

# Creating a conceptual framework for analysis of vascular plant diversity in a coastal landscape: functional aspects and ecosystem services for plants at the Baltic Sea



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UNIVERSITY OF LATVIA

Gederts Ievinsh\*

Department of Ecology, Faculty of Medicine and Life Sciences, University of Latvia, 1 Jelgavas Str., Riga LV-1004, Latvia

\*Corresponding author, E-mail: [gederts.ievins@lu.lv](mailto:gederts.ievins@lu.lv)

## Abstract

The aim of the study is to develop a conceptual framework for the analysis of the diversity of coastal plant species of the Baltic Sea in relation to adaptation to specific conditions and participation in the provision of ecosystem services. The possibilities of coastal plant classification for further analysis of their properties will be described, concentrating on both opportunities and weaknesses of each particular system. These will include approaches related to aspects of taxonomy, life forms and functional strategies, geographical- and habitat-related distribution, ecological indicators, species associations forming vegetation, dependence on landforms as well as provision of ecosystem services. All of these approaches make important contributions to the context of coastal plant occurrence. However, at the level of distribution of individuals of plant species, the perspective is in analysis of their relationship with coastal landscape elements, landforms. Abiotic and biotic aspects of the ecological niche should also be taken into account for the analysis of plant functional diversity, together with the morphological, physiological and biochemical characteristics of individuals. The importance of plants in the functional diversity of coastal ecosystems should be linked to their contribution to ecosystem services.

**Key words:** Baltic Sea, coastal landscape, ecological indicators, ecosystem services, environmental heterogeneity, functional traits, physiological adaptations, plant diversity, vegetation classification.

**Abbreviations:** CRWs, crop wild relatives.

## Introduction

Coasts of oceans and seas represent unique ecosystems in respect to biological diversity, as many plant species are coastal-specific and possess unique adaptive features, and plants are both important physical constituents and one of the functional driving forces in the coastal environment. Scientific interest in the coast as a complex and important natural and socio-economic system has always been significant. However, coastal landscapes have gained systemic scientific interest only within recent decades, leading to appearance of conceptualized theories of the importance of coastal areas (Döring, Ratier 2018). However, the role of plants in the multiple dimensions of coastal landscape functioning has been only seldom assessed.

The presence of particular plant species in a certain location is used to define different hierarchical levels of biosphere, from biomes to habitats, and at all levels plants play are key components around which the functioning of these systems takes place. Usually, an environment-centered approach in plant distribution analysis has been used (Chauvier et al. 2021; Passos et al. 2024; Zurell et

al. 2024). In this approach, when trying to answer the question of why certain plants grow in certain places, we ask what environmental factors are responsible for this distribution pattern. However, if we use a plant-oriented approach, we ask what particular characteristics are these plants possessing making them suitable for this site. Such a question means that we should focus on learning the characteristics of plants that are important in the process of adaptation of an individual to specific conditions, at all levels of biological organization (morphological, physiological, biochemical, molecular). On the other hand, the outcome of the success of adaptation can be described using both simply the presence of the individual and also by biomass production rate, physiological performance, or reproduction intensity. A plant-oriented approach not only gives an opportunity to understand why plants grow in specific places, linking genotype to phenotype through interaction with the environment, but also forms the basis for more practically relevant questions. Thus, we can look for an answer to the question of how climate change as an anthropogenic impact will affect plant functionality and distribution, in further affecting also functions of the whole ecosystem.

To be able to ensure the fulfillment of such a goal, it is necessary to understand how it is possible to classify and analyze plant diversity. So far, the most widely used approaches in the coastal context have been analysis of presence of individuals of plant species in coastal habitats or establishment of characteristic species associations. Focus on floristic composition in the creation of typologies of coastal ecosystems has been rightly criticized, and the need for conceptual framework(s) at multiple spatial scales has been postulated (Yando et al. 2023). Biological aspects have been only seldom used for analysis of coastal plant diversity, but it is evident that this approach can add to dimensions of plant diversity analysis. In this context, functional characteristics of adaptive nature are target properties of individuals of coastal plant species, acting as evidence for evolutionarily-acquired genetically based successful adaptation to prevalent environmental conditions. The functional basis for a coastal-specific distribution of certain plant species can also be found by means of analysis of physiological adaptations. Thus, in order to understand the role of plants in coastal ecosystems, plant diversity need to be analyzed as their functional diversity linking plant characteristics related to adaptation to a specific set of conditions on the seacoast with ecosystem functioning and contribution to ecosystem services.

The Baltic Sea has a coastline of about 8000 km, exhibiting large ecosystem diversity formed by geological differences as well as gradients of temperature, salinity, traditional land use etc. (Carstensen et al. 2020). Although from the point of view of hydrogeography, the Baltic Sea is defined in a limited area that does not include the Danish Straits, usually also the Straits and even the region of Kattegatt have been considered in its context, referring to them as “transition area” (Pätsch et al. 2019; Carstensen et al. 2020). Taking into account the continuity of the landscape on the Danish and Swedish coasts, also this study analyzes the Baltic Sea coastal ecosystem in an expanded version, in principle including areas from the Norwegian-Swedish border in the east and the northern point of the Skagen Odde Peninsula in the west.

Vegetation development in the Baltic Sea region started with the end of the ice age through postglacial colonization and this affected species distribution and range in addition to the dominant influence of climate (Normand et al. 2011). In contrast to other ecosystems, the sea coasts are heavily affected by the dynamic nature of geomorphological processes, and, in interaction with climatic variables, lead to high spatial and temporal variation of vegetation systems.

Although, in general, the diversity of plants and vegetation on the Baltic Sea coast has been investigated relatively well, no comprehensive studies of the entire territory can be found. Most reported studies are within national borders, but in some cases broader comparisons are also available (Remke et al. 2009; Peyrat, Fichtner 2011; Strandmark et al. 2015; Hulisz et al. 2016; Pätsch et al. 2019).

The global goal of this study is to approach a possibility of analyzing the functional diversity of coastal plants of the Baltic Sea and their importance in the existence of the ecosystem and the services it provides. To be able to move in this direction, the main question within the present review is about the selection of relevant approaches and creating a conceptual framework for such analysis.

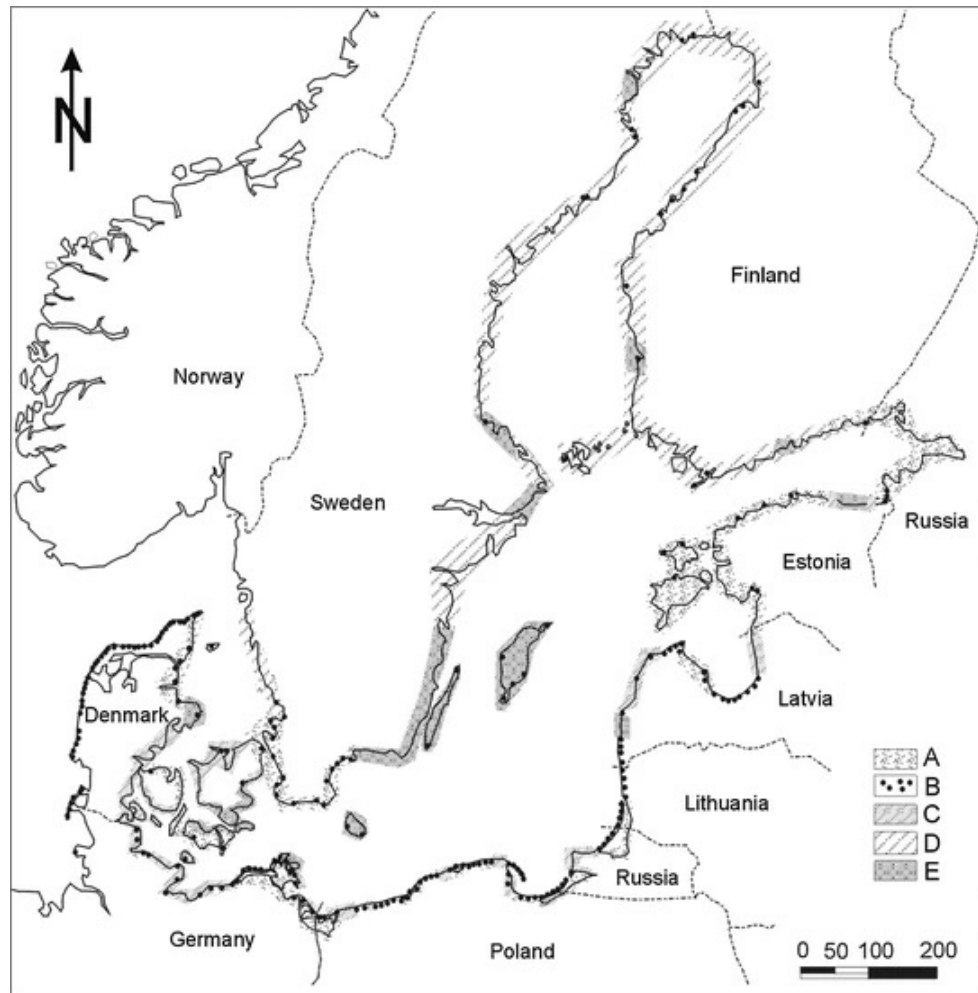
### **Environmental heterogeneity in coastal habitats**

One of the most fundamental features of environmental conditions in ecosystems is represented by their heterogeneity. Environmental heterogeneity is a concept that characterizes the degree of non-uniformity of environmental factors both in space (spatial heterogeneity) and time (temporal heterogeneity) (Dronova 2017). Understanding and practical definition of environmental heterogeneity in nature is made very difficult by its manifestation at different time and space scales. The problem of environmental heterogeneity has received a scientific attention from different points of view, including its role in plant adaptations to the environment (Levinsh 2006; Levinsh 2014), importance for ecosystem services (Dronova 2017), and participation in shaping plant diversity (Daleo et al. 2023). While coastal habitats are often characterized as “extreme” or “stressful”, it is becoming evident that mainly the very large differences in contrasting environmental factors in a coastal ecosystem are what make up this specific environment (Levinsh 2006). Thus, heterogeneity is a characteristic feature of the coast, and there is no doubt that it significantly affects the distribution and physiological status of plants.

Coastal environmental heterogeneity is largely determined by the heterogeneity in geomorphological processes. The role of climatic factors in coastal dynamics of the Baltic Sea has been analyzed, and it was concluded that changes in sea level, long-shore currents and storm surges are among the main factors leading to geomorphological changes (Łabuz 2015). On the other hand, differences in coastal types cause a different level of consequences in the changes of the coastal landscape under the influence of the dominant climate factors. Coastal types in the Baltic Sea region are shown in Fig. 1 (Łabuz 2015).

A complete analysis of differences in environmental factors in coastal habitats is out of the scope of the present paper. Instead, a general overview of more coastal-specific constraints related to particular situation of the Baltic Sea will be given here. More detailed information can be found in specialized literature (Lee, Ignaciuk 1985; Levinsh 2006).

Water availability in soil is one of major limiting factors for distribution of plants. Coastal habitats exhibit extremely high temporal and spatial heterogeneity in respect to soil water content (van der Maarel 1981). The control of soil moisture conditions during the growing season is dominated by irregular inundation with seawater or inundation with fresh water during significant periods of



**Fig. 1.** The prevalent coastal types in the Baltic Sea region. A, soft moraine cliffs; B, sandy barriers and sandy dunes; C, rocky cliffs; D, skerries; E, low coast, meadows, organic/wetlands. The map is reproduced from Łabuz 2015 (CC BY).

rain. However, both sea-related and land-related processes are responsible for formation of the two characteristic types of habitats in respect to moisture conditions, sand dunes and salt marshes. Sandy soils on dunes are characterized by high porosity and poor water-holding capacity together with low organic matter content. In high temperature conditions when sand surface heats up to 45 – 50 °C, high evaporation rates lead to constant water shortage near the soil surface (Ritsema, Dekker 1994). With increase of organic matter, the ability to retain water and mineral nutrients rises. Salt marshes as wetlands are characterized by high overall soil saturation (waterlogging) and periodic rise of water level above soil surface (flooding or submergence). Due to waterlogging, soil oxygen deficiency creates permanently or periodically anaerobic soil conditions together with low redox potential, accumulation of toxic soluble organic compounds, fluctuating soil salinity and other problems that also need specific adaptative responses to cope with them (Irfan et al. 2010). Flooding completely eliminates gas exchange between the soil and the atmosphere.

In contrast to the rather widespread idea that the characteristic surface seawater gradient across the Baltic

Sea also determines the salinity of coastal soil and, consequently, the decrease of salt-tolerant plant species in the west-east direction and, in particular, in the Gulf of Finland and the Gulf of Bothnia, it is evident that the specific salinity of the soil at a particular site depends on the interaction of various factors (Hulisz et al. 2016). Thus, salt patches of soil can develop as a result of topsoil drying or uplift of fossil salt deposits, further affected by irregular seawater flooding or freshwater impact due to heavy rains. These interactions result in high temporal and spatial heterogeneity of soil salinity, as shown in numerous studies (Samsonov, Ievinsh 2018; Ievinsh et al. 2020d; Ievinsh et al. 2021).

Coastal marshes are subjected to periodic flooding with sea water (Colmer, Flowers 2008). In tidal salt marshes, flooding with sea water occurs on daily basis, and in non-tidal marshes this event has a more or less seasonal character. As a result, the soil pore water salinity level may become higher or lower than that of seawater, besides sea-affected flooding depending also on complex action of both evaporation and precipitation (Barnett-Lennard 2003). Rainwater inputs effectively dilute salt concentration in

soils of non-tidal marshes. On the other hand, evaporation can cause pore water salinity to become higher than that of seawater.

Salt spray with wind-driven particles of sea water is generally thought to be a main factor causing elimination of typical inland plants from coastal regions, therefore contributing to establishment of a specific species community of halophytic plants (Du, Hesp 2020). However, sea coasts are not equally intensively affected by wind-driven salt spray. There are places in temperate regions that are affected by salt spray only during the autumn-winter period when there is no actively functioning herbaceous vegetation. Even in coastal sites with intense wind-driven salt spray throughout the vegetation season, dominating inland species as far as 3 km from the shore are significantly affected by the factor, in some places even at a higher intensity than plants on foredunes (Yura, Ogura 2006).

Geomorphological processes on the sea coast greatly affect plants growing on shore and coastal dunes. One of most important effects of these processes on vegetation is related to changes of sand level (Gilbert, Ripley 2010). Net change of sand level on the sea coast is extremely variable. It depends mostly on the amount of sand deposited on the seashore by waves as well as on various environmental factors. The subsequent wind-driven sand transport towards coasts represents a major environmental force on coastal dunes. Due to differences in microenvironmental conditions plant burial by sand in a community is not uniform (Owen et al. 2004). Strong sand accretion in a particular place of a dune system may be concomitant by neighboring sand erosion. Therefore, plants on mobile or semi-mobile sand dunes must possess adaptations to withstand both sand accretion and erosion.

Mineral nutrient heterogeneity is another characteristic of coastal soils in the Baltic Region. While there are some global patterns in wetland soil characteristics in the Baltic Sea region (Hulisz et al. 2016), the degree of spatial heterogeneity of plant-available mineral nutrients in different coastal habitats, both dunes and salt-affected grasslands, is extremely high (Karlsons et al. 2011; Andersone-Ozola et al. 2017; Karlsons et al. 2017; Ievinsh et al. 2020d). In seawater-affected habitats, high correlation occurs between concentration of various plant mineral nutrients, indicating the importance of the salinity and water regime in the regulation of the availability of minerals. However, as based on these studies, it seems that coastal plants have developed efficient adaptive mechanisms to cope with mineral nutrient heterogeneity.

There is no doubt that other environmental factors are important in shaping characteristic vegetation in coastal habitats, as daily and periodically changing high temperature and high light intensity, but also less frequent changes with both potentially deleterious and growth-improving effects on vegetation, such as deposition of algal mats (Ievinsh 2022).

## Systems of coastal plant classification

### *Coastal specificity*

Empirical observations show that there are certain plant species whose individuals are found only in the coastal ecosystem. In some cases, species with a wider distribution in central Europe, in the northern part of their range are exclusively associated with coastal habitats. The question of coastal-specific plant species has never really been addressed from a scientific point of view. Few researchers in the Baltic Sea region have addressed this issue. For Denmark, a list of plants found in salt-affected coastal meadows according to specificity of their association with this habitat was made (Vestegaard 2000). Three groups were designated: (i) species that exclusively or predominantly occur in hydrolittoral or geolittoral (salt-affected) zones of salt meadows; (ii) freshwater species that regularly appear in the hydrolittoral or geolittoral zone of salt meadows, possibly, as specific subspecies; and (iii) species that are present in the epilittoral (salt unaffected) part of salt meadows. Interestingly, several of these species were listed both in group I and II, as *Armeria maritima*, *Ononis spinosa*, *Plantago coronopus*, and *Plantago maritima*. Looking at this list from the point of view of ecophysiology, one might think that coastal specificity is related to salt tolerance, since all plants in the first group are recognized as halophytes. It is therefore not surprising that many of the salt marsh species that are coastal specific in the Baltic region are also found in inland salt marshes in Central Europe (Piernik 2012) or along roadsides in Western and Central Europe as a response to increased salinity due to winter anti-icing treatments (Gerstberger 2001; Fekete et al. 2022).

No comprehensive analysis for coastal specificity has been performed for beach or dune species, but several coastal-specific species from these habitats are represented by *Cakile maritima*, *Calamagrostis arenaria*, *Crambe maritima*, *Honckenya peploides*, and *Leymus arenarius*. However, in a study of ecological indicators and trait values for Swedish plants, occurrence of each species in broadly defined vegetation types has been evaluated, and two particular types roughly cover coastal habitats: (i) sandy/stony/rocky sea shores and (ii) sea shore meadows (Tyler 2021). As a numeric value between 0 and 10 is given for each species indicating incidence in the total Swedish population for the particular vegetation type, it appears that the species with a total summed value of 10 for both of these types can be considered coastal-specific. Among 721 species, 66 indeed corresponded to this criterion.

It could be assumed that beach, dune and wetland specialist species can be allocated as adapted to a prevalent set of environmental conditions. However, these conditions have not been fully evaluated experimentally from the point of view of the species optimal conditions. It is possible that certain species really reach their optimum only under



the influence of a specific factor, such as euhalophytes in the case of increased salt or dune-forming species in the case of sand accretion. Alternatively, considering the specific environmental conditions of the coast, one might think that the appearance of a specific species is related to both the relatively high tolerance to the specific factor (salinity, accretion with sand, lack of minerals) and their weak competitive ability in “normal” conditions on the background of high availability of resources.

In the event that a generally distributed species appears in coastal habitats with very specific environmental conditions (salinity, sand inundation), one might think that the coastal populations are represented by plants that are genetically different from the rest of the population. Thus, existence of coastal-specific ecotypes or even subspecies can be assumed and has been shown for a number of species, including *Agrostis stolonifera* (Tiku, Snaydon 1971; Kik 1989) and *Festuca rubra* (Rozema et al. 1978; Rubinigg et al. 2002). However, one might reasonably suspect that the evaluation of potential ecotypes is influenced by the experimental approaches used. In some studies, existence of coastal and inland ecotypes of a species has been postulated as based on anatomical and morphological analysis of field-collected material, as for *Adenophora triphylla* (Ohga et al. 2013). However, there is a reason to believe that the differences found were due to phenotypic plasticity of the species in different environmental conditions. Another approach is to use transplants of putative ecotypes from different habitats for cultivation in controlled conditions, as for coastal perennial and inland annual ecotypes of *Mimulus guttatus* (Lowry et al. 2008). In this case, it is highly likely that variation in “physiological memory” between plants initially grown in different conditions resulted in different physiological responses.

Existence of ecotypes differing in tolerance to seawater flooding of *Trifolium repens* plants from saline grassland at different points along a salinity gradient was postulated (White et al. 2014). However, in this study, large rooted shoot fragments collected in the field were used as stock plants for obtaining stolons for establishment of experimental plants. Therefore, effects of physiological or epigenetic memory cannot be excluded. In another experiment, rhizome fragments from coastal and inland populations of *Calystegia sepium* were used for establishment of stock plants further cultivated for several months in controlled conditions, and later experimental plants were established from rooted stolon fragments (Jākobsone, Ievinsh 2022). As a result, significant differences in physiological responses to salinity were found, most likely associated with genetical diversity. A more appropriate approach seems to be using seed material of putative ecotypic populations for establishment experiments in the same conditions (controlled study or common garden experiment), but existence of epigenetic effects cannot be ruled out even in this case. Using seed material, three putative ecotypes (coastal short, coastal tall, and inland) were found for *Setaria viridis* (Itoh 2021). It is

evident that this type of experiments needs to be performed in connection with molecular genetic analysis, as was carried out for coastal and inland populations of *Trifolium fragiferum* (Andersone-Ozola et al. 2021; Jēkabsone et al. 2022; Ruņģis et al. 2023).

