka Dune),

which cross the migrating dunes and lead to the beach. The pathways are marked with spiles, which do not, however, prevent the trespassing of the protected area. Hence small plants which are susceptible to trampling, such as *Linaria loeselii*, are menaced by tourists (Stasiak 1987). As These two paths are the only ones in the area, the dune fields in the middle of the Łeba Bar are more or less unaffected by human pressure.

### Climate and soil

The climate at the Łeba Bar is strongly influenced by the Baltic Sea (Piotrowska 1988). The mean annual temperature in February is  $-1.6^{\circ}\text{C}$  and  $16.2^{\circ}\text{C}$  in August, the annual precipitation 700 mm (Figure 2) (Borówka 1980). Prevailing winds are westerly and strong (8 to 14 m/s) to very strong ( $>14$  m/s). The soil, consisting of quartz sand is non-calcareous and susceptible to acidification (Piotrowska 1988).



**Figure 2** Precipitation and temperature for Łeba (adapted from Borowka 1980).

### Nature value and protection status of the Łeba Bar

The Łeba Bar is protected as 'Słowiński National Park' ('Słowiński Park Narodowy'), which was established in 1966 and categorized as a World Biosphere reserve in 1980 (Wojterski 1993). The migrating dunes of the Łeba Bar are outstanding natural features and unique in Europe. Due to seaside lakes, peat bogs, meadows, forests and open dune areas, which create exceptionally rich landscape mosaics, this area was included in an international network of protected areas, like HELCOMBSPA, World Nature Sanctuary, Ramsar wet-land area and NATURA 2000 (von Nordheim and Boedeker 1998).

## Material and methods

A vegetation map from Hueck (1932) drawn on a topographic map (scale 1:25,000, Meßtischblatt 171 Leba-See, 1928) and an actual aerial photograph (scale 1:5000, 2006) from the Łeba Bar, served as basis for the cartometric investigations. Both maps were digitalized and transformed into a geographical reference system. Polygons were defined with ArcView GIS 3.2 for each plant community. Based on the vegetation maps the percentage cover of each plant community was calculated. Nomenclature of vascular plants follows Flora Europaea (Royal Botanic Garden Edinburgh 2009), nomenclature of plant communities are used according to Matuszkiewicz (1980).

The vegetation composition in 1932 is described on a vegetation map from Hueck (1932). Actual vegetation investigations were undertaken by Fałtynowicz (2003) and Jackowiak (2003). Interpretation of aerial photographs and a field study in 2008 in combination with the vegetation investigation from 2003 were used to draw an actual vegetation map. To enable comparison of the plant communities, those used by Hueck (1932) were transferred to the nomenclature of plant communities described by Fałtynowicz (2003) and Jackowiak (2003), modified according to Matuszkiewicz (1980) (Table 1).

In Hueck's map from 1932 dune slack communities had been clearly divided into a *Polytrichum-Lycopodium inundatum*-association (similar to the *Polytrichum commune* var. *perigonale*-*Pohlia nutans*-*Drosera rotundifolia*-community described by Zoladeski (1991)), a *Ranunculus reptans*-*Radiola linoides*-community and vegetation of the *Nardo-Callunetea*. Zoladeski (1991) also differentiates between vegetation of the *Nardo-Callunetea* and the *Polytrichum commune* var. *perigonale*-*Pohlia nutans*-*Drosera rotundifolia*-community. The investigations of Fałtynowicz (2003) and Jackowiak (2003) just list deflation fields. In the present study they are grouped as 'dune slack communities'. In addition to the comparison of the distribution area of plant communities the vegetation maps of 1932 and 2006 were compared to reveal decrease, increase or stability within four defined 'landscape types'. Therefore *Empetro-Pinetum cladonietosum*, *Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum* were grouped into 'woodlands' and the *Elymo-Ammophiletum* and *Helichryso-Jasionetum litoralis* into 'open grasslands'. The *Polytrichum-Lycopodium inundatum*-association (Hueck 1932) (similar to the *Polytrichum commune* var. *perigonale*-*Pohlia nutans*-*Drosera rotundifolia*-community described by Zoladeski (1991)), the *Ranunculus reptans*-*Radiola linoides*-community (Hueck 1932) and communities of the *Nardo-Callunetea* were grouped into 'dune slack communities'. The migrating dunes without vegetation formed the fourth group.

## Results

### Comparison of vegetation

The comparison of the vegetation maps from 1932 and 2006 (Figures 3, 4) revealed obvious differences. On both maps the eastern part of the study area was dominated by huge migrating dunes. Since 1932 these dunes have been migrating eastwards at an average of about 10 m per annum, which implicated a total rate of 708 m (Figure 5). In 2006 most of the dunes had already reached the Łebsko Lake with their southern slope, whereas in 1932 only a small part was directly emerging into the lake. On their way to the lake the dunes buried different grass communities, such as *Elymo-Ammophiletum* and *Helichryso-Jasionetum litoralis* and *Carici elongatae-Alnetum*, *Phragmitetum communis* and woodlands (*Empetro-Pinetum cladonietosum*, *Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum*) growing in front of the migrating dunes' slip face. In the western part of the study area two small fields with bare sand disappeared since 1932 and were overgrown by *Helichryso-Jasionetum litoralis*, *Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum*.

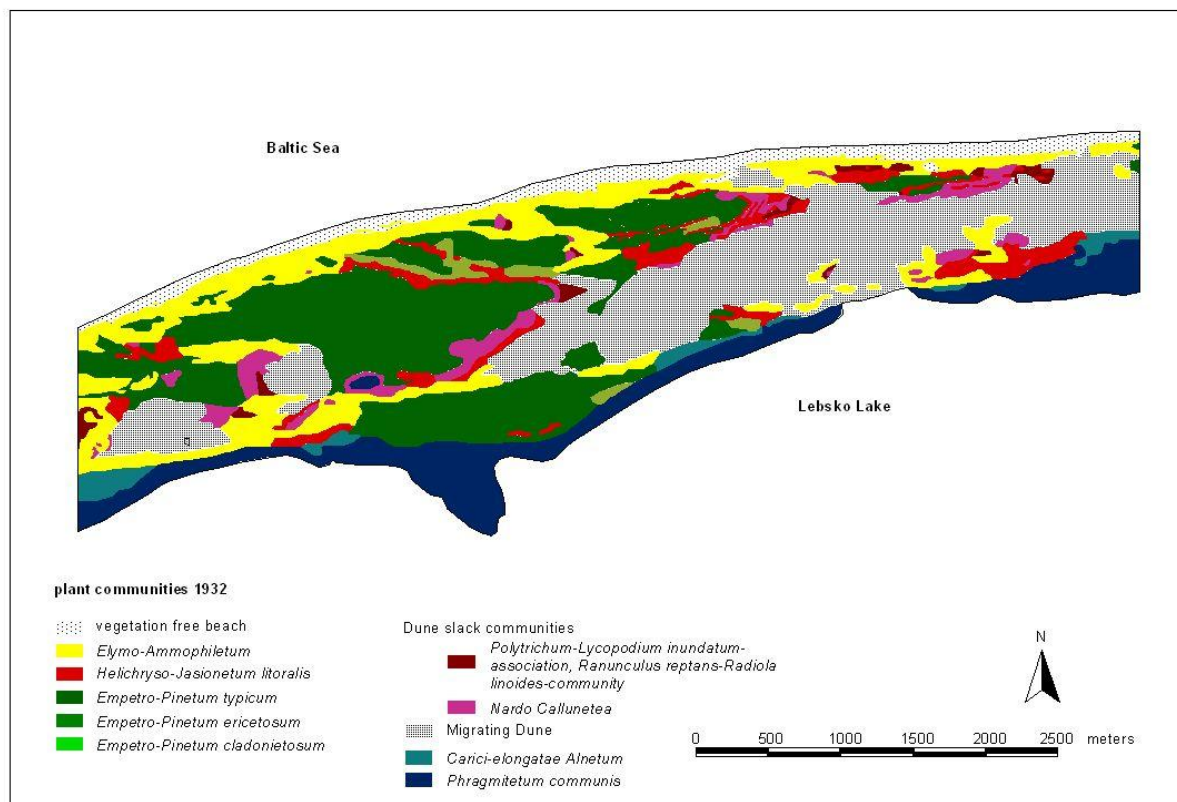
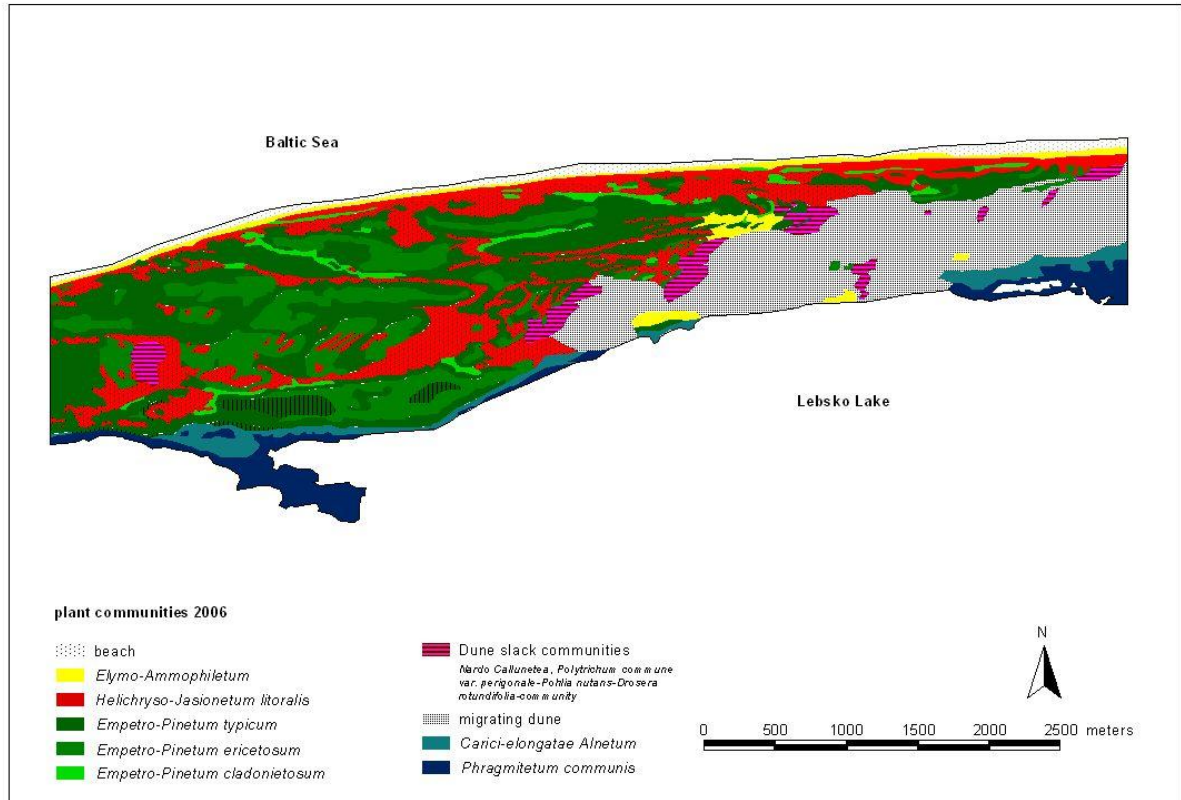
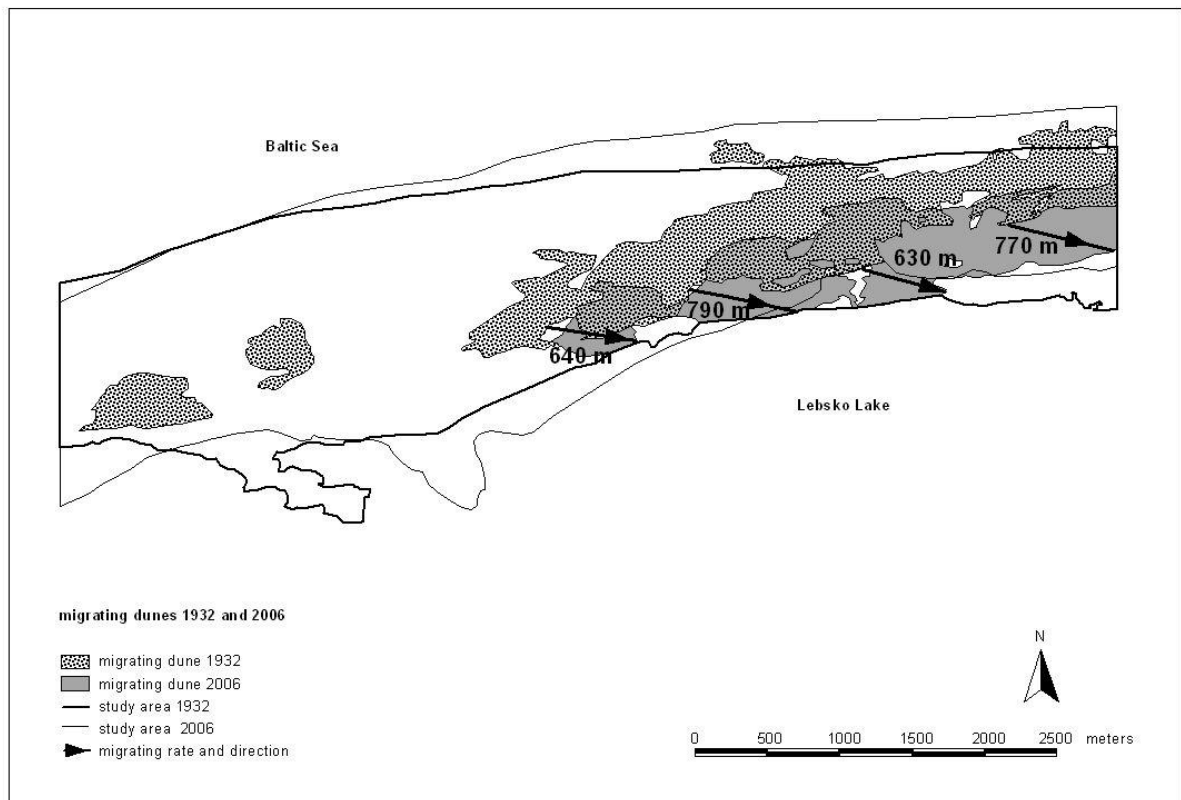