### Taxonomy

Taxonomical hierarchy of plant classification is a phylogenetically-oriented system emphasizing species relatedness as based on their common evolutionary history. While for centuries taxonomical classification was based predominantly on morphological characteristics, recent developments in molecular genetic analysis have resulted in significant changes in plant systematics. Although species have similar characteristics within the boundaries of higher taxa, it is clear that the diversity of different morphological and physiological characters is very large even within genera. Therefore, taxonomic affiliation alone does not allow us to judge the characteristics that are essential for the adaptation of a species to specific environmental conditions. On the other hand, the taxonomic system at the level of plant families and genera is convenient to use, as it is easy to interpret and apply even without specialized knowledge. For this reason, it can serve as a basis for describing the diversity of species, further focusing on the description of adaptively important traits and a more detailed classification by groups of traits.

On the applied side, species serve as basic taxonomic units in various other classification systems, most notably, vegetation analysis and habitat-related plant distribution. However, due to rather specific characteristics of several taxonomic groups, some broad classifications have been traditionally used. Thus, it is reasonable to distinguish grasses (species from Poaceae family), other monocotyledonous species, legumes (species from Fabaceae family), and non-legume dicotyledonous species.

### Geographical distribution

Geographical distribution of plant species can be analyzed from a perspective of species range relative to biogeographic regions. Regarding the distribution of species of the Baltic Sea coast, it would be rational to take into account the existence of the corresponding biogeographical regions of Europe defined by the European Environment Agency (Fig. 2). It is evident that the central part of the Baltic Sea is included in the hemiboreal region, with the northern part in the boreal region and the southern part in the nemoral-continental region. However, when analyzing geographical distribution of habitats for a particular territory or region, coastal habitats can be excluded from a particular biogeographical region (domain) where that territory is located, and a specific “coastal domain” can be designated, as reported for Belgium (Hermy 1993).

When inspecting the occurrence of various coastal species on the Baltic Sea coast (distribution data from <https://www.gbif.org>, last assessed 2024.06.25.), one can

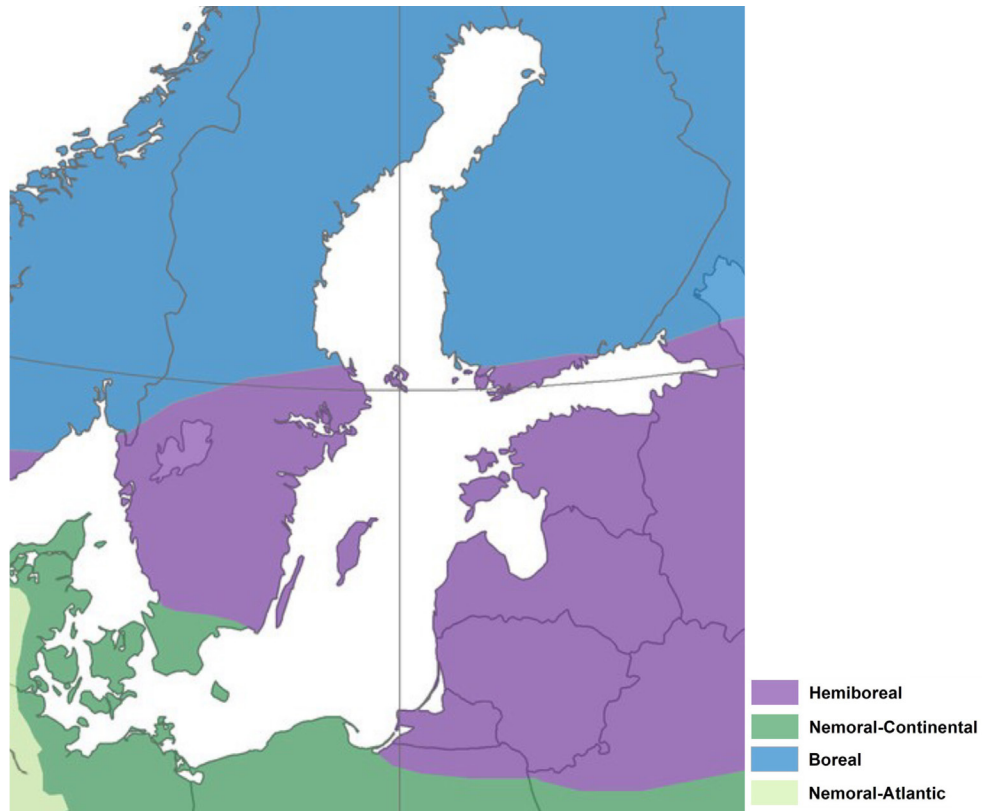


Fig. 2. Biogeographical regions of the Baltic Sea. Modified from Preislerová et al. 2024 (CC BY).

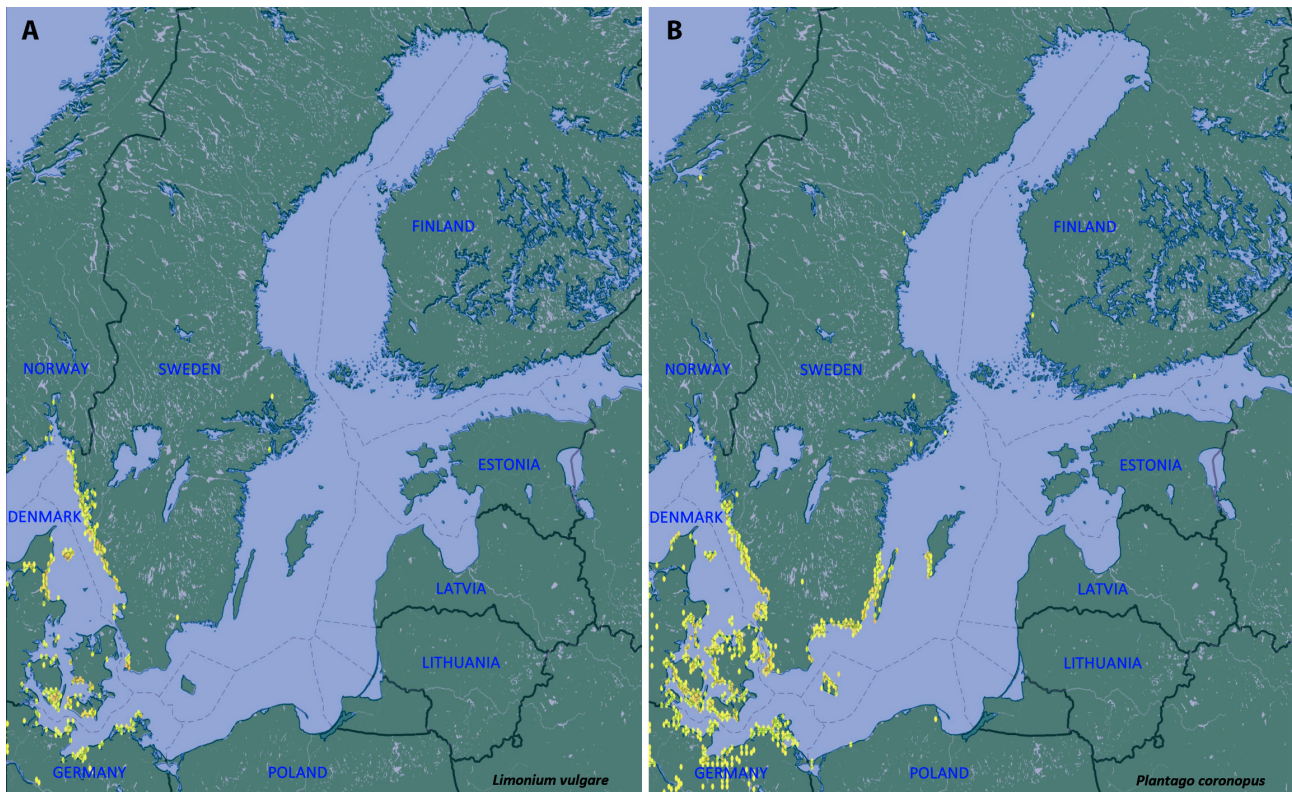


Fig. 3. Examples of typical distribution patterns for several coastal plant species of the Baltic Sea. A, *Limonium vulgare*; B, *Plantago coronopus*; C, *Lotus maritimus*; D, *Lathyrus japonicus*; E, *Puccinellia capillaris*; F, *Deschampsia bottnica*. Distribution data are from <https://www.gbif.org>.

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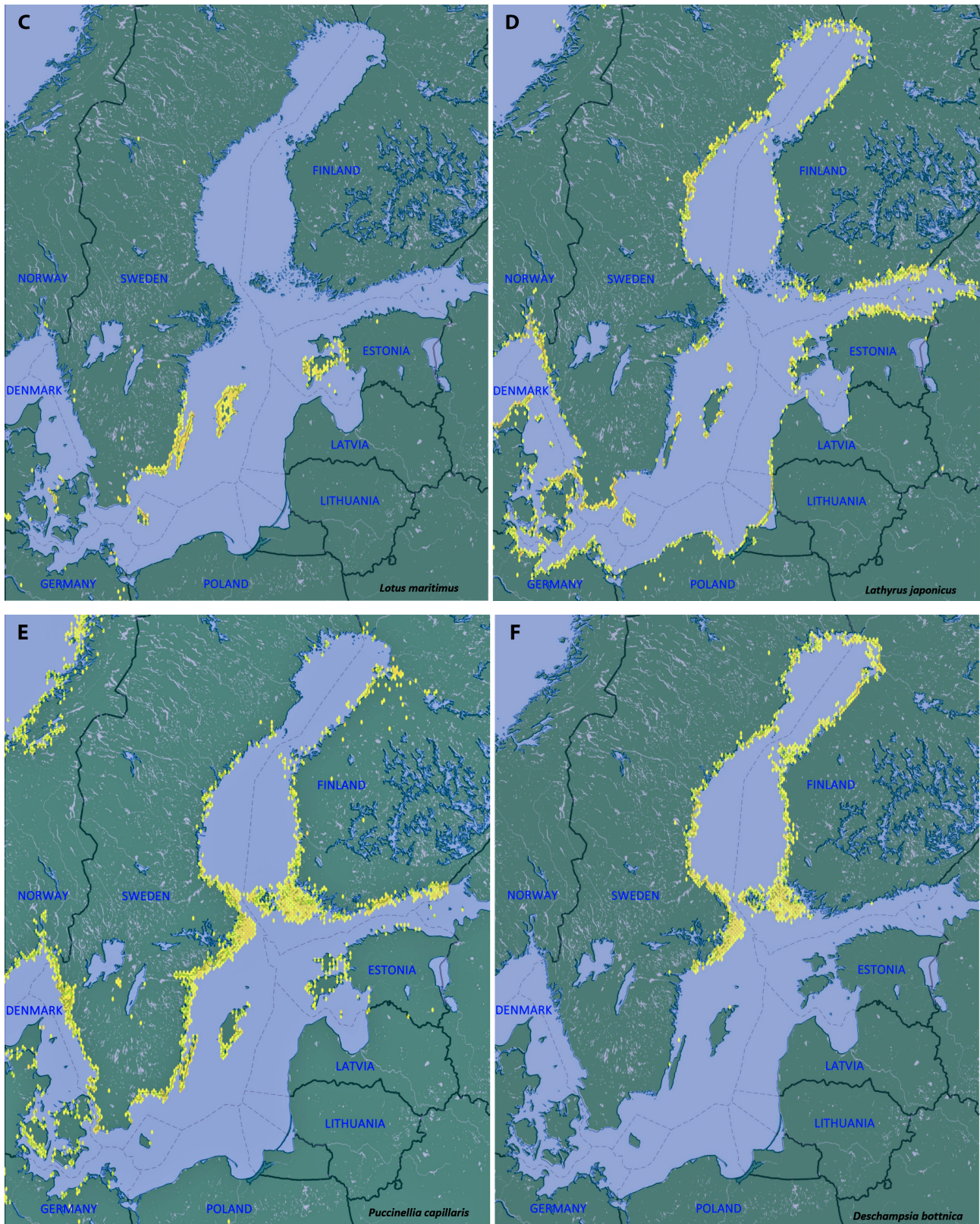


Fig. 3. Continued

see various typical examples of distribution in relation to geographical location. Thus, the salt marsh species *Limonium vulgare* that is typical for Atlantic parts of Europe occurs predominantly on coasts of Kattegat, Danish Straits

and Germany (Fig. 2A), while typical disturbed coastal ground species *Plantago coronopus* can be found also on the island of Bornholm, in southern Sweden and also in southern Gotland (Fig. 2B). The legume species *Lotus*

*maritimus* is distributed only in a relatively narrow central Baltic region from Bornholm to the Estonian archipelago (Fig. 2C). Another legume species characteristic of embryonic dunes and gravel beaches, *Lathyrus japonicus*, is evenly distributed along the entire coast of the Baltic Sea (Fig. 2D). The coastal-specific grass species, *Puccinellia capillaris*, is present predominantly in the northern part of the Baltic Sea (Fig. 3E), but another grass species, *Deschampsia bottnica*, is specifically located only starting from the Stockholm archipelago in the west and Finnish archipelago in the east, and distributed throughout the coasts of the Bothnian Sea and the Bothnian Bay (Fig. 3F). There is no doubt that, besides climatic factors, also availability of appropriate habitats can affect distribution of particular species in the coastal region.

Possible effect of geographical factors on establishment of floristic gradients in shore meadows of the Baltic Sea has been analyzed (Tyler 1969). A pronounced gradient of surface water, presence of seasonal water level fluctuations together with irregular fluctuations caused by winds and changes in air pressure instead of diurnal tidal movements, isostatic land upheaval in Fennoscandia and subsidence in the southern part, as well as climate differences caused by south-north extension are analyzed as the main causes for existence of differences in geographical distribution of coastal species in the Baltic Sea region. Ten standard regional areas have been chosen for comparative analysis (six from Sweden, two from Finland, one from Germany and one from Estonia), and existence of regional-specific species composition has been established.

By combining species distribution data with results of molecular genetic studies, it is possible to perform phylogeographical analysis establishing the link between evolution and dispersal history of the species. Several comparative European scale phylogeographical studies of coastal plant species have been performed (Clausing et al. 2000; Kadereit et al. 2005; Brock et al. 2007; Kadereit, Westberg 2007; Lambracht et al. 2007; Westberg, Kadereit 2009). It appears that propagule dispersal by sea currents has been the main mechanism that led to postglacial recolonization of the northern coasts by coastal species like *Calystegia soldanella*, *Cakile maritima*, *Eryngium maritimum*, *Halimione portulacoides*, *Salsola kali*, *Suaeda maritima* etc. These results support the view that coastlines represent linear biogeographic systems (Clausing et al. 2000). However, recolonization from inland salt-affected populations might have been possible, as shown for *Triglochin maritima* (Lambracht et al. 2007).

#### *Habitat-related distribution*

In a broader sense of a habitat, plants can be classified as terrestrial, aquatic (hydrophytes or macrophytes), aerial (epiphytes) or lithophytes, or according to typical environmental conditions in their habitats in respect to water content or salinity. Habitat classification system in Europe is based on initiatives of the European Environment

Agency further formally developed by a group of scientists as based on analysis of the European Vegetation Archive (Chytry et al. 2020). According to this system, the following coastal habitats are the targets of the current analysis of plant biodiversity of the Baltic Sea coast: MA232, *Baltic coastal meadow*; N11, *Atlantic, Baltic and Arctic sand beach*; N13, *Atlantic and Baltic shifting coastal dune*; N15, *Atlantic and Baltic coastal dune grassland (grey dune)*; N18, *Atlantic and Baltic coastal Empetrum heath*; N1A, *Atlantic and Baltic coastal dune scrub*; N1D, *Atlantic and Baltic broad-leaves coastal dune forest*; N1F, *Baltic coniferous coastal dune forest*; N1H, *Atlantic and Baltic moist and wet dune slack*; N21, *Atlantic, Baltic and Arctic coastal shingle beach*; N31, *Atlantic and Baltic rocky sea cliff and shore*; and N34, *Atlantic and Baltic soft sea cliff*. In the real situation, scientific research often allows various deviations from the existing system, which will be further analyzed.

Often, the physical boundary between sea and land is difficult to determine, because both the water level in the sea and the influence of rainwater create a spatially dynamic and temporally heterogeneous effect. Therefore, there may be hard-to-define transition zones that can be attributed to both marine and terrestrial types. For example, from the point of view of habitat classification, salt marshes are in principle classified as marine habitats, even though typical terrestrial plant species mostly grow in these wetlands. In the context of the Baltic Sea, the situation with the habitat Baltic coastal meadows is rather paradoxical, which due to certain similarities (evidently, in connection with possible inundation with sea water and increased soil moisture) is included in the group of marine habitats. Due to these classification peculiarities, in Nordic countries, all different forms of coastal salt marshes (including “salt meadows”, “coastal meadows”, “tidal marshes” and “reed belts”) are included in the system of Blue Carbon habitats (Krause-Jensen et al. 2022).

Definition of particular coastal habitats can differ in complexity. Coastal topography, presence of plants, land use, water table, type of sediment are among the most important determinants in the definition. Fragmented and non-consistent nature of coastal habitat classification has been admitted, which require significant improvements to better match their real diversity (Vehmaa et al. 2024). Most importantly, besides characterization of vegetation, habitat structure and function need to be taken into the account. The coastal marsh habitat classification system has been recently revised in the Nordic region, including both the Baltic Sea as well as Atlantic coast habitats of Norway (Vehmaa et al. 2024). As a result, a gap in the European habitat classification system was found in respect to the Baltic Sea coastal marshes. It was suggested that the only one habitat type defined for coastal marshes in the Baltic Sea region is MA232 *Baltic Sea coastal meadow*, in reality including large variety of habitat types. While the absence of tidal influence together with relatively low but variable salinity result in a unique floristic characteristics



of this habitat type, differences in environmental and geomorphological features between different regions of the Baltic Sea result in existence of recognizable subtypes of coastal marsh habitats.

Therefore, in practice, separate hierarchical classification systems of coastal wetland vegetation in the Baltic region are often created. Thus, in a study in Estonia, the distinction was made between grasslands and open vegetation, in further leading to seven main types of wetland vegetation, e.g. open pioneer, club-rush swamp, reed swamp, lower shore grassland, upper shore grassland, tall grassland, and scrub and developing woodland (Burnside et al. 2007).

In spite of the accepted system of habitat classification in Europe, including also coastal habitats, in scientific studies very often various traditional classification systems are used. Thus, in the context of the Baltic Sea, in a series of studies, the term “salt grasslands” has been used, defining them as “grassland systems in the geolittoral of the Baltic Sea region”. Another term, “shore meadows” has been relatively widely used in studies performed in Finland, Sweden, and Estonia (Jutla 1999). Similar to that, traditional terms have been used in description of dune vegetation, often using the terms “yellow dunes”, “dune grassland of grey dunes”, and “shrub/woodland of brown dunes” (Peyrat, Fichtner 2011).

Vegetation zonation in coastal ecosystems is a well-visible phenomenon and it is known to be related to existence of pronounced environmental gradients, but a plant-associated functional basis for appearance of typical zonation patterns is poorly understood. It seems to be evident that such patterns reflect important adaptive characteristics of the located species to specific environmental conditions.

Tidal salt marshes have clear zonation created by the tidal regime and visible as differences in vegetation. In the direction from the sea to the land, these zones are open pioneer communities (covered except by the lowest tides), lower marsh (covered by most tides), middle marsh

(covered only by spring tides), upper marsh (covered only by highest spring tides), and transition zone to the adjacent areas (covered only occasionally by storm surges) (Adam 1978; Bertness, Ellison 1987). Thus, regular seawater flooding is the main factor leading to the characteristic vegetation zonation in such marshes. Plant distribution patterns in non-tidal coastal marshes seem to be affected by different combinations of environmental factors. Thus, in Mediterranean coastal marshes, annual flooding events are caused by autumn and winter rains, but increased evapotranspiration in summer results in increased soil salinity (Vélez-Martín et al. 2020).

However, for non-tidal coastal wetlands of the Baltic Sea, another system of vegetation zonation was developed in Scandinavia by Swedish botanist Du Rietz, in principle resembling the one used for tidal wetlands, but caused by less dynamic processes of changes in water level (Fig. 4). Four littoral zones were established based on water level fluctuations and topographical conditions. Starting from the sea, the sublittoral zone completely belongs to marine habitats and is completely submerged even at the lowest water level. Further inland, the hydrolittoral zone is formed, which extends from the sublittoral zone to the mean water level. This zone is frequently submerged and has the highest salinity level. The following geolittoral zone is where characteristic salt marsh vegetation develops, and it is further divided up to high waterline in lower and medium geolittoral zones, and in upper geolittoral that is situated landward of the high waterline and is affected by seawater only during seasonal storms. Finally, the epilittoral zone is never submerged but can be affected by seawater in the form of airborne salt particles. Therefore, even in the epilittoral vegetation, the presence of salt tolerant plants may occur. While the system was developed for coastal wetlands and meadows, it can be used also for more dynamic coasts where formation of shingle and sand beaches occur.