Figure 3 Plant communities in 1932, adapted from Hueck (1932).



**Figure 4** Plant communities in 2006, adapted from Fałtynowicz (2003) and Jackowiak (2003).



**Figure 5** Migrating rate and direction of the open dune fields between 1932 and 2006.

Dune slack communities occurred on the western slope of the retreating migrating dunes in 1932, as well as in 2006. In 2006 most of the western part of the study area was dominated by woodlands such as *Empetro-Pinetum cladonietosum*, *Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum*, whereas in 1932 a mosaic of woodlands, open grasslands and bare sand could be observed. *Elymo-Ammophiletum* and *Helichryso-Jasionetum litoralis*, covering huge parts of the yellow and grey dunes along the whole coast of the area in 1932, were pushed back until 2006 to a small stripe on the western part of the area, whereas the eastern part seemed to stay unchanged. The mean width of this vegetation zone clarifies this fact as it decreased from 175 m in 1932 to 140 m in 2006.

Moreover, the lakeshore has changed considerably over the last 74 years. Figure 5 demonstrates that the lakeshore in the eastern part moved approximately 220 m to the south, whereas in the western part the lakeshore has retreated by 210 m since 1932. The small peninsula of *Phragmitetum communis* growing in the Łebsko Lake was even displaced to the west by 750 m. The beach migrated to the south by 210 m. In a period of 74 years the width of the beach decreased from approximately 186 m to 50 m, which means a decrease of nearly 300 %.

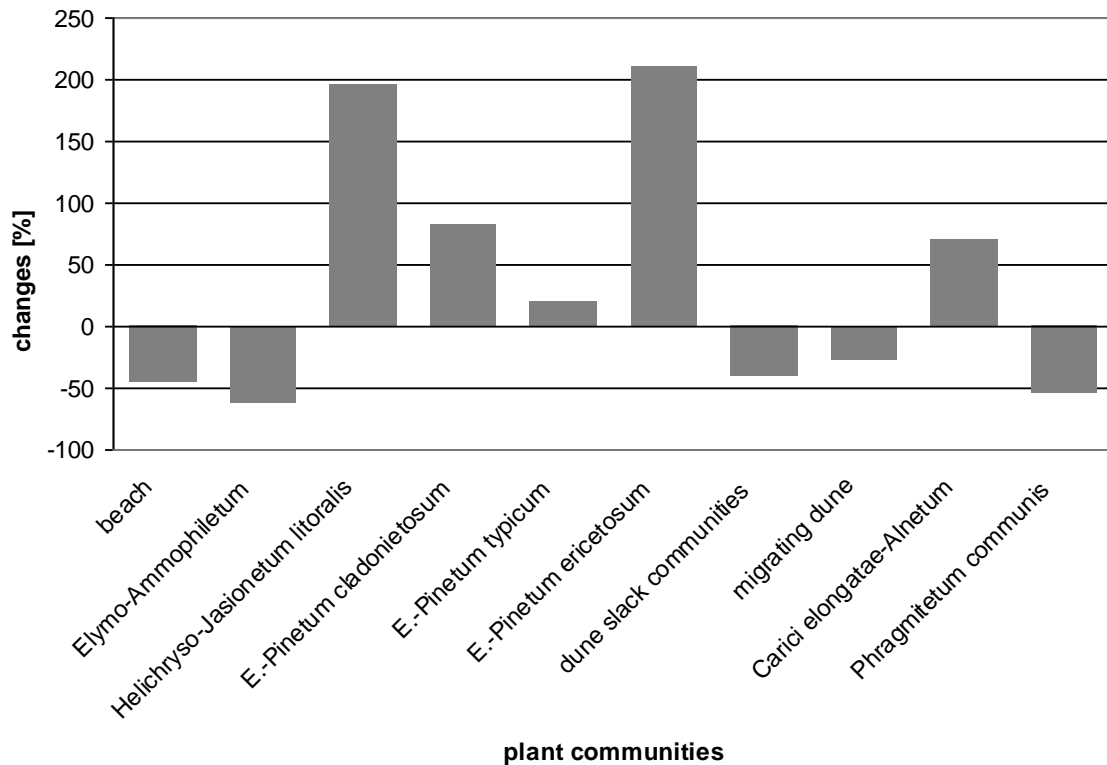
### Distribution of plant communities

A considerable change in the percentage area of plant communities during this 74-year period emerges from these maps (Figures 3 and 4). Woodlands (*Empetro-Pinetum cladonietosum*, *Empetro-Pinetum typicum* and *Empetro-Pinetum ericetosum*) increased from a total area of 28 % in 1932 to 43 % in 2006. At the same time the *Helichryso-Jasionetum litoralis* increased by 195 %. The total area of the beach and the *Elymo-Ammophiletum* diminished from 6 % and 17 % in 1932, to 4 % and 6 % in 2006. Dune slack communities and the *Phragmitetum communis* also denoted a negative balance. The total area of the migrating dune showed the least change comparing the vegetation maps of 1932 and 2006 (Table 2, Figure 6).

**Table 2** Distribution area of plant communities (%) in 1932 and 2006, as well as the percentage change of their distribution.

	percentage of the total area (%)		changes (%)
	1932	2006	
beach	6	4	-45
<i>Elymo-Ammophiletum</i>	17	6	-63
<i>Helichryso-Jasionetum litoralis</i>	6	18	+195
<i>Empetro-Pinetum cladonietosum</i>	1	3	+82
<i>Empetro-Pinetum typicum</i>	22	26	+20
<i>Empetro-Pinetum ericetosum</i>	5	14	+211
dune slack communities	5	3	-41
migrating dune	25	18	-27
<i>Carici elongatae-Alnetum</i>	2	3	+70
<i>Phragmitetum communis</i>	11	5	-54





**Figure 6** Changes (%) of the plant communities between 1932 and 2006.

## Changes within the distribution area of 'vegetation types'

### *Open grasslands*

Fortynine % (210 ha) of the open grasslands in 1932 are today replaced by woodland (108 ha), are under the sea (48 ha) or are covered by sand from the migrating dunes (36 ha) (Table 3). During the same period, 39 % (169 ha) of the open grasslands developed on the bare sand of the migrating dunes (73 ha) or on the area covered by woodland (62 ha) in 1932. A minor part of the open grasslands (47 ha) did not change its appearance.