Taking into account the obvious and pronounced

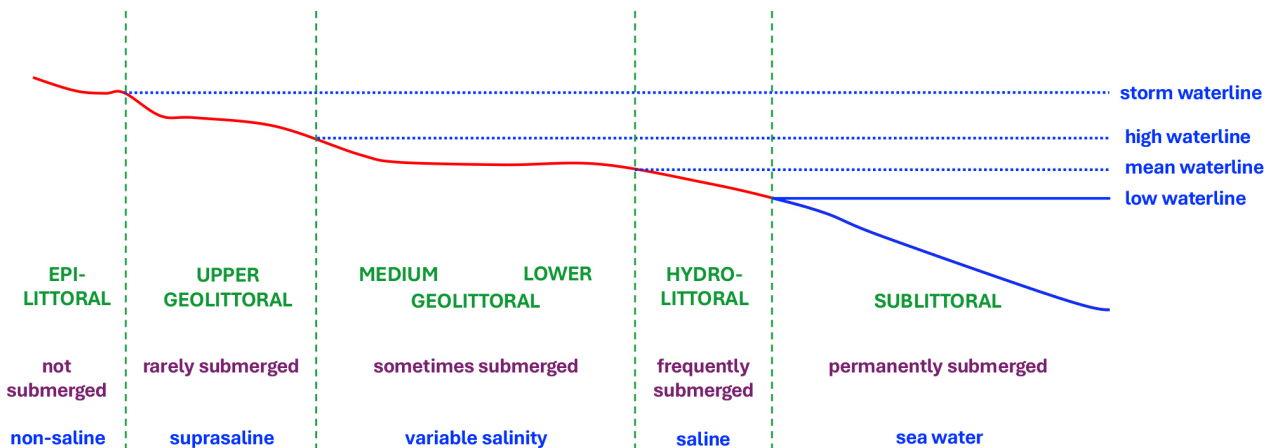


Fig. 4. Traditional zonation for non-tidal coastal shores used in Scandinavia emphasizing differences in submergence and salinity due to changes in waterline.

heterogeneity of environmental conditions, which is especially emphasized in relation to the coastal situation, it is understandable that it is almost impossible to describe a certain set of conditions in places where individuals of a species grow. Such an approach can be facilitated to some extent by proper choice of a spatial scale, by finding certain points on a gradient of a prevailing factor, such as are formed along the sea coast. For example, on sand-accumulating shores, one can see the following gradient in terms of sand accretion intensity, which decreases landward. It would be logical to assume that in areas of intense sand accumulation, species with high burial resistance will mostly be found.

In tide-affected marshes the possibility of periodic inundation with seawater varies with distance from the coast and other factors, and forms certain belts of plants in relation to their potential salt and flooding tolerance. In non-tidal wetland systems, as the ones on the shores of the Baltic Sea, plant submergence and soil waterlogging depend on changes in sea water level and wind activity. Therefore, while clear spatial vegetation patterns can be evident, these usually are fragmented and on a low scale, with low and fluctuating number of individuals of each species present.

The concept of “dominant” and “indicator” plant species has been often used in practical studies related to changes in vegetation in coastal habitats, as due to grazing abandonment (Burnside et al. 2007). Usually, these species are selected within each specific study. However, under the EUNIS habitat classification system, “diagnostic species”, “constant species”, and “dominant species” have been described for each habitat type (Chytrý et al. 2020). According to the concept, individuals of a diagnostic species occur mostly in a particular habitat, and are rare or absent in other habitats. Although they may be absent at many sites. Constant species occur frequently in a particular habitat but can be frequent also in other habitats. Threshold occurrence frequency of 10% was used as a criterion for inclusion for constant species. Individuals of a dominant species form a substantial cover in a particular habitat creating its floristic recognition. Cover above 25% in at least 5% vegetation plots was used as a criterion for inclusion as dominant species.

### *Species associations*

Plant species associations form a basis for one of the most intensively used plant classification systems, vegetation classification, defining different vegetation types or plant communities. A typical example of a hierarchical vegetation classification system is well represented by the European system based on phytosociological principles developed by Braun-Blanquet. Defining diagnostic species is one of the basic approaches in the analysis of societies, giving the opportunity to practically create a hierarchical system. The current European vegetation classification system of vascular plants (EuroVegChecklist1) includes 109 classes, 300 orders and 1108 species alliances (Mucina et al. 2016). However, further classification of vegetation

classes does not follow a clear hierarchical system, being formed by three types of classes: classes corresponding to vegetation zonality according to biomes (arctic, boreal, temperate, Mediterranean), intrazonal classes formed within the respective zones, and azonal classes grouped according to the main ecological features (alluvial forests and scrub, swamp forests and scrub, vegetation of coastal cliffs and dunes, vegetation of rock crevices and scree, vegetation of arctic-alpine vegetation of snow rich habitats etc.). However, within the azonal group of classes, further grouping is by geographic location.

Vegetation classification systems in Europe that apply to the coast are regularly revised. Recently, the most proposed changes are in the dune vegetation. A revision on vegetation of shifting and stable coastal dune vegetation has been proposed (Marcenò et al. 2018; Marcenò et al. 2024). Thus, 18 alliances have been defined for Atlantic and Baltic coasts of Europe, the Mediterranean Basin and the Black Sea region as based on biogeographic and macroclimatic differences between these regions, as well as due to ecological differences between shifting and stable dunes (Marcenò et al. 2018). Vegetation associations in Atlantic-Baltic dunes made a common group with six clusters each under well-differentiated groups of shifting and stable dunes. Two major classes were established: *Koelerio-Corynephoretea canescentis* for stable dunes and *Honckenyo-Elymetea arenarii* for shifting dunes. However, this classification by definition should not include associated beach and wetland vegetation, but several species with diagnostic value for dunes appear also in non-dune habitats. Thus, for example, *Crambe maritima*, *Honckenya peploides*, and *Leymus arenarius*, which are embryonic dune species, often occur on rocky and pebbly beaches on the Baltic Sea coast.

Classical studies on classification of tidal saltmarsh vegetation have been performed in Great Britain (Adam 1978; Adam 1981) and the Netherlands (Beeftink 1985). Vegetation classification of salt-affected grasslands of the Baltic Sea also has been reconsidered relatively recently (Pätsch et al. 2019). As a result, 33 vegetation types have been described, with the main source of floristic variation caused by regional phytogeographic patterns. Among environmental factors, it was suggested that soil salinity together with moisture are key differentiators between the vegetation types, but availability of minerals also matters.

On the other hand, vegetation types could be most confusing for a non-specialist, as functional aspects underlying this type of association are poorly understood, being based on plant physical coexistence without any actual information on physiological interaction between individuals of different species on the background of spatial and temporal environmental heterogeneity. High variation in vegetation types, resulting in description of many subtypes, is related to differences in both microenvironmental and geographical factors, including microbiological functional diversity (Ievinsh 2022).

Description of plant associations on coastal habitats is





**Fig. 5.** Examples of distribution of solitary individuals of plant species in coastal habitats of the Baltic Sea. A, *Vicia cracca* on island of Kihnu, Estonia; B, *Bolboschoenus maritimus* together with *Ranunculus sceleratus* in Melnsils, Latvia; C, *Tripolium pannonicum* together with *Plantago maritima* on island of Bornholm, Denmark; D, *Phalaris arundinaceae* on island of Öland, Sweden; E, *Geranium robertianum* on island of Färö, Sweden; F, *Barbarea vulgaris* together with *Crambe maritima* on island of Gotland, Sweden.

not always possible. Coastal areas are very common where only sparsely distributed individuals of one or several species are present and such can be found on either sandy, rocky and pebbly coasts, as well as in mud belts (Fig. 5). Usually, sparse presence of separate individuals on “bare ground” is treated as an indication of “pioneer vegetation”. However, due to intense action of aeolian and littoral processes on active sandy coasts, any presence of vegetation is only temporary and mostly depends on deposited drift line organic matter.

Vegetation changes over time were first observed and described in the coastal dune ecosystem. It is usually thought that pronounced zonation of plants and their habitats in sandy coasts directly reflects vegetation dynamics. In the boreo-nemoral region of Europe, the climax community is represented by forest. Therefore, the majority of grasslands are management-dependent, but open coastal areas are formed due to persistence of factors unfavorable for tree development, such as sand accretion, flooding with seawater, absence of significant soil layer on rocks etc. However, it is also suggested that coastal grassland habitats on the Baltic coasts have developed as the result of hay making and cattle grazing, protecting them from development of reed beds and woodlands (Jutla 2001; Ingerpuu, Sarv 2015).

It seems that the existing system of vegetation

classification is poorly suited for analysis of functional aspects in coastal ecosystems. Historically, there have been several attempts to classify natural vegetation based on prevalent physiological mechanisms of plant adaptation. Thus, Kuiper (1978) distinguished three types of vegetation. Type 1 vegetation is limited by environmental factor(s) resulting in low species diversity. Examples include salt marsh, peat bog and dry heath. Type 2 vegetation represents a situation where key environmental factor(s) promote high rate of biomass accumulation. Examples include eutrophic vegetation on lake banks and nutrient-rich meadows. Type 3 vegetation is the most species-diverse with wide variety of life forms, but it is of relatively low productivity as environmental conditions are highly heterogeneous.

There have been recent attempts for inclusion of ecological indicator values into the vegetation classification system in Europe. Importantly, one of the goals for this analysis was “to help understand this classification to non-specialists” (Preislerová et al. 2023). Within this analysis, in comparison to widely used indicator systems for plant individuals of the species based on the one of Ellenberg, ecological indicators used for vegetation classification purposes have less gradations (categories) of particular indices. For example, soil moisture has five categories, soil pH and salinity only three, and nutrient status four (Preislerová et al. 2023). In addition to ecological indicators,

also other types of information have been included, as plant life forms, phenological optima, biogeographical regions, azonality-related types etc.

### *Ecological indicators*

An attempt has been made to link the occurrence of plants in a specific place with the complex of environmental conditions through the theory of ecological niches. The so-called fundamental niche reflects physiological optima for individual environmental factors of the given species, resulting in a potential set of conditions where the species can exist. In contrast, the realized niche represents ecological optimum of incidence of individuals of the species, where, apart from a set of environmental factors, the existence of an individual is influenced by interactions with other groups of organisms and persisting various plant species (Russell et al. 1985). This concept makes it possible to explain why the specific species occurs in nature outside the optimum intensity of a certain environmental factor and also why the intensity of biomass accumulation and reproduction in natural conditions differ from those that can be observed in experimentally defined “optimal conditions”. Also, the terms “physiological optimum” and “ecological optimum” have been used to describe fundamental vs. realized niche (Funabashi 2016).

Nevertheless, in practice, the realized niche can be accessed through the use of the system of ecological indicators. The establishment of such a system is mainly associated with work of Ellenberg for Central Europe (Ellenberg et al. 1992) and further adapted to different geographical regions and widely used in vegetation science. Among them, salt content indicator value is one of the most important in the context of coastal plant ecophysiology. Although indicator values are primarily used to describe the requirements of the species, they are more often used as surrogates for indirect characterization of environmental variables as based on species composition of associated vegetation (Tichý et al. 2023). While, in the context of the present paper, it is intended to use ecological indicator values for characterization of ecological optimum conditions for particular species.

Attempts have been made to relate ecological indicators to morphological or ecophysiological traits, essentially trying to correlate ecological and physiological optima through particular functional plant characteristics. For example, it was intended to find such characteristics (aka determinants) corresponding to values for a number of ecological indicators (soil pH, soil moisture, nitrogen/nutrient availability, light, temperature, and continentality) (Bartelheimer, Poschold 2016). The largest number of determinants ( $n = 16$ ) were found for nitrogen/nutrient values, followed by these for soil pH ( $n = 11$ ). However, several determinants were found to be rather unspecific. Thus, relative growth rate, specific leaf area and leaf area ratio correlated with four ecological indicator values (nitrogen/nutrients, soil moisture, soil pH, light), which

probably reflects adaptive adaptation of plant growth rate and morphology to adverse conditions.

In the Baltic Sea region, a system of ecological indicators has been established for the flora of Sweden (Tyler et al. 2021). This system is especially useful for the needs of the present study, as it covers a large part of the coast of the Baltic Sea, and, most important, includes also information on plant ecological and vegetation traits relevant for analysis of functional properties of plants and their associations. Thus, in addition to typical indicators of soil edaphic factors (moisture, soil pH, nitrogen, phosphorus, salinity) and the main environmental determinants (temperature, light), also trait values important for biotic interactions (biodiversity relevance, nectar production, pollinator dependence, nitrogen fixation, mycorrhiza, carnivory, parasitism), reproduction (phenology, seed dormancy, seed bank, seed dispersal), photosynthetic pathway, tolerance to grazing/mowing and soil disturbance, as well as quantitatively evaluated possible association of the species with different vegetation types. The only obvious shortcoming of the system could be the absence of information on plant clonality characteristics.

### *Life forms, growth forms and functional strategies*

Plant life forms were introduced by Raunkiaer, based on main morphological characteristics as related to survival in unfavorable periods specifically regarding the preservation of the apical meristem, and further revised several times (Du Rietz 1931; Dansereau 1950; Ellenberg, Mueller-Dombois 1965; Whittaker 1975; Halloy 1990). The system partially includes habitat-related information, allowing to distinguish between terrestrial and aquatic plants. Life forms have been broadly used to obtain quantifiable data regarding plant diversity and solving various ecological problems. This classification system is also used in coastal plant research. Efforts to further improve this system have resulted in classification of plant functional types, which will be discussed below. Growth form is another morphology-based plant classification system that uses canopy structure and height as the main determinants, but also some ecological information is included, as separating submerged and floating aquatic plants, as well as epiphytes and stem parasites (Box 1996; Ewel, Bigelow 1996; Cornelissen et al. 2001). One major problem with these two classification systems is that they do not include the aspect of plant clonality. It is only relatively recently that clonal plants have been recognized as having a very important role in natural ecosystems (Brooker 2017; Herben, Klimešová 2020), including salt-affected coastal habitats (Ievinsh 2023).

A concept of functional types arose from studies performing comparison of plant characteristics obtained in laboratory experiments with the distribution of these plants in different habitats with the aim to identify major ecological factors leading to patterns of trait variation (Grime 2014). These studies led to establishment of the theory of



primary functional types of plants, also known as the CSR (competitive/stress-tolerant/ruderal) theory (Grime 1974). It needs to be emphasized that the CSR theory operates at the population level and cannot be directly attributed to the functions of individual plants, as is often mistakenly done. The CSR system uses two main groups of environmental factors designated as “stress” and “disturbance”. Stress-related factors are those leading to growth suppression by some environmental variables, such as suboptimal water, light and mineral nutrient availability. Disturbance results in biomass destruction of established plants and can result from anthropogenic and biotic factors as well as due to “extreme climatic events” (erosion, fire, drought, frosts, wind etc.). By quantification of total intensities of stress and disturbance, three possible sets of environmental conditions and characteristic plant strategies are defined, e.g. competitiveness (C) in conditions of low disturbance and low stress, stress tolerance (S) in conditions of high stress and low disturbance, and ruderality (R) in conditions of low stress and high disturbance. Also, intermediate types were recognized, designated as CR, SR, RC, and CSR (Hodgson et al. 1999). For the practical functional type allocation, measurements of only seven predictor variables are necessary, including canopy height (six gradations), dry matter content (as percentage from fresh mass), flowering period (duration in months), start of flowering (six gradations), lateral spread (six gradations), leaf dry weight, and specific leaf area (area per dry mass) (Hodgson et al. 1999).

From a biological point of view, “plant functional traits” mostly represent morphological characteristics only indirectly related to “functions” but showing correlation with intensity values of some environmental factors. These include different leaf traits (size, dry matter content, phenology, lifespan etc.), and other aboveground (stem specific density, twig dry matter content, bark thickness etc.) and belowground (specific root length, diameter of fine roots etc.) traits (Cornelissen et al. 2003). Functional trait theories and classification systems have met serious criticism many times. Most important, the absence of sound mechanistic understanding makes the use of functional types useless, as in climate impact prediction, mainly because “correlation is not causality” (Mason 2014).

#### *Physiological adaptations*

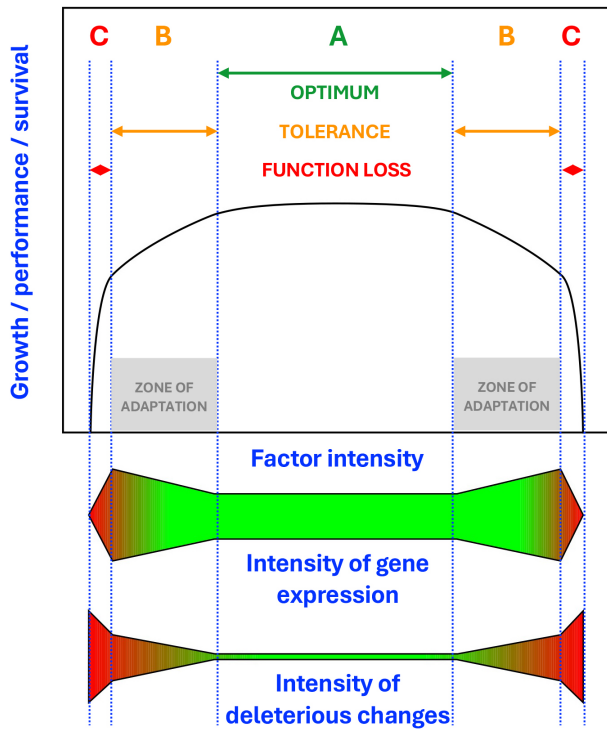
It is usually argued that different suites of correlated plant traits, resulting in defining various functional groups, strategies etc. correlate with adaptive responses to environmental conditions (Dyer et al. 2001). However, such assumptions are usually made in the correlation system of plant presence/set of environmental conditions, without analyzing plant responses directly in the input-response causality system. In contrast to the variability of environmental conditions in time (temporal heterogeneity) and differences in space (spatial heterogeneity) existing in natural conditions, studies with plants are usually

conducted under controlled conditions, strictly limiting the range of factor intensity fluctuations.

The role of environmental heterogeneity in coastal ecosystems has been stressed in the second chapter. Most importantly, plants possess the basic mechanism to adjust the metabolism and physiology of the individual to this heterogeneity. Instead of static morphological characteristics, physiological adaptations represent a mechanism by which evolutionary-acquired genetic adaptation of the species is realized in a life of individual through phenotypic plasticity, allowing for changes in morphological and biochemical characteristics best suited for a particular set of environmental conditions. Differential gene expression due to perception of environmental cues acts as the main mechanism to achieve the “optimum” phenotype of the individual of particular species.

The amount of scientific information accumulated in ecophysiology studies with wild plant species, including those that specifically grow on the seashore, is very large, but there are problems with the generalization of this information. Defining any characteristic coastal conditions (sand accretion, soil erosion, seawater inundation, drought, salt spray) as “stress” or “disturbance”, we lose awareness of the specific adaptations that coastal plants possess towards the specific factor. Apparently, there is a lack of a unified theory about how an individual, as a result of differential gene expression during its development, obtains the best-adapted phenotype for a given set of environmental conditions. Such a theory could explain the process of physiological adaptation, as a result of which, based on phenotypic plasticity, the genetic potential of an individual shows the adaptive capacity acquired in the course of evolution. Some basic concepts useful for development of theory of physiological adaptations have been described previously (Ievinsh 2006; Alonso-Blanco et al. 2009; Nacry et al. 2013; Ievinsh 2014; Köner 2016; Zandalinas et al. 2018; Jia et al. 2021).

Among the important physiological adaptations of coastal plants, adaptations to variable soil salinity, changing moisture levels and flooding, sand accretion, trampling, erosion and other soil disturbances, high intensity of solar radiation and heat, mineral imbalances and the influence of heavy metals should definitely be mentioned (Ievinsh 2006). For each of these types of adaptations, both common inducible characteristics related to general tolerance to adverse conditions (such as protection against endogenous oxidative stress and protection of macromolecules by molecular chaperones) as well as specific properties related to adaptation to a specific factor or group of factors can be analyzed. Detailed analysis of particular adaptation mechanisms of coastal species to characteristic environmental conditions are out of the scope of the present review and will be published elsewhere. Instead, overview of a basic sequence of events during the adaptation process of individual plant will be outlined here as based on physiological optimality of environmental conditions.



**Fig. 6.** Plant performance in respect to changes in intensity of an essential environmental factor (resource or condition) as related to gene expression, intensity of deleterious changes and physiological adaptation. A, zone of optimum; B, zones of tolerance; C, zones of function loss.

While it is usually thought that suboptimal resource availability directly results in growth inhibition, it is evident that a certain level of changes in intensity of environmental factors act as signals first. In respect to the optimality of the particular factor, these changes can be in different directions (decrease or increase) and also different in relation to the values of the optimal intensity of the factor. The signals inducing adaptation to an environmental factor can be changes in the intensity of this same factor, as well as changes in the intensity of another, seasonally variable, factor. For example, growth reduction in salinity occurs when root cell receptors perceive increase in soil salinity (Shabala et al. 2015), but the first phase of cold tolerance in vegetative buds is induced as a result of day length reduction in autumn (Preston, Sandve 2013).

Further physiological events in the plant after sensing environmental changes can be viewed from the perspective of factor optimality by analyzing a classic does/response plot (Fig. 6). In the case of optimum intensity of a particular environmental factor (zone A), plant physiological performance (also growth rate, survival, reproduction etc.) is at its maximum possible level. This is achieved by normally functioning metabolism as a result of basic physiological control mechanisms at a certain level of gene expression. Therefore, the intensity of deleterious structural and metabolic changes is low. When the factor intensity changes to suboptimal (either too low or too high; zones

B), new regulation systems connect to control physiological processes, leading to general increase of gene expression as associated with synthesis of proteins involved in adaptation mechanisms. Therefore, metabolism becomes expanded, but newly acquired adaptation-related characteristics do not allow rapid decline of physiological performance. However, as duration or intensity of environmental changes increase, also intensity of deleterious changes escalates and a plant individual enters the function loss zone (zones C), where intensity of deleterious changes increases in a short time to a level that leads to metabolic disturbances, loss of control capabilities, decreased gene expression, and ultimately changes incompatible with life functions.

*Contribution to ecosystem services*

GENERAL ASPECTS

In addition to the purely dogmatic position that any ecosystem is intrinsically valuable and therefore best preserved in a completely intact form, as well as the completely utilitarian approach that all resources are freely available for profit, there is the possibility of objectively analyzing the benefits offered by ecosystems. This option is also applied to coastal ecosystems and uses the concept of ecosystem services. Most importantly, since the approach is oriented towards decision-making in the choice of management methods, it uses quantifiable indicators. Background information on classification of ecosystem services, their valuation and, particularly, analysis of ecosystem services in a coastal zone are provided by several reviews (Barbier et al. 2011; Barbier 2013; De La Cruz 2021; Lakshmi 2021).

So far, coastal ecosystem services of the Baltic Sea have been analyzed mostly in the marine area, for habitats such as mussel beds, seagrass meadows and macroalgal communities (Heckwolf et al. 2021). On a regional scale, ecosystem services from coastal habitats have been evaluated in Sweden (Rönnbäck et al. 2007). The importance of biodiversity was especially stressed, indicating a present or future potential in making a commercially important discovery for the needs of agricultural and pharmaceutical industries. However, this and similar studies often concentrate on coastal marine habitats instead of looking at terrestrial coastal habitats. As a result, vascular plant diversity has not been much analyzed from a point of providing ecosystem services. Ecosystem services for coastal dunes in Italy have been analyzed, and their role as carbon sinks and source of biological diversity has been emphasized (Drius et al. 2016).

In contrast to direct contribution to carbon capture, biogeochemical cycling, flood and erosion control and other regulating services, the role of vascular plants in provisioning services is less pronounced. Any gathering of plants in coastal habitats could have negative consequences due to the rather fragile nature of coastal ecosystems. However, coastal grasslands traditionally serve as supplier of animal feed in the form of hay or as pasture. Among

cultural services, recreation and aesthetic appreciation of coastal landscapes have been much recognized, with vegetation being considered as important landscape elements.

Among different types of ecosystem services of coastal and marine habitats, the group of cultural services is often undervalued, and the most critical situation is related to formal scientific knowledge, which constitutes scientific value of the ecosystem (Friess et al. 2020). In this respect, coastal ecosystems represent unique opportunities for fundamental and applied scientific studies in various fields of science. Evidently, in contrast to marine ecosystems, providing different direct benefits in a form of provisional services, coastal land plants are more important as a scientific resource in the context of their potential use. It is clear that targeted scientific research is needed in order to realize the potential of using plants of the seacoast, including around the Baltic Sea. Therefore, the next section will be devoted to a detailed analysis of these possibilities.

Most importantly, coastal ecosystems have been recognized as sites for maintenance of genetic diversity. Apart from the view of the need to preserve all diversity, relatively recently a concept of crop wild relatives (CWRs) has emerged, which has gained broad scientific interest within the last decades as potential sources for improvement or development of new crops (Zhang et al. 2017). Several international strategies, especially, at the European level, have been developed in recent decades aiming at conservation, study and sustainable exploitation of crop genetic diversity. According to the current targets of the Convention on Biological Diversity, national inventories of CRWs need to be performed in order to identify necessary conservation measures (Maxted et al. 2007). Several species designated as European priority human food or animal feed CWRs are frequently found in coastal habitats, such as *Daucus carota*, *Festuca rubra*, *Lotus corniculatus*, *Plantago lanceolata*, *Trifolium fragiferum*, *Trifolium pratense*, *Trifolium repens*, etc. (Rubio Teso et al. 2020).

#### FOOD PLANTS

In a historical context, coastal plants have been used as food source (Svanberg, Ægisson 2012). One such example includes the dune and beach species *Eryngium maritimum*, with roots cooked in syrup but young shoots and leaves used as salad (Isermann, Rooney 2014). Presently, gathered wild coastal plants are used for food both in household conditions as well as in restaurants (for example, see Tardío et al. 2006; Łuczaj et al. 2012; Dolina et al. 2014; Dolina et al. 2016; Petropoulos et al. 2018). Among these plants, *Beta vulgaris* subsp. *maritima* is the only halophilic progenitor of a major food crop, beetroot (Koyro et al. 2006).

The “biosaline concept” was introduced in agriculture as early as in 1970s, but only relatively recently significant progress has been reached in developing practical cropping systems of halophyte crops (Glenn et al. 2013; Ventura, Sagi 2013; Panta et al. 2014). Many agrotechnical problems

were encountered, mostly related to maintenance of moisture/salinity balance in field conditions, indicating that halophyte crops could be more useful in novel small-scale production systems aimed at specialty products or fresh gourmet market. Due to high concentration of different secondary compounds in halophyte species, potential directions of application of halophytes include pharmacognosy, functional foods and nutraceuticals (Buhmann, Papenbrock 2013).

Previous studies have shown that several of the potential crop halophytes found also in coastal habitats of the Baltic Sea region have a chemical profile suitable for use as foods or food ingredients. For example, *Triglochin maritima* was found to be a good source of Fe and contained also a significant amount of polyunsaturated fatty acids, protein and polyphenols (Sánchez-Faure et al. 2020). *Tripolium pannonicum* subsp. *pannonicum* (syn. *Aster tripolium*) and *Plantago coronopus* have been shown to be rich in minerals, polyphenols and several vitamins (Ventura et al. 2013; Centofanti, Bañuelos 2019). However, no in-depth analysis of other nutritional and antinutritional factors of these potential crop halophytes has been performed. Most importantly, it needs to be established how cultivation at optimum and tolerable rootzone salinity levels affects nutritional properties of potential crop halophytes in comparison to non-saline conditions.

Potential crop halophytes explored so far are palatable and rich in protein, minerals, fatty acids and vitamins (Centofanti, Bañuelos 2019). High tissue water content (related to induced succulence) of salt tolerant plants grown at increased substrate salinity promotes their palatability. In respect to mineral nutrient content, it is argued that special attention needs to be focused on increased levels of Na and Cl in edible parts of vegetable halophytes, but this aspect has been only seldom assessed experimentally. From a functional point of view, Na usually accumulates in older senescing leaves, often not used as food, and is excluded from younger parts (Ievinsh et al. 2020), but gourmet products are consumed in low quantities and can be prepared without addition of salt. One of the multiple aspects of salinity tolerance involves increased production of antioxidative enzymes and low molecular weight antioxidants to cope with oxidative damage (Türkan, Demiral 2009). Enrichment of plant-derived food with carotene and polyphenolic types of antioxidants by using crop halophytes seems to be desirable for the human diet (Centofanti, Bañuelos 2019) and can be useful as a functional food.

However, as in wild plants in general, there is a chance that halophyte plant parts contain chemical components undesirable for human consumption. These could include toxic substances (alkaloids, tannins, oxalate, cyanogenic glycosides, nitrate) and antinutritional factors (saponins, phytate, proteinase inhibitors). For example, oxalic acid is a common constituent of several coastal Amaranthaceae and Polygonaceae species (*Beta vulgaris*, *Rumex* spp.), but it is

not known in the required detail how its concentration is affected by increased salinity (Morales et al. 2014). Also, extremely high activity of oxidative enzymes together with increased concentration of phenolic compounds in plant material can lead to formation of oxidized phenolic species after tissue disruption, further leading to increased antinutritive activity after food consumption.

#### FEED PLANTS

Possibilities of using salt tolerant plants as a feed resource for livestock production have been discussed in the context of the Mediterranean region, with an emphasis on phytotherapeutic effects (Oliveira et al. 2021). Halophytic species from the genera *Atriplex*, *Salicornia*, *Salsola*, and *Suaeda* have been the most frequently considered for this purpose (Attia-Ismail 2018). However, considering that coastal meadows of the Baltic Sea have been used as pastures for a long time, also facultatively halophytic coastal species could be interesting in such studies. There is a high chance of finding tolerant legume and grass ecotypes in salt-affected coastal grasslands. For example, recent studies have shown that *Trifolium fragiferum* accessions from coastal habitats have high tolerance against salinity, soil waterlogging, trampling and cutting (Anderson-Ozola et al. 2021; Jekabsone et al. 2022).

#### BIOENERGY AND BIOMASS PLANTS

Seeds of several coastal halophytic species have emerged as a source of oil, including *Crithmum maritimum* (Atia et al. 2010), *Salicornia* spp. (Cárdenas-Pérez et al. 2021), and *Suaeda* spp. (Du et al. 2009). A number of halophyte species can be used as a source of lignocellulosic biomass (Sharma et al. 2016). In this sense, the most advantageous are the salt-resistant perennial grasses and *Typha* spp., with relatively high growth rate and whose biomass can be obtained every year without large investments. Achieving practical solutions is quite challenging, as it is necessary to find the most suitable genotypes for local conditions with sufficiently high salt tolerance.

#### SOURCE OF BIOLOGICALLY ACTIVE SUBSTANCES

Many coastal halophytic plant species are reported to be rich in antioxidant compounds with high capacity for sequestration of free radicals and reactive oxygen species (Ksouri et al. 2008; Lopes et al. 2016). In addition, many of these plants possess also antimicrobial activity and other biotic effects (Ksouri et al. 2012). These properties have been associated with high content of phenolic compounds. Several plant species characteristic for habitats of the Baltic Sea have been shown to exhibit different types of potentially useful pharmacological activity *in vitro* and in animal test systems, as *Calystegia soldanella* (Lee et al. 2014), *Eryngium maritimum* (Yurdakok, Baidan 2013), *Salicornia europaea* (Samule et al. 2017), etc. On the other hand, several coastal non-specific species frequently appearing in salt-affected

coastal habitats of the Baltic Sea, are well-known for their pharmacological potential, as *Achillea millefolium* (Abou Baker 2020), *Chenopodium album* (Choudhary et al. 2020), and *Lythrum salicaria* (Lamela et al. 1986), etc. Further research is needed on how coastal conditions, especially salinity, affect the chemical properties and biological activity of these species.

Wild aromatic plant species of the Lamiaceae family, widely available in the Baltic Sea region, represent a valuable plant resource of essential oils both for indigenous as well as industrial uses. In addition, a dune species of Apiaceae, *Eryngium maritimum*, is a valuable source of essential oils (Kikowska et al. 2020). Within European CWRs, the medicinal and aromatic plant group is represented by several species (Heywood, Zohary 1995), and *Mentha × piperita* and *Mentha spicata* are included in the list of the priority species (Rubio Teso et al. 2020). However, *Mentha aquatica* is one of wild ancestral forms of modern *Mentha* cultivars, and genetic and chemical diversity of native *M. aquatica* accessions is still an attractive resource for further exploration (Vining et al. 2019). *M. aquatica* is often found in sea-affected wetland habitats of the Baltic Sea region. Identification of *M. aquatica* genotypes with desirable chemical profiles and resistance is an important constituent in the ongoing domestication process of the mint crop (Vining et al. 2020). Essential oils from *M. aquatica* have high antioxidative and antiradical activity, but biological activity of essential oil from *M. aquatica* includes both antibacterial and fungicidal effects, and other types of activity, which can be assessed in different test systems (for example, Mancuso 2020; de Oliveira Braga et al. 2022).

#### ORNAMENTAL PLANTS

The ornamental value of coastal or halophytic species has not been specifically assessed. However, many species characteristic for coastal habitats of the Baltic Sea have long history of ornamental use, and some even have large numbers of diverse cultivars available (*Alyssum montanum*, *Armeria maritima*, *Eryngium maritimum*, *Gladiolus imbricatus*, *Gypsophila paniculata*, *Iris pseudacorus*, *Limonium humile*, *Limonium vulgare*, *Lobularia maritima*, *Lythrum salicaria*, *Pulsatilla pratensis*, *Silene uniflora*, and *Tripolium pannonicum*). In addition, potential use of native coastal halophytic species in landscaping has been discussed (Cassaniti, Romano 2011).

#### PHYTOREMEDIATION AND RESTORATION OF DEGRADED LAND

Traditionally, salt accumulating halophytes have been used for reclamation of saline soil. For example, a field study with *Suaeda salsa* showed that the plants were able to remove about 3800 kg salt ha<sup>-1</sup> year<sup>-1</sup> during a three year period (Wang et al. 2021). A significant ion accumulation potential has also been observed in many coastal species of the Baltic Sea, both under natural (Ievinsh et al. 2021)



and controlled conditions (Ievinsh et al. 2022a; Jekabsone et al. 2023).

The principles and mechanisms of use in plants for treatment of contaminated lands and waters by phytoremediation have been reviewed in several recent papers (DalCorso et al. 2019; Ievinsh et al. 2020a; Kafle et al. 2022; Shen et al. 2022). There is a growing body of evidence that coastal plant species represent important targets for studies focusing on finding potential solutions in phytoremediation systems (Ievinsh et al. 2020a). Several species from coastal habitats of the Baltic Sea have been shown to be useful in development of practical environmental phytoremediation systems (Ievinsh et al. 2020a; Ieviņa et al. 2023), including *Armeria maritima* (Purmale et al. 2022), *Rumex hydrolapathum* (Ievinsh et al. 2020c), *Ranunculus sceleratus* (Ievinsh et al. 2022b), *Alyssum montanum* subsp. *gmelinii* (Ievinsh et al. 2020b), and *Hylotelephium maximum* (Ievinsh et al. 2022c). Such systems could include growing plants in contaminated soil, as well as various treatment systems for contaminated water and even sewage. For example, different halophyte species have been used for desalination of domestic wastewater using a constructed wetland system in 1000 L water tanks with vertical flow (Fountoulakis et al. 2017). This system can be also used for pathogen removal. Similarly, *Mentha aquatica* has been used to remove both pathogens and heavy metals in conditions of a laboratory experiment (Dahija et al. 2019) and together with other macrophyte species in a hybrid constructed wetland to treat wastewater from cheese production (Reeb, Werckmann 2005). Moreover, use of *Mentha aquatica* plants in constructed wetlands of horizontal subsurface flow allowed for efficient removal of coliform bacteria from primary treated sewage (Avelar et al. 2014). In addition, a coastal accession of *Mentha aquatica* showed a prominent potential for use in hydroponic-based biological air purification systems, facilitating development of a beneficial microbiome (Kalniņš et al. 2022).

#### *Association with landscape elements*

In a certain way, the coastal landscape is uniformly dominated by the component of the presence of the sea, making it clearly recognizable and unique. On the other hand, the terrestrial component is quite diverse in the spatial aspect, forming significant variation of the landscape. The influence of the large open areas of the marine component on the coastal landscape makes it visually vast, even making it difficult to perceive other landscape elements and the plants located on them. This feature is to some extent related to the observer's point of view, looking in the direction from land to sea. Therefore, the possible consolidated landscape model of the inland part of the coast should be created with a view from the sea side to the land, in order to emphasize the landscape elements located there and the vegetation associated with them.

Coastal landscape diversity in the Baltic Sea region is large due to both geological and climate differences and it includes wide open sandy shores with lagoons, fragmented moraine landscape interrupted by estuaries, as well as boreal archipelagos (Carstensen et al. 2020). Large landscape variation appears as a result of differences in dominant driving processes in erosional and accumulating coasts, with a wide range of contrasts in respect to geomorphological features as well as input of sediment and energy. As analysis of land forming processes and other aspects of coastal landscape diversity is out of the scope of the present review, for detailed information, readers are invited to refer to specialized literature.

Based on empirical observations in the landscape of the Baltic Sea coast and relevant literature, within the framework of this review it seemed essential to create an approximate generalized coastal model that would include the diversity of the landscape and its elements (Fig. 7). In low energy coasts, stability of processes allow for soil formation, and sea level fluctuations result in establishment of distinct vegetation zones, as saltmarshes or wet coastal meadows in hydrolittoral and lower geolittoral zones, which successively transform into transitional grassland in the upper geolittoral that is sometimes flooded with sea water, and further into a dry meadow in the epilittoral zone.

On active high energy coasts, conditions do not allow for formation of permanent soil, and an essential source of mineral nutrients is represented by microbial-driven mineralization of drift litter, resulting of establishment of annual drift-line-dependent vegetation formed by halophytic and nitrophilic species (Ievinsh 2022). This type of vegetation is extremely dynamic and even within a single season, such groups of plants can form and perish as a result of wave action several times in a given location. Depending on the type of substrate forming the base and availability of accumulating material, different shore types are formed, from rocky beach to shingle and gravel beach, as well as sand beach differing in the degree of moisture. Typical dune zones in sand-accumulating coasts are formed, consisting of embryonic dunes, foredunes or white dunes, and grey or stabilized dunes. Dune slacks are frequently formed in dune blowout places where the water table is relatively high. Further inland, depending on geomorphological conditions, pH and disturbance intensity, dune heath (on acidic substrate), dry calcareous grassland (on alkaline substrate) or dune scrub (low disturbance) can be distinguished. Seasonal puddles or more permanent pools are formed in appropriate places supporting establishment of annual or perennial vegetation, usually supported by accumulation of drift deposits. In spring-rich areas, as at the foot of the sand cliffs, specific freshwater vegetation of wet places is formed, while the favourable hydrological regime allows the development of wet embryonic dunes towards the sea.



Fig. 7. Coastal landscape model of the Baltic Sea. Author Santa Ieviņa.

### Biotic interactions and anthropogenic impact

Besides the determining role of abiotic environmental factors in shaping plant diversity in coastal habitats, the evolutionary development of a set of organisms of different systematic groups is no less important, but an understudied phenomenon. There is no doubt that plant-centered biotic interactions are important constituents of functional and structural organization of coastal ecosystems. When considering possible effects from biotic interactions to shifting physiological optima (fundamental niche) to ecological optima (realized niche), it is important to suggest both growth loss from competition as well as growth enhancement by symbiotic relationships, mycorrhizae and nitrogen-fixing rhizobacteria (Funabashi 2016). Here, first of all, it should be understood that “growth” includes not only the increase of biomass, but also, in the context of the ecological optimum, the success of reproduction, as well as the generative and clonal spread of individuals. In addition, beneficial effects may also be related to positive interactions between plant species (facilitation) and the presence of free-living plant growth-promoting rhizosphere microorganisms. Similarly, variation in diversity and abundance of other soil microorganisms can cause an indirect positive effect by stimulating accelerated

mineralization of organic matter or a negative effect by changing the redox potential of the soil and causing changes in the availability of minerals or by the accumulation of toxins produced by microorganisms (Ievinsh 2022). Besides clearly negative biotic interactions, such as effect of pathogens and herbivores, selective growth reduction by parasitic plant species is an important factor shaping plant distribution and diversity in coastal grasslands (Ievinsh 2024). Presence of root hemiparasitic plants reduces performance of preferred host species but increases growth of avoided host plants due to less competition pressure.