### *Woodlands*

During the last 74 years, 43 % (242 ha) of the actual woodland either replaced open grasslands (106 ha) or developed on bare sands of the migrating dunes (91 ha) (Table 3). 37 % of the area covered by woodland in 1932 remains so to this day. Only 108 ha (19 %) of the woodland disappeared and has mostly been replaced by open grasslands (65 ha), the migrating dunes (9 ha) or has been washed to the Łebsko Lake (12 ha).

### *Dune slack communities*

By 2006, 57 ha (64 %) of dune slack communities had already disappeared and were mainly replaced by woodlands (24 ha) and open grasslands (17 ha) (Table 3). This decrease is compensated by a gain of 31 ha (35 %), due to new created dune slacks

mostly on bare sand. Only 1 % of current dune slack communities were also dune slack communities in 1932.

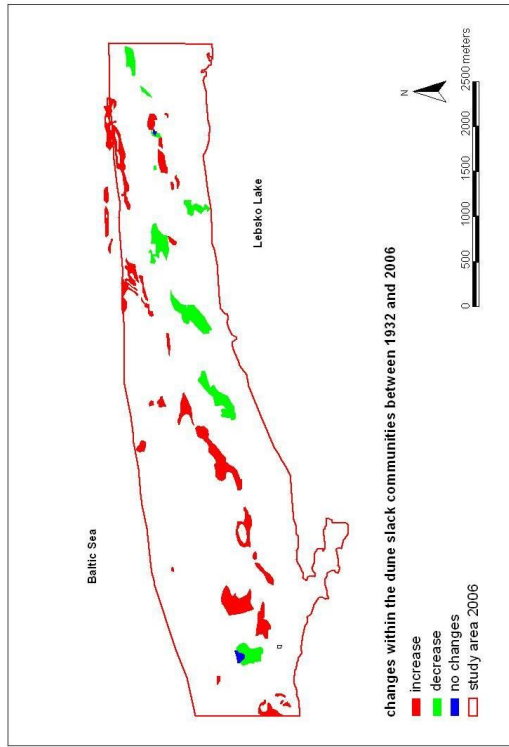
### *Migrating dunes*

The migrating dunes have lost 54 % (205 ha) of their total area since 1932 and became overgrown by woodlands (88 ha) and open grasslands (77 ha) (Table 3). On the other hand, the migrating dunes expanded their total area by 25 % (96 ha), almost the same amount (78 ha) stayed remained unchanged.

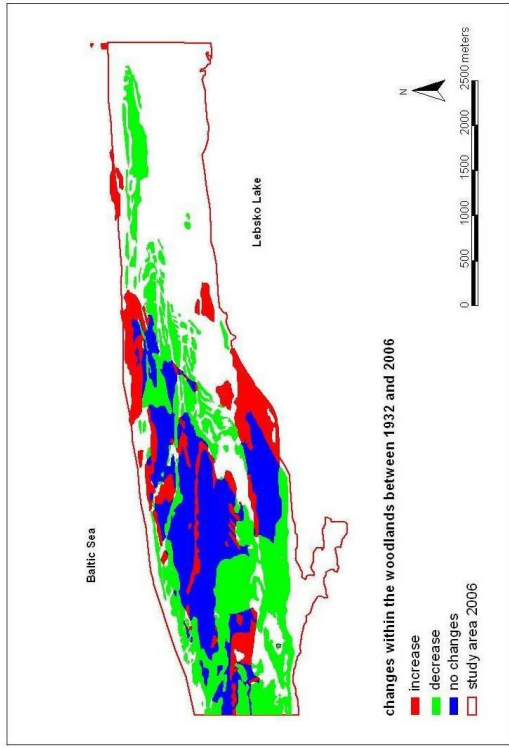
**Table 3** Decrease, increase and no changes within the 'landscape types' between 1932 and 2006 and their distribution in ha and % (with total ha and %).

	Open grasslands		Woodlands		Dune slack communities		Migrating dunes	
	ha	%	ha	%	ha	%	ha	%
Developed to:								
Baltic Sea	48	11	5	1	6	7	14	4
Beach	12	3	4	1	4	5	7	2
Open grasslands			65	12	17	19	77	19
Woodlands	108	25			24	27	88	23
Dune slack communities	1	0	5	1			22	6
Migrating dunes	36	9	9	2	5	6		
<i>Carici elongatae-Alnetum</i>	0	0	4	1				
<i>Phragmitetum communis</i>	3	1	3	1				
Łebsko Lake	2	0	12	2				
<b>Decrease total</b>	<b>210</b>	<b>49</b>	<b>108</b>	<b>19</b>	<b>57</b>	<b>64</b>	<b>205</b>	<b>54</b>
Developed from:								
Baltic Sea	2	0						
Beach	7	2	2	0				
Open grasslands			106	19	1	0	29	8
Woodlands	62	15			5	6	4	1
Dune slack communities	21	5	24	4			5	1
Migrating dunes	73	17	91	16	23	25		
<i>Carici elongatae-Alnetum</i>	2	0	4	1			5	1
<i>Phragmitetum communis</i>	1	0	15	3			35	9
Łebsko Lake	1	0	1	0	2	3	18	5
<b>Increase total</b>	<b>169</b>	<b>39</b>	<b>242</b>	<b>43</b>	<b>31</b>	<b>35</b>	<b>96</b>	<b>25</b>
No changes	47	11	209	37	1	1	78	21
<b>TOTAL</b>	<b>426</b>	<b>100</b>	<b>559</b>	<b>100</b>	<b>89</b>	<b>100</b>	<b>379</b>	<b>100</b>

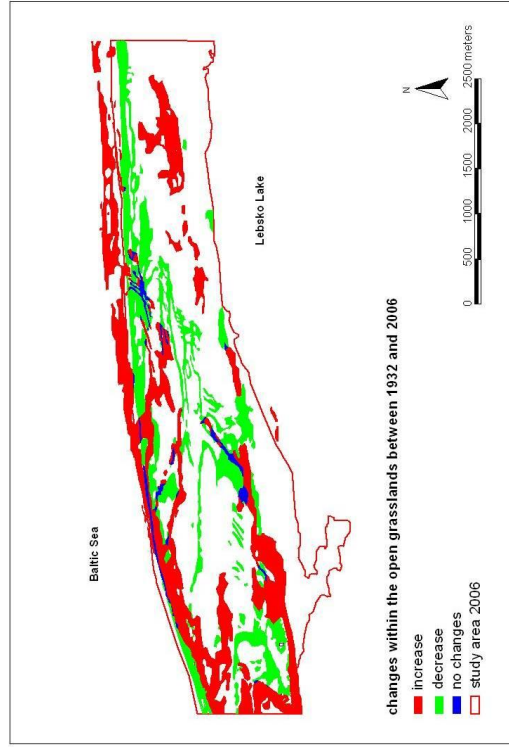
Figures 7–10 illustrate the development trends of the vegetation types. Between 1932 and 2006 the migrating dunes moved eastwards, decreasing in the west and increasing in the east. The dune slack communities were dislocated eastwards. The decreasing shoreline of the beach led to a loss of open grasslands to the Baltic Sea. New grass-communities settled on the dislocated yellow and grey dunes as well as on the western slope and on deflation fields of the retreating migrating dunes. Woodland spread, on a large scale, on the deflation plains and on bare sand or was lost to the Łebsko Lake.



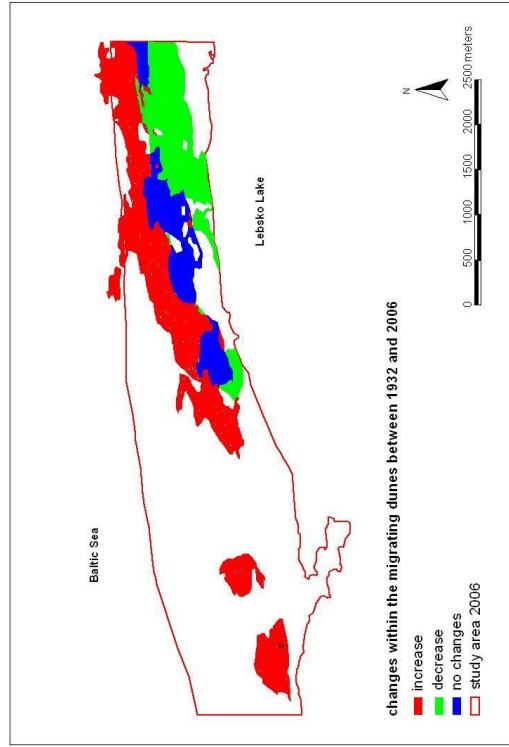
**Figure 7** Changes within the dune slack communities between 1932 and 2006.



**Figure 8** Changes within the woodlands between 1932 and 2006.



**Figure 9** Changes within the open grasslands between 1932 and 2006.



**Figure 10** Changes within the migrating dunes between 1932 and 2006.

## Discussion

The results reveal a clear change in the distribution of plant communities. The natural vegetation succession on sand is probably profoundly changed by three main factors: plantings and following dune stabilisation, intensified human pressure, and especially by nutrient input due to aerial pollution (Remke et al. 2009). Land use changes like recreation pressure and afforestation effected also species composition of the dune vegetation and resulted in a strong increase of synanthrop species (Piotrowska 1988). Other Polish areas, such as coastal meadows are more affected by land use changes due to agriculture development (Rabski 2002).