Other biotic interactions or anthropogenic impacts are of significant relevance in coastal habitats. For example, grazing by small animals has been considered as an important factor in evolution of coastal grasslands (Juttila 1999; Ingerpuu, Sarv 2015). Also, cattle grazing is an essential component of coastal marsh management today. Cattle grazing has a dual effect on vegetation through removal of biomass of preferred food plants and by plant trampling and soil compaction. Mowing also has been used as a management method in coastal grasslands, but most efficient biodiversity maintenance approaches combine both cattle grazing and mowing.

When it comes to strongly negative anthropogenic impacts on coasts, pollution (Rana et al. 2021) and trampling



of vegetation (Santoro et al. 2012; Farris et al. 2013) are most often discussed and assessed. When analyzing the effects of these factors on coastal vegetation, it should be taken into account that different plant species have significant differences in their tolerance to these impacts. Thus, many coastal plant species are highly tolerant to heavy metal pollution with high metal accumulation capacity in plant tissues (Ievinsh et al. 2020a).

**Conceptual framework of functional diversity analysis**

All the above analysis suggests that no single classification system can serve as a basis for understanding the functional diversity of plants and their role in supporting ecosystem functionality. Any system of plant classification has its strengths and weaknesses, depending on what type of relationships the particular system is based. Systems based on community analysis can be important for solving ecological questions, but are less appropriate for analysis of distribution (appearance) of plant individuals and their functional aspects. Habitats seem to be most realistic and often can be easily identified in nature, as plant coexistence is based on microenvironmental differences in abiotic factors as well as interactions between individuals and other types of interactions (microbial symbioses etc.).

However, specific locations of individuals of a particular plant species on a border between different habitats make it difficult to map/classify individuals unequivocally and accurately. Nevertheless, a habitat classification system seems to be most appropriate as a basis for functional analysis of coastal plants. In contrast to functional analysis on plant community basis, as in the CSR system (Grime 1974), individual-based functional analysis system relies on ecophysiological information, as related to particular plant characteristics.

Attempts have been made previously to establish relationships between ecosystem functioning and biological diversity. One of approaches looks at biodiversity maintenance mechanisms as the main supporting feature for ecosystem functioning, and calls for abandoning strict adherence to a deterministic concept of species interactions, emphasizing instead the need for a neutral theory of biodiversity based on stochastic interactions (Funabashi 2016). Although the concept of niches is tempting from the point of view of ease of practical use, its wide utilization has not brought significant achievements in the field of explaining the functional diversity of ecosystems.

Basic taxonomic entities, plant species, will be used as a basis for further analysis (Fig. 8). However, higher level entities, families, can be used for further grouping for sake of systematic analysis. Due to functional similarity, such

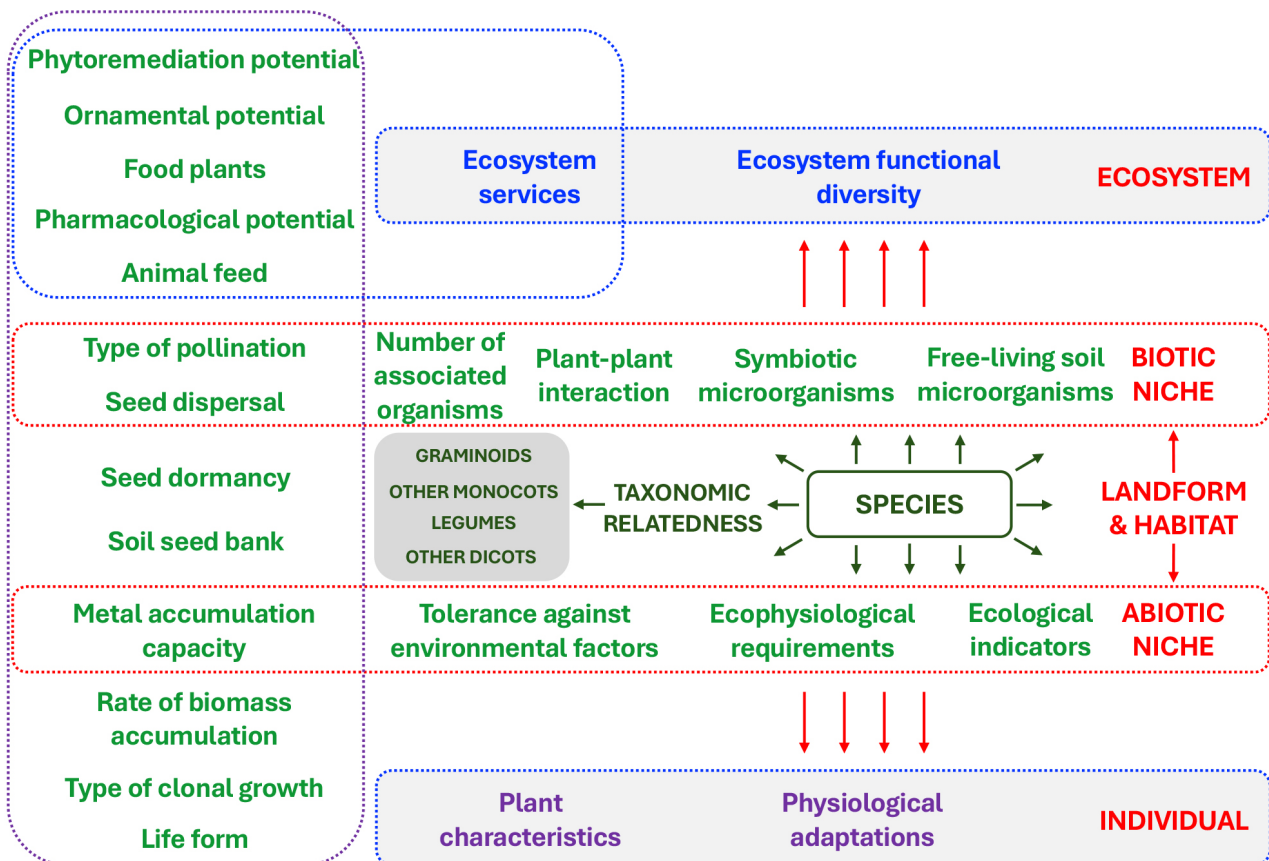


Fig. 8. Developed conceptual framework for analysis of vascular plant diversity in a coastal landscape.

**Table 1.** Taxonomic diversity of coastal plant species of the Baltic Sea, diagnostic values according to the EUNIS, and coastal specificity

| Family          | No. of taxa | No. of diagnostic taxa | No. of constant taxa | No. of coastal-specific taxa |
|-----------------|-------------|------------------------|----------------------|------------------------------|
| MONOCOTS        |             |                        |                      |                              |
| Acoraceae       | 1           | –                      | –                    | –                            |
| Alismataceae    | 4           | –                      | –                    | –                            |
| Amaryllidaceae  | 3           | –                      | –                    | –                            |
| Asparagaceae    | 2           | –                      | –                    | –                            |
| Butomaceae      | 1           | –                      | –                    | –                            |
| Cyperaceae      | 32          | 6                      | 9                    | 13                           |
| Iridaceae       | 4           | –                      | –                    | 2                            |
| Juncaeae        | 11          | 2                      | 2                    | 1                            |
| Juncaginaceae   | 2           | 2                      | 2                    | 1                            |
| Orchidaceae     | 14          | 1                      | 2                    | –                            |
| Poaceae         | 46          | 11                     | 20                   | 8                            |
| Typhaceae       | 3           | –                      | –                    | –                            |
| DICOTS          |             |                        |                      |                              |
| Amaranthaceae   | 24          | 7                      | 5                    | 13                           |
| Apiaceae        | 17          | 2                      | 2                    | 4                            |
| Apocynaceae     | 1           | –                      | –                    | –                            |
| Araliaceae      | 1           | 1                      | 1                    | –                            |
| Asteraceae      | 54          | 6                      | 13                   | 5                            |
| Boraginaceae    | 6           | 1                      | 2                    | 1                            |
| Brassicaceae    | 25          | 2                      | 3                    | 6                            |
| Campanulaceae   | 2           | –                      | 1                    | –                            |
| Caprifoliaceae  | 5           | –                      | –                    | –                            |
| Caryophyllaceae | 34          | 5                      | 7                    | 6                            |
| Cistaceae       | 2           | –                      | –                    | –                            |
| Convolvulaceae  | 5           | –                      | 1                    | 1                            |
| Crassulaceae    | 5           | 1                      | 2                    | –                            |
| Elatinaceae     | 3           | –                      | –                    | –                            |
| Ericaceae       | 5           | 2                      | 4                    | –                            |
| Euphorbiaceae   | 4           | –                      | –                    | –                            |
| Fabaceae        | 34          | 3                      | 5                    | 2                            |
| Gentianaceae    | 8           | –                      | 1                    | –                            |
| Geraniaceae     | 4           | –                      | 1                    | –                            |
| Hypericaceae    | 1           | –                      | –                    | –                            |
| Lamiaceae       | 11          | 1                      | 2                    | –                            |
| Linaceae        | 1           | –                      | –                    | –                            |
| Lythraceae      | 1           | –                      | 1                    | –                            |
| Malvaceae       | 3           | –                      | –                    | –                            |
| Montiaceae      | 2           | 1                      | –                    | –                            |
| Onagraceae      | 4           | –                      | 1                    | –                            |
| Orobanchaceae   | 13          | 1                      | 2                    | 1                            |
| Papaveraceae    | 3           | –                      | –                    | –                            |
| Plantaginaceae  | 18          | 2                      | 5                    | 3                            |
| Plumbaginaceae  | 3           | 2                      | 2                    | 2                            |
| Polygalaceae    | 1           | –                      | –                    | –                            |
| Polygonaceae    | 15          | –                      | 2                    | 1                            |
| Primulaceae     | 5           | 1                      | 1                    | 2                            |
| Ranunculaceae   | 15          | 1                      | 3                    | 1                            |
| Resedaceae      | 2           | –                      | –                    | –                            |
| Rosaceae        | 11          | 1                      | 2                    | –                            |
| Rubiaceae       | 7           | –                      | 4                    | –                            |
| Saxifragaceae   | 1           | –                      | –                    | –                            |
| Solanaceae      | 5           | –                      | 1                    | –                            |
| Urticaceae      | 2           | –                      | 1                    | –                            |
| Violaceae       | 3           | –                      | 1                    | –                            |
| Total           | 491         | 62                     | 76                   | 73                           |



taxonomic categories as “graminoids”, “other monocots”, “legumes” and “other dicots” can be used if necessary. Primary individuals are defined in relation to certain landforms and habitats in order to describe the realized biotic and abiotic niche characteristic of them. Further analysis will focus on the comparison of the realized and the physiological niche, characterizing those features that are essential for adaptations in the conditions of a set of dominant environmental factors. As a result, those adaptive properties of the plant, which play a decisive role in the specific location, should be distinguished. In parallel, the analysis of the set of biological interactions related to the presence of the species will give an opportunity to emphasize the most important of them for the functioning of the ecosystem. From the side of adaptation to abiotic factors, the aspects of plant clonality, the rate of biomass formation, the ability to accumulate metals, etc., should be especially emphasized. In terms of biotic effects, the characteristics of symbiotic interactions and dependence on free-living microorganisms, and the number of free-living organisms associated with a species (including pathogens, herbivores and pollinators) could be the most important characteristics in an ecosystem context. Further analysis should also include aspects related to generative and vegetative propagation of plants, including clonal growth characteristics, pollination characteristics, seed dispersal and dormancy characteristics, and soil seed bank formation. Finally, those plant characteristics that are of particular importance in the context of providing ecosystem services should be distinguished.

### Provisional list of coastal species of the Baltic Sea

A provisional list of vascular plant species from a coastal landscape of the Baltic Sea was prepared as based on available information on coastal distribution of species in numerous literature sources as well as after inspection of the list of EUNIS diagnostic species (Chytry et al. 2020), distribution in coastal habitats according to the study of ecological indicators and traits for Swedish plants (Tyler 2021), personal observations on coastal sites in Latvia, Estonia, Germany, Lithuania, Poland, Denmark and Sweden, and comparison with distribution data available at the Global Biodiversity Information Facility (<https://www.gbif.org>; accessed on 2024.25.06.). The full list appears as Table S1, but summary on taxonomic diversity, diagnostic value and coastal specificity of coastal species is given in Table 1. In total, 491 plant species were identified possibly associated with the coastal landscape of the Baltic Sea. Among monocots, Poaceae and Cyperaceae were the most widely represented families followed by Orchidaceae and Juncaceae. The Cyperaceae family was also the most important in terms of the number of coast-specific species, followed by Poaceae, which had the highest number of diagnostic and constant taxa. Among dicots, species of

Asteraceae were the most widely represented with 54 species, of which five were coastal-specific, but six and 13 species were diagnostic or constant, respectively. Large species representation was also for Caryophyllaceae ( $n = 34$ ), Fabaceae ( $n = 34$ ), Brassicaceae ( $n = 25$ ), and Amarantaceae ( $n = 24$ ). Among these, species of Amaranthaceae were exceptional in respect to coastal specificity ( $n = 13$ ) and the number of diagnostic ( $n = 7$ ) and constant ( $n = 5$ ) species. In total, about 160 species were either coastal specific or diagnostic or constant species in the coastal habitat, or combined several of these features. These species could be considered prime targets for further research using the established conceptual framework.

However, it should be warned that this list cannot be used as a comprehensive source of information regarding coastal plant species. Most likely, it can be perceived as a source of information about those species that could be encountered with a relatively high probability in the coastal landscape of the Baltic Sea. In any case, the location of individual of a certain plant species in a specific place in the coastal landscape on different landforms is associated with both certain regularities as well as random influences as a result of various natural and anthropogenic factors.

### Conclusions

An in-depth analysis of plant diversity classification options has made it possible to see the strengths and problems of different systems. In the context of the functioning of the coastal ecosystem, it has become clear that the greatest lack of knowledge is precisely about the physiological adaptations of plants to a specific set of environmental conditions. The conceptual basis for the analysis of plant characteristics has been created, which combines both the comparison of the fundamental and the realized niche, and the analysis of the main physiological adaptations against the background of a set of environmental factors, with special emphasis on the diversity of biotic relationships, as well as those characteristics essential for the provision of ecosystem services. Based on the created list of vascular plant species of the Baltic Sea coast, it has become possible to conduct an in-depth analysis of the characteristics of the species, especially focusing on 160 of the 491 taxa, with the possible greatest functional significance in the context of the ecosystem. The performed analysis will allow to distinguish the most functionally important plant species related to the specific elements of the coastal landscape and will provide an opportunity to describe the key species for the functioning of the coastal ecosystem, focusing on their physiological adaptation mechanisms and diversity of biotic interactions. The results of the analysis will provide an opportunity to improve the understanding of the importance of plant species in the coastal landscape and form the basis for predicting the effects of climate change and negative load caused by anthropogenic influences.

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**Table S1.** A provisional list of vascular plant species from a coastal landscape of the Baltic Sea. Taxonomy is according to The World Flora Online (<https://www.worldfloraonline.org>).

<sup>1</sup>Data from Chytrý M. et al. 2020. EUNIS habitats of the Baltic Sea: MA232, *Baltic coastal meadow*; N11, *Atlantic, Baltic and Arctic sand beach*; N13, *Atlantic and Baltic shifting coastal dune*; N15, *Atlantic and Baltic coastal dune grassland (grey dune)*; N18, *Atlantic and Baltic coastal Empetrum heath*; N1A, *Atlantic and Baltic coastal dune scrub*; N1D, *Atlantic and Baltic broad-leaves coastal dune forest*; N1F, *Baltic coniferous coastal dune forest*; N1H, *Atlantic and Baltic moist and wet dune slack*; N21, *Atlantic, Baltic and Arctic coastal shingle beach*; N31, *Atlantic and Baltic rocky sea cliff and shore*; N34, *Atlantic and Baltic soft-sea cliff*. Characteristic species are divided into diagnostic (numbers show fidelity), constant (numbers show percentage occurrence frequency), dominant (numbers show percentage frequency of plots with a cover larger than 25%) species.

<sup>2</sup>Data from Tyler et al. (2021). Occurrence of the species in broadly defined vegetation types of sea coast indicate proportion of the species total population in Sweden that is found in these vegetation types (0 to 10). SE sea shores, vegetation on coarse minerogenic substrates periodically inundated by ± salty water; SE shore meadows, grassland vegetation on organic or fine-grained minerogenic soils periodically inundated by ± salty water.

<sup>3</sup>Data from National Plant Monitoring Scheme of Great Britain: Species List (<https://www.npms.org.uk>).

<sup>4</sup>Data from Sterry, Cleave (2023) Coastal Wildflowers of Britain, Ireland and Northwest Europe. Wild Nature Press, Plymouth.

| Species  | EUNIS diagnostic <sup>1</sup>     | EUNIS constant <sup>1</sup>                     | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>  |
|--|-----------------------------------|---|-----------------------------|----------------------------|-------------------------------|----------------------|---------------------------------|
| <b>MONOCOTS</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <b>Acoraceae</b>   |                                   |   |                             |                            |                               |                      |                                 |
| <i>Acorus calamus</i> L.   | -                                 | -   | -                           | 0                          | 0                             | -                    | -                               |
| <b>Alismataceae</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <i>Alisma plantago-aquatica</i> L.   | -                                 | -   | -                           | 0                          | 0                             | -                    | -                               |
| <i>Alisma wahlenbergii</i> (Holmb.) Juz.                                       | -                                 | -   | -                           | 5                          | 0                             | -                    | -                               |
| <i>Sagittaria natans</i> Pall.   | -                                 | -   | -                           | 0                          | 2                             | -                    | -                               |
| <i>Sagittaria sagittifolia</i> L.  | -                                 | -   | -                           | 0                          | 3                             | -                    | -                               |
| <b>Amaryllidaceae</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <i>Allium schoenoprasum</i> L.   | -                                 | -   | -                           | 3                          | 0                             | -                    | damp grassy places on limestone |
| <i>Allium scorodoprasum</i> L.   | -                                 | -   | -                           | 0                          | 0                             | -                    | dry sandy grassland             |
| <i>Allium vineale</i> L.   | -                                 | -   | -                           | 1                          | 0                             | -                    | cliffs / dry grassland          |
| <b>Asparagaceae</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <i>Asparagus officinalis</i> L.  | -                                 | -   | -                           | 2                          | 0                             | -                    | -                               |
| <i>Hyacinthoides non-scripta</i> (L.) Chouard ex Rothm.                        | -                                 | -   | -                           | 0                          | 0                             | cliffs               | -                               |
| <b>Butomaceae</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <i>Butomus umbellatus</i> L.   | -                                 | -   | -                           | 0                          | 0                             | -                    | -                               |
| <b>Cyperaceae</b>  |                                   |   |                             |                            |                               |                      |                                 |
| <i>Blasmus compressus</i> (L.) Panz. ex Link                                   | -                                 | -   | -                           | 0                          | 6                             | -                    | -                               |
| <i>Blasmus rufus</i> (Huds.) Link<br>[ <i>Blasmus rufa</i> (Huds.) Oteng-Yeb.] | MA232: 19                         | -   | -                           | 0                          | 10                            | -                    | saltmarsh / dune slacks         |
| <i>Bolboschoenus maritimus</i> (L.) Palla<br>[ <i>Scirpus maritimus</i> L.]    | -                                 | MA232: 16                                       | -                           | 0                          | 7                             | -                    | margins of brackish water       |
| <i>Carex acuta</i> L.  | -                                 | -   | -                           | 1                          | 0                             | -                    | -                               |
| <i>Carex aquatilis</i> Wahlenb.  | -                                 | -   | -                           | 2                          | 2                             | -                    | -                               |
| <i>Carex arenaria</i> L.   | N15: 28.4<br>N1A: 22.6<br>N1F: 30 | N15: 67; N18: 86<br>N1A: 53; N1F: 70<br>N1H: 17 | -                           | 3                          | 0                             | machair              | dunes                           |
| <i>Carex bigelowii</i> Torr. ex Schwein.<br>[ <i>Carex concolor</i> R.Br.]     | -                                 | -   | -                           | 0                          | 5                             | -                    | -                               |