Since 1932, woodlands have increased considerably at the expense of open habitats. Hundreds of year's abrasion of the Pleistocene cores smoothed the southern Baltic coastline and supported sand accumulation and dune building (Piotrowska 1988). There are various patterns and processes determining aeolian sand dynamic at large as well as at small scales in the study area (Borówka 1980). Nowadays, probably due to coastal erosion combined with less sand accumulation, natural succession led to an increasing vegetation cover and stabilisation of the yellow dunes. As a result the migrating dune areas are cut off from the sand supply from the Baltic Sea. Likewise, dunes in southwestern France such as the Dune du Pyla represent reduced sand dynamics due to marram grass plantings as well as afforestation (Tastet and Pontee 1998). At the Łeba Bar, plants such as *Ammophila arenaria* stabilise the bare sand, and consequently plants less tolerant to sand accumulation such as *Festuca polesica* and *Helichrysum arenarium* begin to spread. Open grasslands and woodland begin to spread on the deflation plain, covering the bare sand. . Moreover, in former times traditional land use forms like burning of woodlands supported heathlands and probably also open dune vegetation (Savukyniené et al. 2003).

The drastic decrease of the beach area and the receding of the shoreline at the Łeba Bar can be observed along the whole Polish coast (Piotrowska 1988). Long-term abrasion and storms had a negative effect on these habitats. However, the situation in the study area is not that drastic as on other parts of the coast. Piotrowska (1988) mentions 15–20 m wide beaches and nearly non-existent yellow dunes as well as fragmented grey dunes with *Helichryso-Jasionetum* on the Polish coast (for example Hel Peninsula and Kopań Bar). Due to a decreasing long-shore drift the beaches along the Polish coast are getting narrower and dunes lower. In spite of a decrease in width and surface area, the beach and dunes in the study area are well developed.

There are still extensive drift sand areas on the Łeba Bar, which provide ideal habitats for pioneer species and open grass communities. The dynamic bare sand blocks the natural succession to more complex developed communities and allows the permanent resettlement of new pioneer stages. On their way eastwards the migrating dunes

cover woodlands and dune slack communities. Once they have reached the Łebsko Lake large parts of the *Phragmitetum communis* and *Caricetum elongatae-Alnetum* are covered by sand.

Two very specific vegetation types on the Łeba Bar are restricted to the dynamic of the migrating dunes. First *Linaria loeselii* forms a species-poor community in deflation hollows of eroded dunes and on sand slopes. This species is endemic to the dune habitats of the southern Baltic coast between Unieście on the Lake Jamno sand bar in Poland, along the Vistula and Curonian Spit up to the Gulf of Riga in Latvia (Stasiak 1987). It is listed in Annex 2 of the European Union Habitats Directive 92/43/EEC (Council of the European Commission 1992). *Linaria loeselii* is often the only pioneer species, which is found on the open dry dune areas. According to Stasiak (1987) mechanical destruction by trampling from holidaymakers, damage of their habitat by storms as well as eutrophication by rubbish dumping could lead to the distinction of this species.

The second are dune slacks, a typical and unique type of wetland ecosystem, occurring at the windward slope of the migrating dunes. This vegetation type ranks highly on the international conservation agenda because of the occurrence of many rare and endangered plant species and their associated fauna (Grootjans et al 1998). Ecologically, they present some of the few examples of primary succession series with a high degree of facilitation between functionally distinct groups of plants and a strong impact of the interannual variation of the water table. Zoladeski (1991) claims that the *Ranunculus reptans-Radiola linoides* community, described by Hueck (1932) has disappeared since 1932 due to more xeric conditions caused by the stabilisation of the foredunes and probably due to a changed water regime due to increasing woodlands. This led to a decrease of sand supply from the Baltic Sea and contributed to a general levelling of the landscape mosaic.

As most of the Łeba Bar is largely protected from major land use changes, the migrating dunes and dune ridges provide suitable habitats especially for these pioneer vegetation types. They are endangered or already absent on coastal habitats at the southern Baltic Coast. Coastal protection, such as plantings and fixation of bare sand led to the disappearance of these habitats. The migrating dunes of the Curonian Spit (Russia/Lithuania) are, for example, threatened by plantings, which stabilized the bare sand and prevent erosion (Peyrat 2008). Likewise large afforestation led to the disappearance of open dune areas on the Vistula Spit/Poland. Nevertheless, the open dune areas on the Łeba Bar are endangered. Ostrowski and Symonides (1995) predict the disappearance of the migrating dunes due to the diminishing sand supply from the Baltic Sea, their spreading along the route of their passage and their natural fixation by vegetation. A possible measure could be the removal of surrounding pine-stands or rather the creation of forest aisles, which may raise the influence of the

wind and support the sand drift and dynamic (van der Meulen and van der Maarel 1993, Hasse and Daniëls 2006). Generally in Europe, there is a beginning of evaluating linked possibilities of both coastal protection and more dynamic landforms, for example to support sand transport from source to near eroding areas, as well as to re-establish natural dynamic to maintain species and landscape diversity (Nordstrom et al. 2007).

The other coastal habitats of the Łeba Bar are also listed in Annex 1 of the European Union Habitats Directive and the fixed coastal grey dunes with herbaceous vegetation (2130) even gain priority in conservation. The area represents a region with high geomorphologic diversity and with various geomorphologic forms (Borówka 1990). The Slowinski Nationalpark is part of the European NATURA 2000 Network and has already reached a high administrative conservation status. We would like to stress the outstanding heritage of the area for natural coastal dynamic processes as it is the only large dune area on the southern Baltic Coast where the full series of large shifting migrating dunes with newly created dune slacks and residual dune ridges ('Gegenwälle') still exist.

## **Conclusion**

This work underlines the importance of natural dynamic for endangered plant species and communities. They can only exist as long as the dynamic is preserved and not changed by plantings, dune fixations and too high human pressure. According to the European Habitats Directive 92/43/EEC (Council of the European Commission 1992) the dunes of the Łeba Bar form important habitats for special coastal vegetation, which is endangered and generally decreasing along the Baltic Coast. Therefore, sustainable protection of natural spatial and temporal dynamics of patterns and processes is one of the most important conservation aspects, necessary to maintain biodiversity of plant species, vegetation as well as landscapes. Interferences have to be avoided and the self-regulation of the area has to be supported.

## **Acknowledgements**

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Dune grassland on the Darsser Ort, DE (Photo: Peyrat 2009).

Chapter 6

# Synthesis

## Summary of results

People have drastically altered coastal dune landscapes around the Baltic coast for almost 1,000 years through exploitation and economic development. Today, the nine countries bordering the Baltic Sea have a population of approximately 40 million people who are living in the immediate coastal proximity (Schiewer 2008). The presence of industry and highly developed agricultural systems results in heavy pollution of the Baltic Sea and adjacent coastal areas, which are among the most polluted regions worldwide. Moreover, increasing demands from tourism put the coasts of the Baltic under severe pressure for development. Baltic coastal ecosystems especially with their fragile environments and endemic species would be threatened further by this kind of development.

### Diversity and habitat conditions of Baltic coastal dunes

In the present work, comparable coastal sites around the Southern Baltic coast were chosen and reviewed with reference to literature and visits to sites. All 15 sites are situated within protected areas of the 'Sundic Baltic Sand Dune Vegetation Complex' and are characterised by a wide range of partly species-rich habitats such as open dunes, grasslands and forests. Compared with the Atlantic sand-dune vegetation of the North-Sea coast, the dunes of the southern Baltic coast are less diverse (Bohn and Gollup 2003). All study sites have a  $\text{pH}_{\text{NaCl}} < 7.0$  of the parent sand material and a precipitation of 520–755 mm yr<sup>-1</sup>.

The vegetation of Baltic coastal dunes is well preserved in pristine or minimally disturbed dune ecosystems (chapter 5). Such areas contain a high biodiversity of native or endemic coastal species (chapter 3). We found a total of 232 species in the studied dunes (chapter 2). Vascular plants represent 61 %, lichens 28 % and bryophytes 11 % of the total recorded species. The species occurred in a zonal distribution in relation to distance from the sea, forming distinctive plant communities. These plant communities are typical for dry coastal dunes along the southern and western Baltic coast (Wojterski 1993, Isermann 1996, Piotrowska 2002, Stankevičiūtė 2006). Yellow dunes along the beach are covered by perennial tall grasslands (*Elymo-Ammophiletum arenariae*). In the interior parts of the dunes, more stable conditions led to the development of acidophilous short grasslands (*Helichryso-Jasionetum litoralis*, *Festucetum polesicae*) with varying coverage of lichen and bryophytes. Older stabilised dunes are occupied by low shrublands (*Hieracio-Empetretum nigri*) and coastal pine forests (*Empetro-Pinetum sylvestris*). *Astragalus arenaria*, *Cakile maritima* subsp. *baltica* and *Tragopogon heterospermus* are species with distribution ranges limited to the Baltic region. Along the Baltic from Germany eastwards continental species such as *Helichrysum arenarium* and *Festuca polesica* become more abundant because of change from an atlantic to a more continental macroclimate.

Variations in diversity and in distributional character of plant species, and in plant communities result mainly because of the interplay between plant succession, exposure, disturbance and resource availability. The further from the the sea, environmental indicator values, that were used to describe dynamics in the dune habitats, showed a decline in light and temperature, accompanied by higher soil moisture due to accumulation of organic matter. We observed an increase in species richness and species diversity on young grey dunes after surface stabilisation when compared to species poor yellow dunes (chapter 4). Older stabilised dune communities with low frequency or intensity of disturbance and environmental conditions showed much lower species richness than grey dunes, where the highest species richness was measured. These findings confirm the intermediate disturbance theory (Connell 1978) stating that highest species richness is found in habitats with intermediate levels of environmental and disturbance gradients.