Continued

Table S1. Continued

| Species  | EUNIS diagnostic <sup>c</sup> | EUNIS constant <sup>1</sup>   | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                           |
|--|-------------------------------|-------------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|--|
| <i>Carex distans</i> L.  | -                             | -                             | -                           | 0                          | 7                             | -                    | upper saltmarsh / margins of pools                       |
| <i>Carex extensa</i> Gooden.   | -                             | -                             | -                           | 0                          | 7                             | -                    | upper saltmarsh / margins of pools                       |
| <i>Carex flacca</i> Schreb.  | -                             | NIH: 24                       | -                           | 0                          | 0                             | dunes                | -  |
| <i>Carex glareosa</i> Schkuhr ex Wahlenb.  | -                             | -                             | -                           | 7                          | 3                             | -                    | -  |
| <i>Carex</i> × <i>halophila</i> F.Nyl.   | MA232: 21.7                   | -                             | -                           | 5                          | 5                             | -                    | -  |
| <i>Carex hirta</i> L.  | -                             | -                             | -                           | 1                          | 1                             | -                    | -  |
| <i>Carex mackenziet</i> V.I.Krecz.   | MA232: 21.6                   | MA232: 11                     | -                           | 0                          | 10                            | -                    | -  |
| <i>Carex maritima</i> Gunnerus   | -                             | -                             | -                           | 4                          | 4                             | -                    | -  |
| <i>Carex nigra</i> (L.) Reichard   | -                             | MA232: 11<br>NIF: 11; NIH: 32 | -                           | 0                          | 0                             | -                    | -  |
| <i>Carex oederi</i> Retz [ <i>Carex viridula</i> Michx.]   | -                             | -                             | -                           | 0                          | 2                             | -                    | -  |
| <i>Carex paleacea</i> Schreb. ex Wahlenb.  | MA232: 18.3                   | -                             | -                           | 10                         | 0                             | -                    | -  |
| <i>Carex panicea</i> L.  | -                             | NIH: 14                       | -                           | 0                          | 1                             | -                    | -  |
| <i>Carex pulicaris</i> L.  | -                             | -                             | -                           | 0                          | 0                             | cliffs               | -  |
| <i>Carex punctata</i> Gaudin   | -                             | -                             | -                           | 10                         | 0                             | -                    | -  |
| <i>Carex tomentosa</i> L.  | -                             | -                             | -                           | 0                          | 1                             | -                    | -  |
| <i>Carex vacillans</i> Drejer  | -                             | -                             | -                           | 0                          | 10                            | -                    | -  |
| <i>Eleocharis acicularis</i> (L.) Roem. & Schult.  | -                             | -                             | -                           | 0                          | 3                             | -                    | -  |
| <i>Eleocharis mamillata</i> (H.Lindb.) H.Lindb.  | -                             | -                             | -                           | 0                          | 2                             | -                    | -  |
| <i>Eleocharis palustris</i> (L.) Roem. & Schult.   | -                             | NIH: 20                       | -                           | 0                          | 2                             | -                    | damp ground  |
| <i>Eleocharis parvula</i> (Roem. & Schult.) Link ex Bluff, Nees & Schauer  | -                             | -                             | -                           | 0                          | 10                            | -                    | -  |
| <i>Eleocharis quinqueflora</i> (Hartmann) O.Schwarz  | -                             | -                             | -                           | 0                          | 2                             | -                    | -  |
| <i>Eleocharis uniglumis</i> (Link) Schult.   | MA232: 43.1                   | MA232: 45                     | -                           | 0                          | 3                             | -                    | damp ground  |
| <i>Eriophorum angustifolium</i> Honck.   | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Schoenoplectus tabernaemontani</i> (C.C.Gmel.) Palla<br>[ <i>Scirpus validus</i> Vahl]<br>[ <i>Schoenoplectus validus</i> (Vahl) A.Löve & D.Löve] | -                             | -                             | -                           | 0                          | 7                             | -                    | grassland / lagoons / saltmarshes / dune slacks          |
| <i>Schoenus nigricans</i> L.   | -                             | NIH: 11                       | -                           | 0                          | 0                             | -                    | dune slacks / sea cliffs / upper saltmarsh               |
| <b>Iridaceae</b>   |                               |                               |                             |                            |                               |                      |  |
| <i>Gladiolus imbricatus</i> L.   | -                             | -                             | -                           | -                          | -                             | -                    | -  |
| <i>Iris orientalis</i> Mill.   | -                             | -                             | -                           | 0                          | 10                            | -                    | -  |
| <i>Iris pseudacorus</i> L.   | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Iris spuria</i> L.  | -                             | -                             | -                           | 0                          | 10                            | -                    | -  |
| <b>Junaceae</b>  |                               |                               |                             |                            |                               |                      |  |
| <i>Juncus articulatus</i> L.   | NIH: 18.9                     | NIH: 37                       | -                           | 0                          | 0                             | -                    | margins of pools in dune slacks and calcareous grassland |
| <i>Juncus balticus</i> Willd.  | -                             | -                             | -                           | 7                          | 0                             | -                    | dune slacks  |
| <i>Juncus bufonius</i> L.  | -                             | -                             | -                           | 0                          | 1                             | -                    | dune slacks / marshes / damp hollows                     |

Continued

Table S1. Continued

| Species   | EUNIS diagnostic <sup>1</sup> | EUNIS constant <sup>1</sup>   | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                     |
|---|-------------------------------|-------------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|--|
| <i>Juncus bulbosus</i> L.                                       | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Juncus capitatus</i> Weigel                                  | -                             | -                             | -                           | 0                          | 0                             | -                    | damp bare ground                                   |
| <i>Juncus compressus</i> Jacq.                                  | -                             | -                             | -                           | 1                          | 3                             | -                    | -  |
| <i>Juncus conglomeratus</i> L.                                  | -                             | -                             | -                           | 0                          | 1                             | -                    | damp grazed grassland                              |
| <i>Juncus effusus</i> L.  | -                             | -                             | -                           | 0                          | 0                             | -                    | overgrazed grassland                               |
| <i>Juncus gerardii</i> Loisel.                                  | MA232: 38.8                   | MA232: 78                     | MA232: 32                   | 0                          | 7                             | saltmarsh            | upper saltmarsh / saline grassland                 |
| <i>Juncus maritimus</i> Lam.                                    | -                             | -                             | -                           | 0                          | 10                            | -                    | upper saltmarsh / rocks                            |
| <i>Juncus ramariius</i> Songeon & E.P.Perrier                   | -                             | -                             | -                           | 0                          | 6                             | -                    | -  |
| <b>Juncaginaceae</b>  |                               |                               |                             |                            |                               |                      |  |
| <i>Triglochin maritima</i> L.                                   | MA232: 32.9                   | MA232: 58                     | -                           | 3                          | 7                             | saltmarsh            | saltmarsh  |
| <i>Triglochin palustris</i> L.                                  | MA232: 16                     | MA232: 24                     | -                           | 0                          | 0                             | -                    | -  |
| <b>Orchidaceae</b>  |                               |                               |                             |                            |                               |                      |  |
| <i>Cephalanthera rubra</i> (L.) Rich.                           | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Corallorhiza trifida</i> Châtel.                             | -                             | -                             | -                           | 0                          | 0                             | -                    | dune slacks  |
| <i>Dactylorhiza baltica</i> (Klinge) Nevski                     | -                             | -                             | -                           | -                          | -                             | -                    | dune slacks / coastal woodland                     |
| <i>Dactylorhiza incarnata</i> (L.) Soó                          | -                             | -                             | -                           | 0                          | 0                             | -                    | dune slacks  |
| <i>Dactylorhiza maculata</i> (L.) Soó                           | -                             | -                             | -                           | 0                          | 0                             | -                    | heaths / acid grassland                            |
| [ <i>Orchis maculata</i> L.]                                    | -                             | -                             | -                           | -                          | -                             | -                    | -  |
| <i>Dactylorhiza maculata</i> subsp. <i>fuchsii</i> (Druce) Hyl. | -                             | -                             | -                           | 0                          | 0                             | -                    | dune slacks / calcareous grassland                 |
| [ <i>Dactylorhiza fuchsii</i> (Druce) Soó]                      | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Epipactis atrorubens</i> (Hoffm.) Besser                     | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Epipactis helleborine</i> (L.) Crantz                        | -                             | -                             | -                           | 0                          | 0                             | -                    | -  |
| <i>Epipactis palustris</i> (L.) Crantz                          | -                             | NIH: 14                       | -                           | 0                          | 0                             | -                    | dune slacks  |
| <i>Gymnadenia densiflora</i> A.Dietr.                           | -                             | -                             | -                           | 0                          | 0                             | -                    | calcareous dune slacks                             |
| <i>Liparis loeselii</i> (L.) Rich.                              | -                             | -                             | -                           | 0                          | 0                             | -                    | dune slacks  |
| <i>Neottia cordata</i> (L.) Rich.                               | NIF: 18.8                     | NIF: 16                       | -                           | 0                          | 0                             | -                    | -  |
| <i>Neottia ovata</i> (L.) Hartm.                                | -                             | -                             | -                           | 0                          | 0                             | -                    | dune slacks / dunes                                |
| <i>Platanthera bifolia</i> (L.) Rich.                           | -                             | -                             | -                           | 0                          | 0                             | -                    | undisturbed grassland / dune slacks                |
| <b>Poaceae</b>  |                               |                               |                             |                            |                               |                      |  |
| <i>Achnatherum calamagrostis</i> (L.) P.Beauv.                  | MA232: 32                     | MA232: 25                     | -                           | 0                          | 1                             | -                    | -  |
| [ <i>Calamagrostis neglecta</i> G.Gaertn., B.Mey. & Scherb.]    | -                             | -                             | -                           | -                          | -                             | -                    | -  |
| <i>Agrostis capillaris</i> L.                                   | -                             | N18: 24; N1D: 17              | -                           | 0                          | 0                             | -                    | grassland / dunes                                  |
| <i>Agrostis gigantea</i> Roth                                   | -                             | -                             | -                           | 1                          | 1                             | -                    | -  |
| <i>Agrostis stolonifera</i> L.                                  | MA232: 23.8                   | MA232: 86<br>N1H: 45; N34: 20 | MA232: 34                   | 0                          | 2                             | -                    | brackish grassland / dune slacks / upper saltmarsh |
| <i>Aira praecox</i> L.  | -                             | N15: 14                       | -                           | 0                          | 0                             | -                    | dunes / cliff-tops on acidic soil                  |
| <i>Alopecurus arundinaceus</i> Poir.                            | -                             | -                             | -                           | 2                          | 7                             | -                    | -  |
| <i>Alopecurus geniculatus</i> L.                                | -                             | -                             | -                           | 0                          | 2                             | dunes                | -  |

Continued



Table S1. Continued

| Species   | EUNIS<br>diagnostic <sup>c</sup>    | EUNIS<br>constant <sup>1</sup>   | EUNIS<br>dominant <sup>1</sup> | SE sea<br>shores <sup>2</sup> | SE shore<br>meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>        |
|---|-------------------------------------|--|--------------------------------|-------------------------------|----------------------------------|----------------------|---------------------------------------|
| <i>Anthoxanthum nitens</i> (Weber) V.Schouten & Woldkamp<br>[ <i>Hierochloë odorata</i> (L.) P.Beauv.]            | -                                   | -  | -                              | 0                             | 1                                | -                    | -                                     |
| <i>Anthoxanthum odoratum</i> L.   | -                                   | N18: 17; N1F: 18<br>NIH: 15  | -                              | 0                             | 1                                | -                    | dry grassland / acidic dunes          |
| <i>Briza media</i> L.   | -                                   | -  | -                              | 0                             | 0                                | -                    | dry grassland / dunes                 |
| <i>Bromus hordeaceus</i> L.   | -                                   | N34: 13  | -                              | 1                             | 0                                | cliffs               | cliffs / shingle                      |
| <i>Bromus racemosus</i> L.  | -                                   | -  | -                              | 0                             | 2                                | -                    | -                                     |
| <i>Calamagrostis arenaria</i> (L.) Roth<br>[ <i>Ammophila arenaria</i> (L.) Link]                                 | N13: 36.9<br>N15: 16.8<br>N18: 21.7 | N11: 17; N13: 71<br>N15: 33; N18: 43<br>N1A: 22  | N13: 55                        | 8                             | 0                                | machair              | dunes                                 |
| <i>Calamagrostis arundinacea</i> (L.) Roth  | -                                   | -  | -                              | 0                             | 0                                | -                    | -                                     |
| <i>Calamagrostis epigejos</i> (L.) Roth   | N1A: 23.8                           | N15: 18; N18: 27<br>N1A: 60; N1D: 35<br>NIH: 16  | -                              | 1                             | 0                                | -                    | -                                     |
| <i>Catabrosa aquatica</i> (L.) P.Beauv.   | -                                   | -  | -                              | 0                             | 4                                | -                    | -                                     |
| <i>Corynephorus canescens</i> (L.) P. Beauv.  | N15: 31.2                           | N15: 52; N1F: 11   | -                              | 0                             | 0                                | -                    | dunes / sandy shingle                 |
| <i>Cynosurus cristatus</i> L.   | -                                   | -  | -                              | 0                             | 1                                | -                    | -                                     |
| <i>Dactylis glomerata</i> L.  | -                                   | N1D: 14; N34: 40   | -                              | 0                             | 0                                | -                    | cliffs / dunes                        |
| <i>Deschampsia cespitosa</i> (L.) P.Beauv.  | -                                   | -  | -                              | 0                             | 0                                | -                    | -                                     |
| <i>Deschampsia cespitosa</i> subsp. <i>cespitosa</i><br>[ <i>Deschampsia bottnica</i> (Wahlenb.) Trin.]           | -                                   | -  | -                              | 10                            | 0                                | -                    | -                                     |
| <i>Dupontia fulva</i> (Trin.) Röser & Tkach<br>[ <i>Arctophila fulva</i> (Trin.) Andersson]                       | -                                   | -  | -                              | 0                             | 5                                | -                    | -                                     |
| <i>Elymus athericus</i> (Link) Kerguelen<br>[ <i>Elytrigia atherica</i> (Link) Kerguelen ex Carreras<br>Martinez] | -                                   | N21: 11  | -                              | -                             | -                                | saltmarsh            | upper saltmarsh                       |
| <i>Elymus pungens</i> subsp. <i>campestris</i> (Godr. & Gren.)<br>Melderis  | -                                   | -  | -                              | 7                             | 0                                | -                    | -                                     |
| <i>Elytrigia campestris</i> (Godr. & Gren.) M.A.Carreras ex<br>Kerguelen]   | -                                   | -  | -                              | -                             | -                                | -                    | -                                     |
| <i>Elymus repens</i> (L.) Gould<br>[ <i>Elytrigia repens</i> (L.) Nevski]   | -                                   | MA232: 14<br>N21: 11   | -                              | 3                             | 1                                | -                    | -                                     |
| <i>Festuca beckeri</i> (Hack.) Trautv.<br>[ <i>Festuca polesica</i> Zapal.]                                       | N15: 22.4                           | -  | -                              | 0                             | 0                                | -                    | -                                     |
| <i>Festuca filiformis</i> Pourr.  | -                                   | N18: 17 N1A: 14  | -                              | 0                             | 0                                | -                    | -                                     |
| <i>Festuca ovina</i> L.   | -                                   | N18: 22  | -                              | 0                             | 0                                | -                    | calcareous grassland / cliffs / dunes |
| <i>Festuca rubra</i> L.<br>[ <i>Festuca arenaria</i> Osbeck]  | N34: 15.7                           | MA232: 52<br>N13: 37; N15: 33<br>N18: 18; N1A: 45<br>N1D: 12; NIH: 23<br>N21: 15; N31: 43<br>N34: 70 | -                              | 1                             | 1                                | -                    | upper saltmarsh / cliffs              |

Continued

Table S1. Continued

| Species  | EUNIS diagnostic <sup>c</sup>                     | EUNIS constant <sup>1</sup>                                  | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                  |
|--|---|--|-----------------------------|----------------------------|-------------------------------|----------------------|---|
| <i>Holcus lanatus</i> L.   | -   | N18: 16; N1A: 17<br>N1D: 20; N1H: 31<br>N34: 30              | -                           | 0                          | 0                             | shingle              | meadows / grasslands                            |
| <i>Hordeum secalinum</i> Schreb.   | -   | -  | -                           | 0                          | 10                            | -                    | -   |
| <i>Koeleria glauca</i> (Spreng.) DC  | -   | -  | -                           | 0                          | 0                             | -                    | -   |
| <i>Leymus arenarius</i> (L.) Hochst.   | N11: 25.2<br>N13: 32.1                            | N11: 24; N13: 31<br>N21: 11                                  | -                           | 7                          | 0                             | -                    | dunes / sandy beaches                           |
| <i>Lolium arundinaceum</i> (Schreb.) Darbysh. [ <i>Schedonorus arundinaceus</i> (Schreb.) Dumort.] | -   | -  | -                           | 2                          | 3                             | -                    | -   |
| <i>Parapholis strigosa</i> (Dumort.) C.E.Hubb.   | -   | -  | -                           | 0                          | 10                            | -                    | -   |
| <i>Phalaris arundinacea</i> L.   | -   | -  | -                           | 1                          | 1                             | -                    | -   |
| <i>Phleum arenarium</i> L.   | N15: 21.3   | N15: 15  | -                           | 0                          | 0                             | -                    | dunes / sandy shingle                           |
| <i>Phragmites australis</i> (Cav.) Trin. ex Steud.   | MA232: 15.1                                       | MA232: 50<br>N1H: 31   | -                           | 0                          | 3                             | -                    | margins of pools / damp ground / marshes        |
| <i>Poa annua</i> L.  | -   | -  | -                           | 0                          | 1                             | -                    | -   |
| <i>Poa bulbosa</i> L.  | -   | -  | -                           | 0                          | 0                             | -                    | shingle / dunes                                 |
| <i>Poa pratensis</i> L.  | -   | MA232: 19<br>N15: 12; N18: 12<br>N1A: 49; N1D: 26<br>N1H: 15 | -                           | 0                          | 1                             | -                    | -   |
| <i>Puccinellia distans</i> (Jacq.) Parl<br>[ <i>Puccinellia capillaris</i> (Lilj.) Jansen]         | -   | -  | -                           | 0                          | 3                             | -                    | upper saltmarsh / saline grassland              |
| <i>Puccinellia maritima</i> (Huds.) Parl.  | -   | -  | -                           | 5                          | 5                             | -                    | -   |
| <i>Spartina anglica</i> C.E.Hubb.  | -   | -  | -                           | 0                          | 10                            | saltmarsh            | middle & upper saltmarsh<br>saltmarsh / mudflat |
| <i>Thinopyrum junceum</i> (L.) Á.Löve<br>[ <i>Elytrigia juncea</i> (L.) Nevski]                    | N11: 19.8; N13: 24<br>N11: 41; N13: 49<br>N21: 16 | N13: 26  | N13: 26                     | 10                         | 0                             | -                    | sandy shores                                    |
| <i>Trisetum flavescens</i> (L.) P.Beauv.   | -   | -  | -                           | 0                          | 0                             | -                    | dry dune grassland                              |
| <b>Typhaceae</b>   |   |  |                             |                            |                               |                      |   |
| <i>Sparganium erectum</i> L.   | -   | -  | -                           | 0                          | 0                             | -                    | -   |
| <i>Typha angustifolia</i> L.   | -   | -  | -                           | 0                          | 0                             | -                    | -   |
| <i>Typha latifolia</i> L.  | -   | -  | -                           | 0                          | 0                             | -                    | -   |
| <b>DICOTS</b>  |   |  |                             |                            |                               |                      |   |
| <b>Amarathaceae</b>  |   |  |                             |                            |                               |                      |   |
| <i>Atriplex glabriuscula</i> Edmondston  | N11: 16.8<br>N21: 19.5                            | -  | -                           | 10                         | 0                             | -                    | shingle beach / sandy beach                     |
| <i>Atriplex laciniata</i> L.   | N11: 24.9<br>N21: 15.5                            | N11: 13  | -                           | 10                         | 0                             | -                    | shingle beach / sandy beach                     |
| <i>Atriplex littoralis</i> L.  | N11: 25.2<br>N21: 20.2                            | N11: 26; N21: 21   | -                           | 6                          | 3                             | -                    | saltmarsh strandlines / sea walls / bare ground |
| <i>Atriplex longipes</i> Drejer  | -   | -  | -                           | 0                          | 10                            | -                    | -   |