### **Coastal dunes as habitats for threatened species and plant communities**

Around the Southern Baltic coast we recorded 24 vascular plants, 17 lichens and two bryophytes, which are classified as regionally endangered (chapter 2). Among these species are *Eryngium maritima* and *Pulsatilla vulgaris*, which carry a very high conservation value. They occur in protected dunes in greater quantities than on most other non-protected dunes (Łabuz 2007). Moreover, several varieties of lichens are threatened or have decreasing populations along the German Baltic coast, such as *Cladonia cervicornis*, *Cladonia coccifera*, *Cladonia cornuta*, *Cladonia gracilis*, *Lecanora symnicata* and *Peltigera rufescens*. The dunes of the southern Baltic coast are noted for two plant communities, which are exclusive to this area: First, species-poor annual pioneer vegetation with *Corispermum pallasii*, *Cakile maritima* subsp. *baltica* and the endemic *Linaria loesellii* are specific to dynamic dune fields of the Łeba Bar and the Curonian Spit (chapter 3). *Corispermum pallasii* and *Cakile maritima* subsp. *baltica* are found only on the dunes of the Curonian Spit, whereas the endemic *Linaria loesellii* is distributed along the whole of the southern Baltic seacoast from Pomerania to the Baltic States, and it is also found on the Curonian Spit as well as on the dunes of the Łeba Bar. The neophyte *Corispermum pallasii* is widely replacing the Baltic endemic *Corispermum intermedium*, which has been recorded in the past sharing the same coastal habitats (Preuß 1912, Steffen 1931). The spread of *Corispermum pallasii* on drifting dunes of the Baltic coast in Lithuania has been discovered by Gudžinskas (2000). Today, the current distribution of *Corispermum intermedium* along the Baltic coast is insufficiently known. The second plant community restricted solely to the southern Baltic coast is represented by coastal pine forests of the syntaxon *Empetro-Pinetum sylvestris*. They are restricted to a narrow coastal strip with a main distribution area along the Polish Baltic coast up to the Curonian Spit.

Detailed studies of landscape dynamics in Europe have shown a tendency to increase fixation and succession on coastal dunes during the past century. A large reduction in area of grasslands and open sandy areas associated with an increase in the area of wooded communities are reported for the North Sea and Baltic Sea coast. Ketner-Oostra (1993) and Ketner-Oostra and Sýkora (2004) observed drastic changes of dune vegetation structure on the West Frisian Island Terschelling between 1966 and 1990 as well as a strong decline in lichen diversity. The area of bare sand declined from 25 on the northern and 60 % on the southern dune slopes to less than 1%. Tall grassland communities, such as the *Violo-Corynephorretum* decreased over the same period, while there was a spread of graminoids (*Ammophila arenaria*, *Carex arenaria*, *Festuca rubra*) and mosses (*Dicranum scoparium* and *Campylopus introflexus*). Isermann and Cordes (1992) describe a similar trend of vegetation succession and soil development on the East Frisian Island of Spiekeroog. Here, bare sand declined and is nowadays replaced by grey dune vegetation, where the area of grassland communities showed a strong decline and succession continued towards shrub (*Empetrum nigrum*) and woodland (*Betula spp.*, *Sorbus aucuparia*). Observations on vegetation changes for Baltic dunes are very similar. Schubert (1996) and Remke (2009) describe severe grass encroachment with *Deschampsia flexuosa* and *Carex arenaria* on dry heathlands on the Dünenheide on Hiddensee. During the 1930ies and late 1980ies older successional vegetation units increased at the expense of pioneer stages.

Many authors presume that this tendency is mainly caused by changes in land use, eutrophication through atmospheric nitrogen deposition, impact of climate change and increasing anthropogenic pressure regarding coastal protection and recreation (e.g. Piotrowska and Stasiak 1982, Houston et al. 2001, Labuz 2004, Pruszek and Zawadska 2008, Remke 2009). The decline of open, early succession dune habitats is linked especially to a decline in biodiversity, as these habitats host threatened plant communities and species and are therefore of high conservation value in Europe (Provoost et al. 2009).

Most dune systems along the southern Baltic coast have changed from very mobile to more stable dune systems from the second half of the 19th century onwards. Only a few dune systems with natural coastal dynamics and largely undisturbed vegetation cover of pioneer habitats remain today. One of the most significant dune areas with high geomorphologic and ecologic diversity is found on the Łeba Bar on the Polish Baltic Sea coast. The Łeba Bar is the only large area on the southern Baltic coast, where the full series of large shifting migrating dunes and deflation areas still exists. Along a sea-to-inland gradient the complete succession series could be recognized, from annual communities on the strandline zone of the beach, through lichen-rich grass communities to pine forests on the inland stabilized dunes. Two very specific pioneer vegetation types are found on open dry dune areas and on dune slacks on the

windward slope of the migrating dunes (chapter 5). Although a large part of the Łeba Bar is protected as National Park and is part of the European NATURA 2000 Network, there are several hazards, such as natural erosion due to aeolian processes, plantings, tourism and coastal protection measures which threaten these fragile coastal ecosystems and lead to temporal changes and transitions of plant communities. A GIS based comparison of two aerial photographs of the Łeba Bar from 1932 and 2006 respectively produced vegetation maps that identified vegetation dynamics and temporal changes in the distribution of plant communities that have taken place over the past 74 years (chapter 5).

Since 1932 woodlands and dense grass communities have increased considerably at the expense of open habitats and dune slacks. Woodlands of 1932 spread from a total area of 28 % to 43% in 2006, the *Helichryso-Jasionetum litoralis* increasing by 195 %. At the same time dune slack communities decreased from 5 % to 3 %, and the area of bare sand on the migrating dunes reduced from 25 % to 18 % of the total area.

Observed changes in plant habitats and plant communities on the Łeba Bar are relatively low, when compared with other formerly very active dune fields along the Southern Baltic coast, the. Active dune fields on the Vistula Bar disappeared completely in the 20<sup>th</sup> century due to large afforestation (Baudler 2003). Peyrat (2008) showed also that coastal protection, such as planting and fixation of bare sand, and afforestation do threaten dynamic sandy habitats on the Curonian Spit to this day. Open dynamic habitats dominated large parts of the Curonian spit until the beginning of the 20<sup>th</sup> century. The dunes with all stages of vegetation succession from young short via old to tall grassland had been the focus of intensive research into succession (Preuß 1912, Steffen 1931, Paul 1944, 1953). Between 1938 and 2005 the total area of open dynamic habitats decreased considerably (-66 %), this is mainly replaced by pine plantations (Peyrat 2008).

Results from chapter 5 identify extensive drift sand areas, that are still existing on the Łeba Bar, providing ideal habitats for pioneer species and open grass communities. In 1967 the Słowiński National Park was established and covers a large part of the Łeba Bar. This area of active dune fields, which is situated in the middle of the Łeba Bar, became a core zone where all management and land use is prohibited. The dynamic bare sand hinders the natural succession to more complex developed communities, thus allowing the permanent resettlement of new pioneer stages.

## **Recommendations for maintenance and development of Baltic dunes**

The most important goal for management of Baltic coastal dunes has to be the preservation of open coastal dune habitats with their very specific plant species. These habitats contain a high biodiversity, which declined – at least regionally – around the

Baltic coast. Habitats with high sand dynamic can only exist as long as the natural dynamic is preserved and is not compromised by plantings, dune fixations and human pressure. The present studies prove that highly dynamic habitats with high biodiversity and endangered species can continue to thrive along the southern Baltic coast, such as on the Darß peninsula, the Łeba Bar and in places on the Curonian Spit. Sustainable protection of the natural, spatial and temporal dynamics of patterns and processes is one of the most important conservation aspects necessary to maintain biodiversity of plant species, vegetation as well as landscapes. Interferences have to be avoided and self-regulation of the area has to be supported.

In the past, management of coastal dunes was focused on dune stabilization, as bare dune landscapes and sandy ecosystems were considered of no value and interest (Kutiel 2001). Afforestation and coastal defense measures of grass planting for dune stabilisation has fixed large parts of the southern Baltic dunes. Moreover, changes in nutrient regime through increased atmospheric nitrogen deposition and climate changes (lengthening of the growing season and enhanced CO<sub>2</sub>-concentrations) resulted in an encroachment of grasses and shrubs on coastal dunes. This tendency of landscape fixation was also accelerated by changes in land use, such as abandonment of agricultural practices (grazing, mowing and burning). Over the last decades geomorphological and ecological studies have proved the importance of mobile sand to be an intrinsic part of the dunes (Kutiel 2001).

Therefore, management of sandy dune ecosystems has to comply with the following principles:

- further losses of sandy dune ecosystems have to be prevented,
- intact dune ecosystems have to be put under nature conservation,
- eutrophication and nutrient inputs have to be reduced,
- shrub and tree encroachment have to be prevented,
- invasive neophytic plant species have to be removed,
- traditional management practices should serve as examples for the maintenance of sandy ecosystems.

Rhind and Jones (2009) deem a variety of management practises as necessary to maintain high landscape heterogeneity and to restore the dynamic landscape along with typical local flora and fauna. The management is ranging from total non- or minimal intervention through to intensive management and habitat recreation. Extensive studies are being conducted at present, mainly in Belgium, France, Germany, Great Britain and the Netherlands (table 1). Grazing is believed to be the most appropriate tool to maintain the open character and diversity of dune sites (Lemoine and Faucon 2005, Leten et al. 2005). Cattle and sheep are effective in countering the development of shrubs and have been used in several restoration projects in England (Hewett 1985,



**Table 1** Management practises for dunes (goals, measures, effects, problems and experiences).

Management practise	Goals	Measures	Effects	Problems	Experiences
<b>Grazing</b>	<ul style="list-style-type: none"> <li>• to counteract grass- and scrub-encroachment</li> <li>• to maintain the open character and plant species diversity of dunes</li> </ul>	<ul style="list-style-type: none"> <li>• year round low intensity livestock grazing (cattle or sheep) for maintaining dune grasslands (Boorman and Boorman 2002)</li> <li>• more intensive seasonal livestock grazing (cattle or sheep) to restore dune grasslands (Boorman and Boorman 2002, Houston 2008)</li> </ul>	<ul style="list-style-type: none"> <li>• long-term grazing has positive effects on species diversity, plant communities and habitat condition in dunes (Plassmann et al. 2010)</li> <li>• grazing maintain a fine mosaic pattern with areas of open sand, sand with moss and lichens and low grass vegetation (de Bonte et al. 1999)</li> </ul>	<ul style="list-style-type: none"> <li>• the vegetation will remain denser in areas with high nitrogen deposition and with accumulation of organic matter; therefore grazing has to be combined with turf stripping or deposition of fresh sand (e.g. Houston 2008, Remke 2009)</li> <li>• when grassland is already existing, shrubs have to be removed mechanically at first (van Dijk 1992, Provoost et al. 2004, Houston 2008)</li> <li>• grazing is responsible for shifts in plant community composition and a decrease in plant diversity among grasslands at opposing acidity conditions in coastal dune grasslands (Tahmasebi Kohyani et al. 2009)</li> </ul>	<ul style="list-style-type: none"> <li>• Belgium (Cosyns et al. 2001, Provoost et al. 2004)</li> <li>• The Netherlands (van Dijk 1992, Koijman and de Haan 1995, de Bonte et al. 1999, Boorman and Boorman 2002, van Til 2006)</li> <li>• Germany (Schütz and Grimbach 1994; Schwabe et al. 2002)</li> <li>• Great Britain (Hewett 1985, Boorman 1989, Oates et al. 1998, Simpson et al. 2001)</li> </ul>
<b>Mowing</b>	<ul style="list-style-type: none"> <li>• to counteract grass- and shrub-encroachment</li> <li>• to maintain the open character and plant species diversity of dunes</li> </ul>	<ul style="list-style-type: none"> <li>• mowing with scythes, single axle motor movers or tractor-mounted harvesters (Quinger and Meyer 1995, Houston 2008)</li> <li>• removal of cuttings with wooden rakes (Quinger and Meyer 1995)</li> </ul>	<ul style="list-style-type: none"> <li>• mowing increase the plant diversity, richness and the number of annual herbs (Anderson and Romeril 1992) and maintain a short turf (Hewett 1985)</li> </ul>	<ul style="list-style-type: none"> <li>• ground compaction by using heavy mechanical equipment (Breeds and Rogers 1998)</li> <li>• uneven terrain, steep slopes and hidden hazards hinder the work (Breed and Rogers 1998)</li> <li>• removal of cuttings is expensive and require a disposal area (Breeds and Rogers 1998)</li> </ul>	<ul style="list-style-type: none"> <li>• Belgium (Provoost et al. 2004)</li> <li>• Great Britain (Hewett 1985, Anderson and Romeril 1992, Breeds and Rogers 1998, Simpson et al. 2001, Packham and Willis 2001)</li> </ul>

Management practise	Goals	Measures	Effects	Problems	Experiences
<b>Sod-cutting</b>	<ul style="list-style-type: none"> <li>• to restore and regenerate lichen-rich short dune grasslands</li> <li>• to remove the build up of below-ground biomass stimulated by Nitrogen deposition and the soil enriched with organic matter</li> <li>• to remove invasive mosses (e.g. <i>Campylopus introflexus</i>)</li> </ul>	<ul style="list-style-type: none"> <li>• shallow sod cutting by removing 5cm of the top-soil (Ah-layer) (e.g. van Til and Kooijman 2007, Remke 2009)</li> </ul>	<ul style="list-style-type: none"> <li>• sod-cutting results in a decrease in coarse vegetation and an increase in species-richness (van Til and Kooijman 2007)</li> </ul>	<ul style="list-style-type: none"> <li>• sod-cutting in moss-encroached vegetation is unsuccessful as a management technique to restore the former lichen-rich succession stages; promoting deposition of fresh sand or deep sod-cutting down to calcium rich soil layers will be more effective (Ketner-Oostra and Sýkora 2000)</li> </ul>	<ul style="list-style-type: none"> <li>• The Netherlands (Ketner-Oostra and Sýkora 2000, van Til and Kooijman 2007)</li> </ul>
<b>Removal of plantation</b>	<ul style="list-style-type: none"> <li>• to restructure the plantations on dunes by replacing non-native woodlands by native woodlands</li> <li>• to restore the original dune flora</li> </ul>	<ul style="list-style-type: none"> <li>• clear-felling of conifers</li> <li>• litter removal</li> <li>• removal of self-sown young conifers at regular intervals (Houston 2008)</li> </ul>	<ul style="list-style-type: none"> <li>• typical dune species will resettle the dunes</li> <li>• development of closed thickets and tall heathlands or an open vegetation similar to growing heathlands and grasslands (Lemauviel and Roze 2000)</li> </ul>		<ul style="list-style-type: none"> <li>• Belgium (Bistea and Mahy 2005)</li> <li>• France (Lemauviel and Roze 2000)</li> <li>• Great-Britain (Simpson and Gee 2001, Sturgess and Atkinson 2003)</li> <li>• The Netherlands (van Til et al. 2007)</li> </ul>
<b>Large scale destabilisation</b>	<ul style="list-style-type: none"> <li>• to enhance landscape rejuvenation and to restore dune mobility by increasing aeolian erosion and deposition</li> <li>• to create new possibilities for the development of pioneer vegetation stages</li> </ul>	<ul style="list-style-type: none"> <li>• removal of the vegetation and soil with bulldozers (Lemoine and Faucon 2005, Rhind and Jones 2009)</li> </ul>	<ul style="list-style-type: none"> <li>• massive increase of natural dynamics and aeolian processes</li> <li>• expansion of sand drift areas</li> <li>• natural vegetation succession with a mosaic of bare sand and pioneer vegetation (Arens et al. 2005)</li> </ul>	<ul style="list-style-type: none"> <li>• areas smaller than 50m<sup>2</sup> tend to restabilise to quickly (van Boxel et al. 1997, Rhind and Jones 2009)</li> <li>• new measures to reduce stabilisation need to be required every 10 or 20 years (Arens and Geelen 2006)</li> </ul>	<ul style="list-style-type: none"> <li>• France (Lemoine and Faucon 2005)</li> <li>• The Netherlands (Arens et al. 2005, Terlouw and Slings 2005, Arens and Geelen 2006)</li> </ul>

1985, Boorman 1989, Burton 2001), in the Netherlands (Kooijman and de Haan 1995, Kooijman and van der Meulen 1996, De Bonte et al. 1999) and Belgium (Provoost et al. 2004). The reinstating of grazing into the dunes of the Curonian Spit by allowing local people to keep cattle in grey dunes has been proposed by Armaitienè et al. (2007). To restore lichen-rich short dunes along the Southern Baltic coast, Remke (2009) recommends turf stripping of grasslands, the removal of organic matter enriched soil and liming. These measures may help to counteract acidification and accumulation of organic matter due to increased atmospheric Nitrogen deposition.

Large scale remobilization of stable and senescent dune systems could be undertaken to restore dune mobility. In projects carried out in the Netherlands to enhance landscape rejuvenation (Arens et al. 2005, Terlouw and Slings 2005, Arens and Geelen 2006), the aeolian activity was stimulated by increasing aeolian erosion and deposition. Large scale remobilization would also be a possible action in order to restore and preserve the active migrating dunes of the Curonian Spit. By cutting the forest on the leeward foot of the dunes, blown out sand could be restored artificially to the dune crest (Armaitienè et al. 2007). The constant initiation of dynamic processes appear to be the key factor for the preservation process of biodiversity in early successional plant communities on coastal dunes (Jentsch and Beyschlag 2003).

Nature conservation programs for Baltic dune ecosystems always have to include the history of the dune area, trends in vegetation development, current land use and present ecological conditions, because the dune landscape of the Baltic coast has been influenced by people since their genesis, and it consists today of elements from different periods (Provoost et al. 2009). The dune landscapes on the Łeba Bar and Curonian Spit, for example, are regarded as 'pristine landscape'. To large extend, the dune landscape was formed due to anthropogenic changes in the 17<sup>th</sup> century and is a result or an intermediate stage of anthropogenic processes. Only through extensive study of these semi-natural vegetation and their biotopes, decreases and changes of plant habitats during the last decades their history can be understood (Ihse 1995).

The use and comparison of aerial photographs with a geographic information system (GIS) is a useful tool to receive information about the temporal changes and transitions of these habitats that have taken place in recent decades (Bender et al. 2005). Furthermore, it is possible to demarcate the areas that need urgent attention in terms of management and conservation (Shanmugam and Barnsley 2002). Especially endangered plants, such as *Corispermum intermedium*, should be mapped and protected before the species become extinct. Monitoring of endangered coastal habitats is an important precondition for the management of coastal dune systems, which are highly dynamic in nature.

In conclusion, those responsible for management of coastal dunes have to remember, that the restoration and conservation of open dune habitats present a serious dilem-

ma, as these ecosystems are in a constant change due to natural succession and their plant communities have a relatively short life (Nezadal 1989). The right balance between intensifying the management (to maintain open dynamic habitats) and accepting the gradual move towards an ecologically and geomorphologically stable situation (by natural development with late succession stages) must be the target of nature conservation.

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Coastal woodland close to Prerow, Darss, DE (Photo: Peyrat 2009).

# Summary

In North-West Europe, dunes form extensive systems along the exposed Atlantic, North and Baltic Sea. Coastal dunes contain a high ecological diversity in terms of environmental heterogeneity and variability of species composition. Despite the restricted widths of these coastal ecosystems, there is a complex sea-to-inland gradient with spatial sequences of dune ridges, representing chronological series. Changing environmental conditions as well as the interplay among plant succession, exposure, disturbance and resource availability lead to diverse patterns and rates of succession. Hence, these geomorphologically active and very dynamic systems consist of a fine mosaic of various habitats. Rare and endemic species and plant communities are restricted to coastal dunes and therefore deserve special conservation attention. To safeguard these ecosystems, a range of national parks or nature reserves was established. Furthermore many coastal sites are protected as priority habitats under the European Habitats Directive (Council Directive 92/43/EEC of 21 May 1992) or they are listed as Natura 2000 sites, indicating that these areas should be preserved in their function as habitat for threatened species. Despite their ecological value, almost all European coastal dune systems have been significantly affected by human activities during the last centuries. In many cases, human impact dates back to the development of the dunes. Overgrazing, deforestation, dune stabilization, settlement, tourism, atmospheric pollution and coastal protection have altered the dunes significantly. Natural processes, such as sea-level rise, climate change and lack of sediment led to erosion and fragmentation of many dune systems.