Continued

Table S1. Continued

| Species   | EUNIS<br>diagnostic <sup>c</sup> | EUNIS<br>constant <sup>1</sup> | EUNIS<br>dominant <sup>1</sup> | SE sea<br>shores <sup>2</sup> | SE shore<br>meadows <sup>2</sup> | GB NPMs <sup>3</sup>          | GB, IE, NW Europe <sup>4</sup>                 |
|---|----------------------------------|--------------------------------|--------------------------------|-------------------------------|----------------------------------|-------------------------------|--|
| <i>Atriplex nudicaulis</i> Boguslaw<br>[ <i>Atriplex praecox</i> Hülpf.]                                    | N21: 22.7                        | -                              | -                              | -                             | -                                | -                             | -  |
| <i>Atriplex patula</i> L.   | -                                | -                              | -                              | 2                             | 2                                | -                             | beach / saltmarsh / bare ground                |
| <i>Atriplex prostrata</i> Boucher ex DC.  | N11: 21.3<br>N21: 22.8           | N11: 44<br>N21: 47             | -                              | 4                             | 2                                | -                             | beach  |
| <i>Atriplex prostrata</i> subsp. <i>calothea</i> (Rafn) M.A.Gust.<br>[ <i>Atriplex calothea</i> (Rafn) Fr.] | -                                | -                              | -                              | 5                             | 5                                | -                             | -  |
| <i>Atriplex rosea</i> L.  | -                                | -                              | -                              | 10                            | 0                                | -                             | -  |
| <i>Beta vulgaris</i> L.   | N21: 32                          | N21: 35; N31: 15               | -                              | 7                             | 3                                | saltmarsh /<br>shingle        | cliffs / shingle beach / saltmarsh strandlines |
| <i>Chenopodium album</i> L.   | -                                | -                              | -                              | 3                             | 1                                | -                             | -  |
| <i>Chenopodium chenopodioides</i> (L.) Aellen   | -                                | -                              | -                              | -                             | -                                | -                             | -  |
| <i>Chenopodium glaucum</i> L.<br>[ <i>Oxybasis glauca</i> (L.) S. Fuentes, Uotila & Borsch]                 | -                                | -                              | -                              | 3                             | 4                                | -                             | dung heaps / margins of pools                  |
| <i>Chenopodium rubrum</i> L.<br>[ <i>Oxybasis rubra</i> (L.) S. Fuentes, Uotila & Borsch]                   | -                                | -                              | -                              | 3                             | 4                                | -                             | -  |
| <i>Chenopodium suecicum</i> Murr  | -                                | -                              | -                              | 0                             | 1                                | -                             | -  |
| <i>Chenopodium vulvaria</i> L.  | -                                | -                              | -                              | 0                             | 0                                | -                             | disturbed soils                                |
| <i>Corispermum intermedium</i> Schweigg.  | -                                | -                              | -                              | 0                             | 0                                | -                             | -  |
| <i>Corispermum pallasii</i> Steven  | -                                | -                              | -                              | -                             | -                                | -                             | -  |
| <i>Halimione pedunculata</i> L.   | -                                | -                              | -                              | 0                             | 10                               | -                             | -  |
| <i>Halimione portulacoides</i> L.   | -                                | -                              | -                              | 0                             | 10                               | -                             | -  |
| <i>Salicornia europaea</i> L.   | -                                | -                              | -                              | 0                             | 10                               | -                             | middle, upper saltmarsh / muddy shingle        |
| <i>Salicornia procumbens</i> Sm.  | -                                | -                              | -                              | 0                             | 10                               | -                             | -  |
| <i>Salsola kali</i> L.  | N11: 31.3                        | N11: 55                        | -                              | 9                             | 0                                | -                             | sandy beach                                    |
| <i>Suaeda maritima</i> (L.) Dumort.   | -                                | -                              | -                              | 0                             | 10                               | saltmarsh                     | saltmarsh                                      |
| <b>Apiaceae</b>   |                                  |                                |                                |                               |                                  |                               |  |
| <i>Angelica archangelica</i> L.   | -                                | -                              | -                              | 1                             | 1                                | -                             | -  |
| <i>Angelica sylvestris</i> L.   | -                                | -                              | -                              | 1                             | 1                                | machair                       | -  |
| <i>Anthriscus caucalis</i> M.Bieb.  | -                                | -                              | -                              | 3                             | 0                                | -                             | -  |
| <i>Apium graveolens</i> L.  | -                                | -                              | -                              | 0                             | 10                               | saltmarsh                     | saline grassland                               |
| <i>Bupleurum tenuissimum</i> L.   | -                                | -                              | -                              | 0                             | 6                                | -                             | grassland / upper saltmarsh                    |
| <i>Cicuta virosa</i> L.   | -                                | -                              | -                              | 0                             | 2                                | -                             | -  |
| <i>Conium maculatum</i> L.  | -                                | -                              | -                              | 3                             | 3                                | -                             | lanward sides of beaches and cliffs            |
| <i>Daucus carota</i> L.   | N34: 17.1                        | N31: 16; N34: 50               | -                              | 0                             | 0                                | -                             | grassland / cliffs / dunes                     |
| <i>Eryngium maritimum</i> L.  | N34: 24.1                        | N13: 21                        | -                              | 10                            | 0                                | shingle beach /<br>sand beach | -  |
| <i>Heracleum sphondylium</i> L.   | -                                | -                              | -                              | 0                             | 0                                | saltmarsh                     | grassland / cliffs / dunes                     |
| <i>Kaderia dubis</i> (Schuhr) Lavrova & V.N.Tikhom.<br>[ <i>Selinum abubium</i> (Schkuhr) Leute]            | -                                | -                              | -                              | 0                             | 2                                | -                             | -  |

Continued



Table S1. Continued

| Species                                  | EUNIS diagnostic <sup>c</sup> | EUNIS constant <sup>1</sup> | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup>      | GB, IE, NW Europe <sup>4</sup>           |
|--|-------------------------------|-----------------------------|-----------------------------|----------------------------|-------------------------------|---------------------------|--|
| <i>Ligusticum scoticum</i> L.            | -                             | -                           | -                           | 10                         | 0                             | cliffs                    | cliffs / dunes / shingle                 |
| <i>Oenanthe lachenalii</i> C.C.Gmel.     | -                             | -                           | -                           | 10                         | 0                             | -                         | damp meadows / marshes                   |
| <i>Pastinaca sativa</i> L.               | -                             | -                           | -                           | 2                          | 0                             | -                         | calcareous grassland                     |
| <i>Petroselinum crispum</i> (Mill.) Fuss | -                             | -                           | -                           | 3                          | 0                             | -                         | -  |
| <i>Seseli libanotis</i> W.D.J.Koch       | -                             | -                           | -                           | 0                          | 0                             | -                         | chalk grassland                          |
| <i>Sium latifolium</i> L.                | -                             | -                           | -                           | 0                          | 0                             | -                         | -  |
| <b>Apocynaceae</b>                       |                               |                             |                             |                            |                               |                           |  |
| <i>Vincetoxicum hirundinaria</i> Medik.  | -                             | -                           | -                           | 0                          | 0                             | -                         | -  |
| <b>Araliaceae</b>                        |                               |                             |                             |                            |                               |                           |  |
| <i>Hydrocotyle vulgaris</i> L.           | NIH: 32.6                     | NIH: 41                     | -                           | 0                          | 0                             | saltmarsh                 | dune slacks / shingle hollows            |
| <b>Asteraceae</b>                        |                               |                             |                             |                            |                               |                           |  |
| <i>Achillea millefolium</i> L.           | -                             | -                           | -                           | 0                          | 0                             | machair / cliffs          | dunes / shingle                          |
| <i>Achillea ptarmica</i> L.              | -                             | -                           | -                           | -                          | -                             | -                         | -  |
| <i>Ambrosia psilostachya</i> DC.         | -                             | -                           | -                           | 3                          | 0                             | -                         | -  |
| <i>Arctium minus</i> (Hill) Bernh.       | -                             | -                           | -                           | 0                          | 0                             | -                         | waste ground / verges                    |
| <i>Artemisia absinthium</i> L.           | -                             | -                           | -                           | 3                          | 0                             | -                         | disturbed grassland                      |
| <i>Artemisia campestris</i> L.           | -                             | N15: 13                     | -                           | 1                          | 0                             | -                         | -  |
| <i>Artemisia maritima</i> L.             | -                             | -                           | -                           | 0                          | 10                            | -                         | saltmarsh                                |
| <i>Artemisia rupestris</i> L.            | -                             | -                           | -                           | 0                          | 1                             | -                         | -  |
| <i>Artemisia stelleriana</i> Besser      | -                             | -                           | -                           | 10                         | 0                             | -                         | -  |
| <i>Artemisia vulgaris</i> L.             | -                             | -                           | -                           | 3                          | 1                             | -                         | disturbed ground                         |
| <i>Bellis perennis</i> L.                | -                             | -                           | -                           | 0                          | 1                             | machair                   | grassland / dune slacks / clifftop paths |
| <i>Bidens cernua</i> L.                  | -                             | -                           | -                           | 0                          | 0                             | -                         | -  |
| <i>Bidens tripartita</i> L.              | -                             | -                           | -                           | 0                          | 2                             | -                         | -  |
| <i>Carlina vulgaris</i> L.               | -                             | -                           | -                           | 0                          | 0                             | dunes / cliffs            | dry calcareous grassland                 |
| <i>Centaurea jacea</i> L.                | -                             | -                           | -                           | 0                          | 1                             | -                         | -  |
| <i>Centaurea nigra</i> L.                | -                             | -                           | -                           | 0                          | 0                             | -                         | -  |
| <i>Centaurea scabiosa</i> L.             | -                             | -                           | -                           | 0                          | 0                             | cliffs                    | calcareous soils / cliffs / dunes        |
| <i>Cirsium arvense</i> (L.) Scop.        | -                             | N1A: 16                     | -                           | 2                          | 1                             | dunes / shingle / machair | disturbed ground / grassy areas          |
| <i>Cirsium palustre</i> Scop.            | -                             | -                           | -                           | 0                          | 0                             | -                         | damp grassy places                       |
| <i>Cirsium vulgare</i> (Savi) Ten.       | -                             | N1A: 12; N34: 17            | -                           | 1                          | 1                             | shingle                   | grassland / disturbed ground             |
| <i>Cotula coronopifolia</i> L.           | -                             | -                           | -                           | 0                          | 10                            | -                         | -  |
| <i>Echinops sphaerocephalus</i> L.       | -                             | -                           | -                           | 2                          | 0                             | -                         | -  |
| <i>Erigeron acris</i> L.                 | -                             | -                           | -                           | 0                          | 0                             | -                         | shingle / dunes                          |
| <i>Eupatorium cannabinum</i> L.          | -                             | -                           | -                           | 1                          | 2                             | -                         | -  |
| <i>Helichrysum arenarium</i> (L.) Moench | -                             | -                           | -                           | 0                          | 0                             | -                         | -  |
| <i>Hieracium umbellatum</i> L.           | N18: 17.9                     | N15: 23; N18: 31<br>N1F: 24 | -                           | 2                          | 0                             | -                         | -  |

Continued

Table S1. Continued

| Species   | EUNIS diagnostic <sup>1</sup> | EUNIS constant <sup>1</sup>          | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup>     | GB, IE, NW Europe <sup>4</sup>        |
|---|-------------------------------|--------------------------------------|-----------------------------|----------------------------|-------------------------------|--------------------------|---------------------------------------|
| <i>Hypochaeris maculata</i> L.  | -                             | -                                    | -                           | 0                          | 0                             | -                        | dry grassland                         |
| <i>Hypochaeris radicata</i> L.  | -                             | N15: 20 N18: 11<br>N34: 12           | -                           | 0                          | 0                             | shingle                  | dry grassland                         |
| <i>Inula britannica</i> L.  | -                             | -                                    | -                           | 0                          | 3                             | -                        | -                                     |
| <i>Jacobaea vulgaris</i> Gaertn.<br>[ <i>Senecio jacobaea</i> L.]   | N1A: 20.5 N34: 17.7           | N13: 11; N1A: 35<br>N1D: 12; N34: 30 | -                           | 0                          | 0                             | dunes / shingle          | grassland                             |
| <i>Lactuca serriola</i> L.  | -                             | -                                    | -                           | 1                          | 1                             | shingle                  | shingle / disturbed ground            |
| <i>Lactuca tatarica</i> C.A.Mey.  | -                             | -                                    | -                           | 7                          | 0                             | -                        | -                                     |
| <i>Leontodon saxatilis</i> Lam.   | N34: 15.4                     | N1H: 11; N34: 27                     | -                           | 0                          | 0                             | -                        | dunes / grassland                     |
| <i>Leucanthemum vulgare</i> Lam.  | -                             | -                                    | -                           | 0                          | 0                             | machair                  | dunes / cliffs                        |
| <i>Petasites spurius</i> Rchb.f.  | -                             | -                                    | -                           | 7                          | 0                             | -                        | -                                     |
| <i>Pilosella officinarum</i> Vaill.<br>[ <i>Hieracium pilosella</i> L.]                                       | -                             | -                                    | -                           | 0                          | 0                             | dunes / machair / cliffs | dunes / cliffs / meadows              |
| <i>Pulicaria dysenterica</i> (L.) Bernh.  | -                             | -                                    | -                           | 0                          | 10                            | -                        | -                                     |
| <i>Scorzonoides autumnalis</i> (L.) Moench<br>[ <i>Leontodon autumnalis</i> L.]                               | MA232: 18.7                   | MA232: 33                            | -                           | 1                          | 2                             | -                        | dunes / dry saltmarshes               |
| <i>Senecio sylvaticus</i> L.  | N1A: 15                       | N1A: 14                              | -                           | 0                          | 0                             | -                        | cliffs / sandy beaches                |
| <i>Senecio viscosus</i> L.  | -                             | -                                    | -                           | 1                          | 0                             | -                        | shingle / dunes                       |
| <i>Senecio vulgaris</i> L.  | -                             | -                                    | -                           | 2                          | 0                             | -                        | dunes / cliffs                        |
| <i>Serratula tinctoria</i> L.   | -                             | -                                    | -                           | 0                          | 0                             | -                        | cliff-tops / heaths                   |
| <i>Sonchus arvensis</i> L.  | -                             | N13: 11; N21: 12                     | -                           | 2                          | 2                             | saltmarsh / shingle      | beach / saltmarsh strandlines         |
| <i>Sonchus asper</i> (L.) Hill  | -                             | -                                    | -                           | 0                          | 0                             | shingle                  | disturbed ground / rough grassland    |
| <i>Sonchus maritimus</i> L.   | -                             | -                                    | -                           | -                          | -                             | -                        | -                                     |
| <i>Sonchus oleraceus</i> L.   | -                             | N34: 13                              | -                           | 3                          | 0                             | -                        | -                                     |
| <i>Tanacetum vulgare</i> L.   | -                             | -                                    | -                           | 2                          | 1                             | -                        | -                                     |
| <i>Taraxacum</i> spp.   | -                             | -                                    | -                           | -                          | -                             | -                        | cliffs / dunes / meadows              |
| <i>Tragopogon heterospermus</i> Schweigg.   | -                             | -                                    | -                           | -                          | -                             | -                        | -                                     |
| <i>Tragopogon pratensis</i> L.  | -                             | -                                    | -                           | 0                          | 0                             | -                        | dunes                                 |
| <i>Tripleurospermum inodorum</i> (L.) W.D.J.Koch  | -                             | -                                    | -                           | 3                          | 3                             | -                        | disturbed ground                      |
| <i>Tripleurospermum maritimum</i> (L.) W.D.J.Koch   | N21: 19.2                     | N11: 17; N21: 37                     | -                           | 3                          | 3                             | -                        | shingle beach / sand beach            |
| <i>Tripolium pannonicum</i> (Jacq.) Dobrocz.<br>[ <i>Aster tripolium</i> L.] [ <i>Tripolium vulgare</i> Nees] | -                             | MA232: 13<br>N21: 14                 | -                           | 0                          | 10                            | saltmarsh                | saltmarsh / saline grassland / cliffs |
| <i>Tussilago farfara</i> L.   | -                             | -                                    | -                           | 0                          | 0                             | -                        | -                                     |
| <b>Boraginaceae</b>   |                               |                                      |                             |                            |                               |                          |                                       |
| <i>Asperugo procumbens</i> L.   | -                             | -                                    | -                           | 2                          | 0                             | -                        | -                                     |
| <i>Cynoglossum officinale</i> L.  | N1A: 32<br>N1D: 17.6          | N1A: 32; N1D: 18                     | -                           | 2                          | 0                             | -                        | dry grassy places                     |
| <i>Echium vulgare</i> L.  | -                             | -                                    | -                           | 2                          | 0                             | -                        | dry grassland                         |

Continued

Table S1. Continued

| Species   | EUNIS diagnostic <sup>c</sup> | EUNIS constant <sup>i</sup> | EUNIS dominant <sup>i</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                 |
|---|-------------------------------|-----------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|--|
| <i>Mertensia maritima</i> (L.) Gray   | -                             | -                           | -                           | 10                         | 0                             | -                    | -  |
| <i>Myosotis laxa</i> Lehm.  | -                             | -                           | -                           | 1                          | 2                             | -                    | -  |
| <i>Myosotis ramosissima</i> Rochel  | -                             | N1A: 13                     | -                           | 0                          | 0                             | -                    | stabilized dunes                               |
| <b>Brassicaceae</b>   |                               |                             |                             |                            |                               |                      |  |
| <i>Alyssum montanum</i> subsp. <i>gmelinii</i> (Jord.) Hegi & Em.Schmid [ <i>Alyssum gmelinii</i> Jord. & Fourr.]       | -                             | -                           | -                           | -                          | -                             | -                    | -  |
| <i>Arabisopsis lyrata</i> subsp. <i>petraea</i> (L.) O'Kane & Al-Schehbaz [ <i>Arabisopsis petraea</i> (L.) V.I.Dorof.] | -                             | -                           | -                           | 4                          | 0                             | -                    | -  |
| <i>Barbarea vulgaris</i> W.T.Aiton  | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Berteroa incana</i> (L.) DC.   | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Brassica nigra</i> W.D.J.Koch  | -                             | -                           | -                           | 0                          | 2                             | -                    | cliffs / shingle                               |
| <i>Bunias orientalis</i> L.   | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Cakile maritima</i> Scop.  | N11: 51.3                     | N11: 97; N13: 15<br>N21: 12 | N11: 58                     | 10                         | 0                             | -                    | sandy beach / shingle beach / gravel beach     |
| <i>Capsella bursa-pastoris</i> Medik.   | -                             | -                           | -                           | 0                          | 0                             | -                    | beside tracks                                  |
| <i>Cochlearia danica</i> L.   | N31: 23.6<br>N34: 18.9        | N31: 19; N34: 15            | -                           | 4                          | 6                             | -                    | sandy soils / shingle                          |
| <i>Cochlearia officinalis</i> L.  | -                             | -                           | -                           | 0                          | 10                            | -                    | saltmarsh / cliffs                             |
| <i>Crambe maritima</i> L.   | -                             | N21: 14                     | -                           | 10                         | 0                             | shingle              | shingle beach / sandy beach                    |
| <i>Descurainia sophia</i> (L.) Webb ex Pranti   | -                             | -                           | -                           | 3                          | 0                             | -                    | -  |
| <i>Diploaxis tenuifolia</i> (L.) DC.  | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Draba verna</i> L. [ <i>Erophila verna</i> (L.) DC.]   | -                             | -                           | -                           | 0                          | 0                             | -                    | dunes / shingle / cliffs                       |
| <i>Erysimum cheiri</i> Crantz   | -                             | -                           | -                           | 0                          | 0                             | -                    | cliffs   |
| <i>Hornungia petraea</i> Rchb.  | -                             | -                           | -                           | 0                          | 0                             | -                    | calcareous rocks / dunes                       |
| <i>Isatis tinctoria</i> L.  | -                             | -                           | -                           | 6                          | 0                             | -                    | -  |
| <i>Lepidium coronopus</i> (L.) Al-Schehbaz  | -                             | -                           | -                           | 0                          | 0                             | -                    | disturbed ground                               |
| <i>Lepidium draba</i> L.  | -                             | -                           | -                           | 4                          | 0                             | -                    | disturbed ground                               |
| <i>Lepidium latifolium</i> L.   | -                             | -                           | -                           | 9                          | 0                             | -                    | banks of creeks and ditches / saline grassland |
| <i>Lepidium ruderale</i> L.   | -                             | -                           | -                           | 1                          | 0                             | -                    | -  |
| <i>Lobularia maritima</i> (L.) Desv.  | -                             | -                           | -                           | 3                          | 0                             | -                    | -  |
| <i>Raphanus raphanistrum</i> L.   | -                             | -                           | -                           | 0                          | 0                             | -                    | shingle / dunes                                |
| <i>Sisymbrium altissimum</i> L.   | -                             | -                           | -                           | 2                          | 0                             | -                    | -  |
| <i>Subularia aquatica</i> L.  | -                             | -                           | -                           | 2                          | 0                             | -                    | -  |
| <i>Teesdalia nudicaulis</i> (L.) W.T.Aiton  | -                             | -                           | -                           | 0                          | 0                             | -                    | sandy ground / shingle                         |
| <b>Campanulaceae</b>  |                               |                             |                             |                            |                               |                      |  |
| <i>Campanula rotundifolia</i> L.  | -                             | -                           | -                           | 0                          | 0                             | -                    | dune grassland                                 |
| <i>Jasione montana</i> L.   | -                             | N15: 25                     | -                           | 0                          | 0                             | cliffs               | dry grassland / cliffs / dunes                 |