The present work has focused on coastal dune ecosystems along the Southern Baltic coast, where some stretches of coastline with pristine or minimally disturbed dune ecosystems remain, containing a high biodiversity with native or endemic coastal species. The aim of this study is to compile an overview about the vegetation, environmental problems, plant community dynamics and landscape changes throughout these Baltic coastal dune habitats. The quality and critical environmental factors of these habitats are of permanent interest for the future management and nature protection.

The first objective of this study was to give a general overview of plant species composition and of main plant communities of dry coastal dunes along the Southern Baltic coast by own plant records. Eleven coastal communities with a total of 230 species are considered. Twenty-four vascular plants, 17 lichens and two bryophytes, classified as regionally endangered, are found, testifying the importance of these coastal habitats for the conservation of threatened species. Pioneer communities on young dynamic dunes (*Elymo arenarii-Ammophiletum arenariae*) are dominated by grasses

and have a lower cover and diversity. Further successional stages on stabilised intermediate dunes have a low cover but moderately higher diversity, with sedges and grasses dominating (*Helichryso arenarii-Jasionetum litoralis*). Older stages on stable backdunes have a greater mean cover with an abundance of shrubs and trees (*Hieracio-umbellati-Empetretum nigri* and *Empetro nigri-Pinetum sylvestris*). Environmental changes through natural processes and human activities among these dunes were evaluated by a literature review. These showed that the ecology of the surveyed coastal sites is gradually being degraded by coastal erosion, human impact and atmospheric nitrogen deposition.

A very specific dune vegetation, exclusive to the Southern Baltic coast, is found on active migrating dunes and sand dune fields of the Łeba Bar and Curonian Spit and is represented by 18 vegetation relevés according to Braun-Blanquet. The Baltic endemics *Cakile maritima* subsp. *baltica*, *Corispermum intermedium* and *Linaria loeselii* form open species-poor dune vegetation. This annual vegetation is restricted to high dynamic open dune areas and is threatened by severe losses of habitat through dune afforestation along the Southern Baltic coast. Therefore, the objective was to study this vegetation with reference of landscape changes and species conservation. A comparison of these results with literature records pointed to a gradual replacement of *Corispermum intermedium* by the neophyte *Corispermum pallasii*.

A further objective was to describe patterns of plant species diversity in dry coastal dunes. Plant species richness along a sea-to-inland gradient depends on permanent interactions of abiotic and biotic environmental factors. Environmental indicator values, used to describe dynamics in dune habitats, record a decline of light and temperature due to increased distance from the sea, accompanied by higher soil moisture due to accumulation of organic matter. Species richness shows a humped-shaped curve along the coastal dune gradient, with highest values reached in grey dunes with intermediate levels of environmental and disturbance gradients. Habitats, such as the open dynamic habitats of the migrating dunes, are species poor, but they host endangered and endemic species and contribute to the overall biodiversity as well.

The dune habitats under observation are highly dynamic systems with outstanding conservation value. To observe medium-term natural and anthropogenic changes and development of dune habitats, one well preserved dune area, the Łeba Bar, was chosen for detailed investigation. Cartometric comparison with a Geographical Information System (GIS) gives information about the decrease, increase and stability of vegetation types between 1932 and 2006. It becomes obvious, that there has been a severe reduction in the total area of bare sand and a considerable increase of woodlands and dense grass communities. Nevertheless the remaining extensive drift sand areas on the Łeba Bar are among the most dynamic habitats along the southern Baltic coast, offering important habitats for pioneer species.

Nature conservation programs for Baltic dune ecosystems must always include the history of the dune area, trends in vegetation development, current land use and present ecological conditions, because the dune landscape of the Baltic coast has been influenced by people since the dune's genesis and it consists of elements from different periods. The importance of these coastal habitats is the occurrence of numerous rare and endangered vascular plants, lichens and bryophytes. Management practices of Baltic coastal dunes should aim to restore the open dynamic habitats by encouraging sand drift (e.g. grazing, mowing, or removal of conifer plantations) and maintaining the right balance between large-scale dynamics and succession.

# Zusammenfassung

Ausgedehnte Dünensysteme erstrecken sich entlang der Atlantik- Nordsee- und Ostseeküste. Aufgrund ihrer Umweltheterogenität und Variabilität der Artenzusammensetzung verfügen Küstendünen über eine hohe ökologische Vielfalt. Sie sind, trotz ihrer geringen Breite, durch einen komplexen Küsten-Inlands-Gradienten gekennzeichnet, der aus einer räumlichen und zeitlichen Abfolge von Dünenreihen besteht. Wechselnde Umweltbedingungen, sowie das Zusammenspiel zwischen Sukzession, Exposition, Störungsintensität und Ressourcenverfügbarkeit führen zu unterschiedlichen Sukzessionsmustern und -raten. Daher setzen sich diese geomorphologisch aktiven und sehr dynamischen Dünensysteme aus einem Mosaik unterschiedlichster Lebensräume mit zum Teil seltenen und endemischen Arten und Pflanzengesellschaften zusammen. In der Vergangenheit wurde zum Schutz dieser besonderen Lebensräume eine Reihe von Nationalparks und Naturschutzgebieten eingerichtet. Darüber hinaus sind viele Küstengebiete als prioritäre Lebensräume für bedrohte Arten gemäß der FFH- Richtlinie 92/43/EWG geschützt oder als Natura 2000 Gebiete aufgeführt. Trotz ihres hohen ökologischen Wertes wurden fast alle europäischen Küstendünen in den letzten Jahrhunderten durch menschliche Aktivitäten, wie Überweidung, Abholzung, verstärkte Küstenschutzmaßnahmen, Besiedlung, Tourismus sowie Luftverschmutzung nachhaltig beeinträchtigt und verändert. Zudem führten natürliche Prozesse wie Meeresspiegelanstieg, Klimawandel und fehlende Sedimentation zu Erosion und Fragmentierung von vielen Dünensystemen.

Die vorliegende Arbeit konzentriert sich auf naturnahe Küstendünen entlang der südlichen Ostseeküste, die geringe Störungen aufweisen und eine hohe Biodiversität besitzen. Ziel der vorliegenden Studie war die Erstellung einer Übersicht über Vegetation, Umweltprobleme, Dynamik von Pflanzengesellschaften und Landschaftsveränderungen dieser baltischen Küstendünenlebensräume. Die Qualität und die kritischen Umweltfaktoren dieser Habitate sind von zentraler Bedeutung für deren zukünftiges Management und Naturschutz.

Erstes Ziel der Studie war es, die Artenzusammensetzung der wichtigsten Pflanzengesellschaften in Küstendünen entlang der südlichen Ostseeküste durch eigene Vegetationsaufnahmen zu beschreiben (Kapitel 2). Insgesamt wurden elf Gesellschaften mit 230 Arten berücksichtigt, von denen 24 Gefäßpflanzen, 17 Flechten und 2 Moose als Rote-Liste-Art geschützt sind. Pioniergesellschaften auf jungen dynamischen Dünen (*Elymo arenarii-Ammophiletum arenariae*) sind durch Gräser dominiert und zeigen eine geringe Deckung und Diversität. Weiterführende Sukzessionsstadien auf festgelegten Dünen besitzen ebenfalls eine geringe Deckung, weisen jedoch eine höhere Diversität mit Seggen und Gräsern auf (*Helichryso arenarii-Jasionetum litoralis*).

Ältere Sukzessionsstadien sind durch eine höhere Deckung und das Vorkommen von Sträuchern und Bäumen gekennzeichnet (*Hieracio umbellati-Empetretum nigri* und *Empetro nigri-Pinetum sylvestris*). Durch Literaturrecherche wurden in den untersuchten Dünengebieten Umweltveränderungen durch natürliche Prozesse und menschliche Aktivitäten bewertet. Die Ökologie dieser Küstengebiete wird allmählich durch Erosion, anthropogene Tätigkeiten und erhöhte Stickstoffeinträge aus der Luft verändert.

Die an der Ostseeküste endemischen Arten *Cakile maritima* subsp. *baltica*, *Corispermum intermedium* und *Linaria loeselii* bilden offene, artenarme Bestände, die auf hoch dynamische Dünengebiete beschränkt sind und u.a auf den Wanderdünen der Łeba-Nehrung und der Kurischen Nehrung wachsen. In der vorliegenden Arbeit sind sie in 18 Vegetationsaufnahmen nach Braun-Blanquet vertreten (Kapitel 3). Der Lebensraum dieser annualen Arten ist durch Aufforstungsmaßnahmen entlang der südlichen Ostseeküste stark gefährdet. Ziel war es daher, die Vegetation der Wanderdünen vor dem Hintergrund von Landschaftsveränderungen und Artenschutz zu untersuchen. Ein Vergleich der Vegetationsaufnahmen mit Literaturreferenzen offenbart ein schrittweises Ersetzen von *Corispermum intermedium* durch den Neophyten *Corispermum pallasii*.

Weiter wurde die Struktur der pflanzlichen Artenvielfalt in Küstendünen untersucht (Kapitel 4). Der Artenreichtum entlang eines Gradienten von der Küste landeinwärts ist von ständigen Wechselwirkungen zwischen abiotischen und biotischen Standortparametern abhängig. Ellenberg-Zeigerwerte, die verwendet wurden, um die Dynamik in den Dünenlebensräumen zu beschreiben, zeigen eine Licht- und Temperaturabnahme mit zunehmender Entfernung vom Meer und eine höhere Bodenfeuchte durch Anreicherung von organischer Substanz im Boden an. Der Artenreichtum nimmt mit zunehmender Entfernung zum Meer zu und erreicht die höchsten Werten in den Graudünen, die im mittleren Bereich von Umwelt- und Störungsgradienten liegen. In späteren Sukzessionsstadien, wie der Dünenwald auf den Braundünen, sinkt der Artenreichtum. Dynamische Lebensräume, wie die aktiven offenen Wanderdünen, sind artenarm, besitzen jedoch gefährdete und endemische Arten und tragen daher ebenfalls zur Gesamtartenvielfalt bei.

Die untersuchten Dünenlebensräume sind hochdynamische Systeme mit einem hohen Schutzwert. Um mittelfristige natürliche und anthropogene Veränderungen sowie die Entwicklung von Dünenlebensräumen zu beobachten, wurde die Łeba-Nehrung als gut erhaltenes Dünengebiet für detaillierte Untersuchungen ausgewählt (Kapitel 5). Mit Hilfe eines Geographischen Informationssystems (GIS) wurden Luftbildaufnahmen von 1932 und 2006 verglichen und Aussagen über Abnahme, Zunahme und Stabilität von Vegetationstypen getroffen. Es wird deutlich, dass es zu einer erheblichen Abnahme von offenen Sandflächen und einer deutlichen Zunahme von

Wäldern und Sandtrockenrasen gekommen ist. Dennoch zählen die verbleibenden Flugsandgebiete der Łeba-Nehrung zu den dynamischsten Lebensräumen entlang der südlichen Ostseeküste und stellen wichtige Habitate für Pionierarten bereit.

Naturschutzprogramme für Dünenökosysteme entlang der südlichen Ostsee sollten stets die Geschichte der Dünengebiete, die Richtung der Vegetationsentwicklung, die aktuelle Landnutzung sowie die derzeitigen ökologischen Bedingungen berücksichtigen. Die besondere Bedeutung der Küstenlebensräume liegt in den zahlreichen seltenen und gefährdeten Gefäßpflanzen, Flechten und Moosen die in ihnen vorkommen. Managementpraktiken sollten auf die Wiederherstellung der offenen, dynamischen Lebensräume und der Mobilität des Sandes ausgerichtet sein (z.B. durch Beweidung, Mahd oder dem Entfernen von Nadelbaumforsten) und die richtige Balance zwischen großräumiger Dynamik und Sukzession unterstützen.



## Краткий обзор (Russian summary)

В Северо-Западной Европе дюны формируют обширные системы вдоль открытого побережья северной Атлантики и Балтийского моря. Береговые дюны являются одной из наиболее важных экосистем в Европе, так как отличаются высоким экологическим разнообразием, выраженным в неоднородности окружающей среды и изменчивости видового состава. Несмотря на небольшую ширину прибрежных экосистем, здесь есть комплексный градиент в направлении с моря на сушу с пространственными рядами гребней дюн, представляющими хронологические серии. Изменение условий окружающей среды, так же как и взаимодействие между растительными сукцессиями, воздействием, нарушением и доступностью ресурсов ведут к различному характеру и скорости сукцессии. Таким образом, эти геоморфологически-активные и очень динамичные системы представляют собой мелкую мозаику различных местообитаний. Редкие и эндемичные виды и растительные сообщества ограничены береговыми дюнами и таким образом заслуживают особого внимания с точки зрения охраны природы. Для охраны этих экосистем был создан ряд национальных парков и заповедников. Кроме того многие береговые зоны охраняются Директивой Европейского Союза о местах обитания (Директива Совета ЕС 92/43/ЕЕС от 21 мая 1992 года) как места обитания первостепенной важности, или они включены в экологическую сеть «Натура-2000», что означает необходимость сохранения данных зон как места обитания видов, находящихся под угрозой исчезновения. Несмотря на свою экологическую ценность, в течение последних столетий почти все системы береговых дюн в Европе подвергались значительному влиянию деятельности человека. Во многих случаях антропогенное воздействие ведет начало от периода развития дюн. Чрезмерный выпас, вырубка лесов, закрепление дюн, образование поселений, туризм, атмосферное загрязнение и защита береговой зоны значительно изменили дюны. Естественные процессы, такие как подъем уровня моря, изменение климата и недостаток осадочных пород, привели к эрозии и фрагментации многих дюнных систем.

В центре внимания данной работы находятся экосистемы береговых дюн вдоль южного побережья Балтийского моря, где остались участки береговой линии с нетронутыми или минимально нарушенными дюнными экосистемами, в которых представлено большое разнообразие местных или эндемичных прибрежных видов. Целью данного исследования было составление обзора растительного покрова, проблем окружающей среды, динамики растительного сообщества и изменений ландшафта местообитаний балтийских береговых дюн. Качество и ключевые факторы окружающей среды этих мест обитания

представляют большой интерес для дальнейшего регулирования и охраны природы.

Основной целью данного исследования является общий обзор видового состава растений и главных растительных сообществ сухих береговых дюн вдоль южного побережья Балтийского моря на основе собственных данных о растительности. Рассматривается одиннадцать прибрежных сообществ с общим количеством видов – 230. Найдено двадцать четыре вида сосудистых растений, 17 лишайников и два мха, которые находятся под угрозой исчезновения в регионе, что подтверждает важность этих прибрежных мест обитания для сохранения исчезающих видов. В пионерных сообществах на молодых движущихся дюнах (*Elymo-Ammophiletum*) доминируют злаки, также эти сообщества имеют меньшее покрытие и разнообразие. Следующие стадии сукцессии на стабилизировавшихся переходных дюнах имеют небольшое покрытие, но сравнительно высокое разнообразие с доминированием осок и злаков (*Helichryo-Jasionetum*).

Более поздние стадии на стабильных основных дюнах отличаются большим средним покрытием и большим количеством кустарников и деревьев (*Hieracio-umbellati-Empetretum nigri* и *Empetro nigri-Pinetum*). Изменения окружающей среды за счет естественных процессов и деятельности человека для этих дюн оценивались на основе обзора литературы. Экология исследуемых участков побережья постепенно ухудшалась из-за береговой эрозии, антропогенного воздействия и накопления атмосферного азота.

На активных мигрирующих дюнах и песчаных дюнных полях отмели Леба и Куршской косы найден один тип растительности, встречающийся исключительно на южном побережье Балтийского моря, он представлен 18 описаниями согласно Брауну-Бланке. Балтийские эндемики *Cakile maritima* п/вид *baltica*, *Corispermum intermedium* и *Linaria loeselii* формируют открытый бедный видами растительный покров дюн. Этот однолетний тип растительности ограничен высокоподвижными открытыми дюнными пространствами и находится под угрозой из-за сильного экологического ущерба за счет посадок леса вдоль южного побережья Балтийского моря. Таким образом, целью было изучение данного типа растительности с точки зрения изменений ландшафта и сохранения видов. Сравнение результатов с литературными данными показывает постепенное замещение *Corispermum intermedium* неофитом *Corispermum pallasii*.

Следующей целью было описание примеров видового разнообразия растений сухих береговых дюн. Изобилие видов растений вдоль градиента в направлении с моря на сушу зависит от долговременных взаимодействий абиотических и биотических факторов окружающей среды. Индикаторы

состояния окружающей среды, используемые для описания динамики дюнных местообитаний, показывают снижение количества света и понижение температуры с удалением от моря, которые сопровождаются повышением влажности почвы из-за накопления органического вещества. Изобилие видов представлено куполообразной кривой вдоль градиента береговой дюны, при этом наибольшие значения показаны для серых дюн со средним уровнем градиента окружающей среды и градиента нарушений. Такие места обитания, как открытые подвижные мигрирующие дюны, бедны видами, но являются местообитанием исчезающих и эндемичных видов, а также вносят вклад в общее биоразнообразие.

Наблюдаемые дюнные местообитания являются высокодинамичными системами и представляют большую ценность с точки зрения охраны природы. Для наблюдения среднесрочных естественных изменений и изменений, связанных с деятельностью человека, и для детального исследования был выбран один хорошо сохранившийся дюнный участок, отмель Леба. Картометрическое сравнение с Географической информационной системой (ГИС) дает информацию об уменьшении, увеличении и стабильности типов растительности в период с 1932 по 2006 годы. Становится очевидным, что общая площадь голых песков сильно сократилась, и значительно увеличились площади лесных и густых травяных сообществ. Тем не менее, оставшиеся обширные площади подвижных песков отмели Леба являются одними из наиболее динамичных местообитаний вдоль южного побережья Балтийского моря и представляют собой важные места обитания для пионерных видов.

Природоохранные программы для экосистем балтийских дюн всегда должны включать историю дюнного участка, тенденции развития растительности, современное землепользование и настоящие экологические условия, так как дюнный ландшафт балтийского побережья испытывал влияние человека, начиная со времени своего возникновения, и состоит из элементов различных периодов. Практика управления балтийскими береговыми дюнами должна быть направлена на восстановление открытых динамичных местообитаний путем поддержания движения песка (например, выжигания, перемещения, выпаса или удаления хвойных насаждений) и сохранения правильного баланса между крупномасштабной динамикой и сукцессией.

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# Curriculum vitae

## Persönliches

Name	Jann Peyrat
Geburtsdatum	15.03.1980
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## Schulische und akademische Ausbildung

Ab 01.2011	Lehrer im Vorbereitungsdienst für das Lehramt an Grund-Haupt- und Realschulen an der Haupt- und Realschule Käthe-Kollwitz-Schule, Osnabrück
07.2008 – heute	Promotion am Institut für Natur- und Ressourcenschutz (bei Prof. Dr. H. Roweck) der Agrar- und Ernährungswissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel
30.05.2007	Erste Staatsprüfung für das Lehramt an Grund-, Haupt- und Realschulen (Schwerpunkt Hauptschule und Realschule)
10.2004 – 5.2007	Studium des Lehramtes an Grund-, Haupt- und Realschulen (Fächer Biologie und Chemie) an der Carl-von-Ossietzky-Universität Oldenburg
19.10.2006	Diplom-Landschaftsökologe
10.2000 – 10.2006	Studium der Landschaftsökologie an der Carl-von-Ossietzky-Universität Oldenburg
08.1986 – 06.1999	Schulzeit in Wilhelmshaven; Abschluss mit Allgemeiner Hochschulreife

# Erklärungen

Dipl. Landschaftsökologe Jann Peyrat

## Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorgelegte Dissertation mit dem Titel „*Landscape and vegetation of southern Baltic dune systems – diversity, landuse and threats*“ selbständig und ohne unerlaubte Hilfe angefertigt habe und dass ich die Arbeit noch keinem anderen Fachbereich bzw. noch keiner anderen Fakultät vorgelegt habe.

Kiel, den .....

.....  
(Unterschrift)

Hiermit erkläre ich, dass gegen mich kein strafrechtliches Ermittlungsverfahren schwebt.

Kiel, den .....

.....  
(Unterschrift)