Continued



Table S1. Continued

| Species  | EUNIS diagnostic <sup>1</sup>       | EUNIS constant <sup>1</sup> | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup>         | GB, IE, NW Europe <sup>4</sup>    |
|--|-------------------------------------|-----------------------------|-----------------------------|----------------------------|-------------------------------|------------------------------|-----------------------------------|
| <i>Knaulia arvensis</i> (L.) Coult.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Succisa pratensis</i> Moench  | -                                   | -                           | -                           | 0                          | 0                             | machair                      | -                                 |
| <i>Valeriana excelsa</i> subsp. <i>sambucifolia</i> (J.C.Mikan & Pohl) Holub | -                                   | -                           | -                           | 1                          | 0                             | -                            | -                                 |
| [ <i>Valeriana sambucifolia</i> J.C.Mikan ex Pohl]                           |                                     |                             |                             |                            |                               |                              |                                   |
| <i>Valeriana locusta</i> L. [ <i>Valerianella locusta</i> (L.) Laterr.]      | -                                   | -                           | -                           | 2                          | 0                             | dunes                        | -                                 |
| <i>Valeriana officinalis</i> L.  | -                                   | -                           | -                           | 3                          | 0                             | -                            | -                                 |
| <b>Caryophyllaceae</b>   |                                     |                             |                             |                            |                               |                              |                                   |
| <i>Cerastium arvense</i> L.  | -                                   | N1A: 11                     | -                           | 0                          | 0                             | dunes                        | sand dunes / shingle              |
| <i>Cerastium diffusum</i> Pers.  | N34: 16                             | N34: 12                     | -                           | 10                         | 0                             | -                            | sandy ground                      |
| <i>Cerastium fontanum</i> Baumg.   | -                                   | -                           | -                           | 0                          | 0                             | shingle / machair            | disturbed ground / dunes/ shingle |
| <i>Cerastium semidecandrum</i> L.  | -                                   | N15: 18; N1A: 17            | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Corrigiola litoralis</i> L.   | -                                   | -                           | -                           | 0                          | 0                             | -                            | margins of freshwater             |
| <i>Dianthus arenarius</i> L.   | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Dianthus deltoides</i> L.   | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Dianthus superbus</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Gypsophila fastigiata</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Gypsophila paniculata</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |
| <i>Honckenya peploides</i> (L.) Ehrh.  | N11: 38.8<br>N13: 18.6<br>N21: 32.9 | N11: 40; N13: 19<br>N21: 34 | -                           | 10                         | 0                             | shingle                      | shingle beach / sandy beach       |
| <i>Sagina apetala</i> Ard.   | -                                   | -                           | -                           | 0                          | 0                             | shingle                      | -                                 |
| <i>Sagina maritima</i> Don   | N31: 16.5                           | N31: 14                     | -                           | 6                          | 4                             | -                            | bare ground                       |
| <i>Sagina nodosa</i> (L.) Fenzl  | -                                   | -                           | -                           | 1                          | 2                             | dunes                        | dune slacks                       |
| <i>Sagina procumbens</i> L.  | -                                   | -                           | -                           | 2                          | 0                             | -                            | damp ground on cliffs             |
| <i>Silene boryszenica</i> (Gruner) Walters                                   | -                                   | -                           | -                           | -                          | -                             | -                            | -                                 |
| <i>Silene conica</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | dunes / sandy shingle             |
| <i>Silene dioica</i> (L.) Clairv.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | cliffs / grassland / shingle      |
| <i>Silene flos-cuculi</i> (L.) Greuter & Burdet                              | -                                   | -                           | -                           | 0                          | 1                             | saltmarsh                    | -                                 |
| [ <i>Lychnis flos-cuculi</i> L.]   |                                     |                             |                             |                            |                               |                              |                                   |
| <i>Silene latifolia</i> Poir.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | disturbed ground                  |
| <i>Silene nutans</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | grassland / shingle beach         |
| <i>Silene suecica</i> (Lodd.) Greuter & Burdet                               | -                                   | -                           | -                           | 1                          | 0                             | -                            | -                                 |
| [ <i>Viscaria alpina</i> G. Donn]  |                                     |                             |                             |                            |                               |                              |                                   |
| <i>Silene uniflora</i> Roth  | N31: 16.2                           | N31: 19; N34: 62            | -                           | 5                          | 0                             | saltmarsh / shingle / cliffs | cliffs / shingle                  |
| [ <i>Silene maritima</i> With.]  | N34: 52.8                           |                             |                             |                            |                               |                              |                                   |
| <i>Silene viscosa</i> Pers.  | -                                   | -                           | -                           | 5                          | 0                             | -                            | -                                 |
| <i>Spergula arvensis</i> L.  | -                                   | -                           | -                           | 0                          | 0                             | -                            | -                                 |

Continued

Table S1. Continued

| Species  | EUNIS diagnostic <sup>c</sup> | EUNIS constant <sup>i</sup> | EUNIS dominant <sup>i</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>  |
|--|-------------------------------|-----------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|---------------------------------|
| <i>Spergularia marina</i> (L.) Besser          | -                             | MA232: 13                   | -                           | 0                          | 10                            | saltmarsh            | upper saltmarsh                 |
| [ <i>Spergularia salina</i> J.Presl & C.Presl] | -                             | -                           | -                           | 0                          | 0                             | -                    | -                               |
| <i>Spergularia media</i> (L.) C.Presl          | -                             | -                           | -                           | 0                          | 10                            | saltmarsh            | upper saltmarsh                 |
| <i>Spergularia rubra</i> J.Presl & C.Presl     | -                             | -                           | -                           | 0                          | 0                             | -                    | -                               |
| <i>Stellaria crassifolia</i> Ehrh.             | -                             | -                           | -                           | 0                          | 4                             | -                    | -                               |
| <i>Stellaria fennica</i> (Murb.) Perfil.       | -                             | -                           | -                           | 0                          | 10                            | -                    | -                               |
| <i>Stellaria graminea</i> L.                   | -                             | -                           | -                           | 1                          | 0                             | -                    | -                               |
| <i>Stellaria media</i> (L.) Vill.              | -                             | -                           | -                           | 1                          | 1                             | -                    | disturbed ground / strandline   |
| <i>Stellaria pallida</i> (Dumort.) Crép.       | N1A: 16.3                     | -                           | -                           | 0                          | 2                             | -                    | -                               |
| <i>Stellaria palustris</i> Retz.               | -                             | -                           | -                           | 0                          | 1                             | -                    | -                               |
| <b>Cistaceae</b>                               |                               |                             |                             |                            |                               |                      |                                 |
| <i>Helianthemum nummularium</i> Mill.          | -                             | -                           | -                           | 0                          | 0                             | cliffs               | dry grassland / dunes           |
| <i>Helianthemum oelandicum</i> (L.) DC.        | -                             | -                           | -                           | 0                          | 0                             | -                    | grassy places on limestone      |
| <b>Convulvaceae</b>                            |                               |                             |                             |                            |                               |                      |                                 |
| <i>Calystegia sepium</i> (L.) R.Br.            | -                             | -                           | -                           | 1                          | 1                             | saltmarsh            | -                               |
| <i>Calystegia soldanella</i> (L.) R.Br.        | -                             | N13: 15                     | -                           | -                          | -                             | -                    | dunes /shingle                  |
| <i>Convolvulus arvensis</i> L.                 | -                             | -                           | -                           | 0                          | 0                             | -                    | -                               |
| <i>Cuscuta epithymum</i> L.                    | -                             | -                           | -                           | 0                          | 0                             | -                    | grassy places / heaths          |
| <i>Cuscuta europaea</i> L.                     | -                             | -                           | -                           | 1                          | 2                             | -                    | -                               |
| <b>Crassulaceae</b>                            |                               |                             |                             |                            |                               |                      |                                 |
| <i>Crassula aquatica</i> (L.) Schönland        | -                             | -                           | -                           | 0                          | 4                             | -                    | -                               |
| <i>Hylotelephium maximum</i> (L.) Holub        | -                             | -                           | -                           | 0                          | 0                             | -                    | -                               |
| [ <i>Sedum maximum</i> (L.) Holub]             | -                             | -                           | -                           | 0                          | 0                             | -                    | -                               |
| <i>Sedum album</i> L.                          | -                             | -                           | -                           | 1                          | 0                             | -                    | rocky ground / cliffs / shingle |
| <i>Sedum acre</i> L.                           | -                             | N15: 19                     | -                           | 1                          | 0                             | shingle              | dunes / shingle / gravel        |
| <i>Sedum anglicum</i> Huds.                    | N34: 23.7                     | N34: 20                     | -                           | 5                          | 0                             | -                    | -                               |
| <b>Elatinaceae</b>                             |                               |                             |                             |                            |                               |                      |                                 |
| <i>Elatine hydropiper</i> L.                   | -                             | -                           | -                           | 0                          | 3                             | -                    | -                               |
| <i>Elatine orthosperma</i> Dübén               | -                             | -                           | -                           | 0                          | 3                             | -                    | -                               |
| <i>Elatine triandra</i> Schkuhr                | -                             | -                           | -                           | 0                          | 3                             | -                    | -                               |
| <b>Ericaceae</b>                               |                               |                             |                             |                            |                               |                      |                                 |
| <i>Calluna vulgaris</i> (L.) Hill.             | N18: 16.1<br>N1F: 17.1        | N18: 66; N1F: 69            | N18: 35                     | 0                          | 0                             | cliffs               | heaths                          |
| <i>Empetrum nigrum</i> L.                      | N18: 32.9<br>N1F: 24.8        | N18: 100; N1F: 76           | N18: 84                     | 0                          | 0                             | -                    | -                               |
| <i>Erica tetralix</i> L.                       | -                             | N18: 32; N1F: 15            | -                           | 0                          | 0                             | -                    | -                               |
| <i>Orthilia secunda</i> (L.) House             | -                             | N1F: 13                     | -                           | 1                          | 0                             | -                    | -                               |
| <i>Pyrola rotundifolia</i> L.                  | -                             | -                           | -                           | 0                          | 0                             | -                    | dune slacks                     |

Continued

Table S1. Continued

| Species  | EUNIS<br>diagnosti <sup>c</sup> | EUNIS<br>constant <sup>1</sup>       | EUNIS<br>dominant <sup>1</sup> | SE sea<br>shores <sup>2</sup> | SE shore<br>meadows <sup>2</sup> | GB NPMs <sup>3</sup>            | GB, IE, NW Europe <sup>4</sup>         |
|--|---------------------------------|--------------------------------------|--------------------------------|-------------------------------|----------------------------------|---------------------------------|--|
| <i>Euphorbia esula</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Euphorbia helioscopia</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Euphorbia palustris</i> L.  | -                               | -                                    | -                              | 1                             | 4                                | -                               | -                                      |
| <i>Euphorbia peplus</i> L.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | sandy beach / gravel beach             |
| <b>Fabaceae</b>  |                                 |                                      |                                |                               |                                  |                                 |  |
| <i>Anthyllis vulneraria</i> L.   | N34: 22.4                       | N34: 60                              | N34: 30                        | 0                             | 0                                | -                               | calcareous grassland / shingle / dunes |
| <i>Anthyllis vulneraria</i> subsp. <i>maritima</i> (Schweigg. ex K.G.Hagen) Corb.<br>[ <i>Anthyllis maritima</i> Schweigg. ex K.G.Hagen] | -                               | -                                    | -                              | -                             | -                                | -                               | -                                      |
| <i>Astragalus danicus</i> Retz.  | -                               | -                                    | -                              | 0                             | 3                                | -                               | dunes / machair / cliffs               |
| <i>Astragalus glycyphyllos</i> L.<br>[ <i>Astragalus glycyphyllos</i> L.]  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Cytisus scoparius</i> (L.) Link   | -                               | -                                    | -                              | 0                             | 0                                | -                               | sea-exposed rock faces                 |
| <i>Genista pilosa</i> L.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | heaths / cliffs                        |
| <i>Genista tinctoria</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | cliffs                          | -                                      |
| <i>Lathyrus japonicus</i> Willd.<br>[ <i>Lathyrus maritimus</i> (L.) Fr.]  | N21: 26.8                       | N21: 14                              | -                              | 10                            | 0                                | -                               | shingle beach / sandy beach            |
| <i>Lathyrus latifolius</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Lathyrus palustris</i> L.   | -                               | -                                    | -                              | 0                             | 3                                | -                               | -                                      |
| <i>Lathyrus pratensis</i> L.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | grassland                              |
| <i>Lathyrus sylvestris</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Lotus corniculatus</i> L.   | -                               | N18: 17; N1A: 18<br>N1H: 17; N34: 40 | -                              | 0                             | 0                                | saltmarsh /<br>machair / cliffs | grassy places                          |
| <i>Lotus maritimus</i> L.  | -                               | -                                    | -                              | 0                             | 6                                | -                               | -                                      |
| <i>Lotus pedunculatus</i> Cav.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | dampy grasslands / fens                |
| <i>Lotus tenuis</i> Waldst. & Kit. ex Willd.   | -                               | -                                    | -                              | 0                             | 7                                | -                               | -                                      |
| <i>Medicago falcata</i> L.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Medicago lupulina</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | dunes / machair                 | short grassland                        |
| <i>Medicago sativa</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | -                                      |
| <i>Melilotus albus</i> Medik.  | -                               | -                                    | -                              | 1                             | 1                                | -                               | -                                      |
| <i>Melilotus dentatus</i> (Waldst. & Kit.) Desf.   | -                               | -                                    | -                              | 4                             | 4                                | -                               | -                                      |
| <i>Melilotus officinalis</i> (L.) Lam.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | grassy places                          |
| <i>Ononis spinosa</i> L.   | -                               | -                                    | -                              | 0                             | 6                                | -                               | grassland / grazing marshes            |
| <i>Ornithopus perpusillus</i> L.   | -                               | -                                    | -                              | 0                             | 0                                | -                               | dunes / cliff paths                    |
| <i>Trifolium arvense</i> L.  | -                               | -                                    | -                              | 0                             | 0                                | -                               | sand dunes / cliffs / gravel beach     |
| <i>Trifolium fragiferum</i> L.   | MA232: 24                       | MA232: 31                            | -                              | 0                             | 7                                | dunes                           | grassy places                          |
| <i>Trifolium pratense</i> L.   | -                               | -                                    | -                              | 0                             | 1                                | dunes / machair                 | grassy places                          |

Continued



Table S1. Continued

| Species   | EUNIS diagnostic <sup>1</sup> | EUNIS constant <sup>1</sup>   | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>  |
|---|-------------------------------|-------------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|---------------------------------|
| <i>Trifolium repens</i> L.                      | -                             | MA232: 19<br>N1H: 22; N34: 22 | -                           | 0                          | 1                             | dunes / machair      | grassy places                   |
| <i>Trifolium striatum</i> L.                    | -                             | -                             | -                           | 0                          | 0                             | cliffs               | grassy places on sand or gravel |
| <i>Ulex europaeus</i> L.                        | -                             | -                             | -                           | 0                          | 0                             | cliffs               |                                 |
| <i>Vicia cracca</i> L.                          | -                             | -                             | -                           | 1                          | 0                             | saltmarsh / dunes    | grassy places                   |
| <i>Vicia lathyroides</i> L.                     | -                             | -                             | -                           | 0                          | 0                             | -                    | short grassland                 |
| <i>Vicia lutea</i> L.                           | -                             | -                             | -                           | 0                          | 0                             | -                    | cliff-side grassland / shingle  |
| <i>Vicia sativa</i> L.                          | -                             | -                             | -                           | 0                          | 0                             | -                    | shingle beach / sandy beach     |
| <b>Gentianaceae</b>                             |                               |                               |                             |                            |                               |                      |                                 |
| <i>Blackstonia perfoliata</i> (L.) Huds.        | -                             | -                             | -                           | 0                          | 0                             | cliffs               | -                               |
| <i>Centaurium erythraea</i> Rafn                | -                             | N34: 15                       | -                           | 0                          | 1                             | -                    | dry grassland / dunes           |
| <i>Centaurium littorale</i> (Turner) Gilmour    | -                             | -                             | -                           | 0                          | 6                             | -                    | sandy soils                     |
| <i>Centaurium pulchellum</i> (Sw.) Druce        | -                             | -                             | -                           | 0                          | 8                             | -                    | dunes / damp grassland          |
| <i>Gentianella amarella</i> (L.) Börner         | -                             | -                             | -                           | 0                          | 0                             | machair              | calcareous soil / dunes         |
| <i>Gentiana pneumonanthe</i> L.                 | -                             | -                             | -                           | 0                          | 0                             | -                    | -                               |
| <i>Gentianella campestris</i> (L.) Börner       | -                             | -                             | -                           | 0                          | 0                             | -                    | grassland                       |
| <i>Gentianella uliginosa</i> (Willd.) Harry Sm. | -                             | -                             | -                           | 0                          | 4                             | -                    | -                               |
| <b>Geraniaceae</b>                              |                               |                               |                             |                            |                               |                      |                                 |
| <i>Erodium cicutarium</i> (L.) L'Hér.           | -                             | -                             | -                           | 0                          | 0                             | -                    | bare grassy places              |
| <i>Geranium palustre</i> L.                     | -                             | -                             | -                           | 0                          | 0                             | -                    | -                               |
| <i>Geranium robertianum</i> L.                  | -                             | N10: 21                       | -                           | 1                          | 0                             | shingle              | -                               |
| <i>Geranium sanguineum</i> L.                   | -                             | -                             | -                           | 0                          | 0                             | dunes                | dunes / cliffs                  |
| <b>Hypericaceae</b>                             |                               |                               |                             |                            |                               |                      |                                 |
| <i>Hypericum perforatum</i> L.                  | -                             | -                             | -                           | 0                          | 0                             | -                    | dune grassland                  |
| <b>Lamiaceae</b>                                |                               |                               |                             |                            |                               |                      |                                 |
| <i>Betonica officinalis</i> L.                  | -                             | -                             | -                           | 0                          | 0                             | -                    | cliff tops / dunes              |
| [ <i>Stachys officinalis</i> (L.) Trevis.]      | -                             | -                             | -                           | 0                          | 0                             | -                    | -                               |
| <i>Galeopsis bifida</i> Boenn.                  | -                             | -                             | -                           | 1                          | 0                             | -                    | -                               |
| <i>Lamium purpureum</i> L.                      | -                             | -                             | -                           | 0                          | 0                             | -                    | disturbed ground                |
| <i>Lycopus europaeus</i> L.                     | -                             | -                             | -                           | 0                          | 1                             | -                    | -                               |
| <i>Marrubium vulgare</i> L.                     | -                             | -                             | -                           | 0                          | 0                             | -                    | dry disturbed ground            |
| <i>Mentha aquatica</i> L.                       | N1H: 20                       | N1H: 36                       | -                           | 0                          | 3                             | -                    | -                               |
| <i>Prunella vulgaris</i> L.                     | -                             | N1H: 20                       | -                           | 0                          | 0                             | machair              | -                               |
| <i>Scutellaria galericulata</i> L.              | -                             | -                             | -                           | 1                          | 0                             | -                    | dune slacks / marshes           |
| <i>Scutellaria hastifolia</i> L.                | -                             | -                             | -                           | 0                          | 6                             | -                    | -                               |
| <i>Stachys palustris</i> L.                     | -                             | -                             | -                           | 1                          | 2                             | -                    | -                               |
| <i>Thymus serpyllum</i> L.                      | -                             | -                             | -                           | 0                          | 0                             | -                    | -                               |
| <b>Linaceae</b>                                 |                               |                               |                             |                            |                               |                      |                                 |
| <i>Linum catharticum</i> L.                     | -                             | -                             | -                           | 0                          | 1                             | -                    | machair                         |

Continued

Table S1. Continued

| Species   | EUNIS<br>diagnosti <sup>c</sup> | EUNIS<br>constant <sup>1</sup> | EUNIS<br>dominant <sup>1</sup> | SE sea<br>shores <sup>2</sup> | SE shore<br>meadows <sup>2</sup> | GB NPMS <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                 |
|---|---------------------------------|--------------------------------|--------------------------------|-------------------------------|----------------------------------|----------------------|--|
| <i>Lythrum salicaria</i> L.   | -                               | N1H: 11                        | Lythraceae                     | 2                             | 1                                | -                    | -  |
| <i>Althaea officinalis</i> L.   | -                               | -                              | Malvaceae                      | 0                             | 6                                | -                    | wetlands / upper saltmarsh                     |
| <i>Malva neglecta</i> Wallr.  | -                               | -                              | -                              | 0                             | 0                                | -                    | coastal tracks / strandline / disturbed ground |
| <i>Malva sylvestris</i> L.  | -                               | -                              | -                              | 1                             | 1                                | -                    | grassy verges / disturbed ground / near cliffs |
| <i>Claytonia perfoliata</i> Donn ex Willd.<br>[ <i>Montia perfoliata</i> (Donn ex Willd.) Howell]                             | N1A: 23.9                       | -                              | Montiaceae                     | 3                             | 0                                | -                    | dry sandy soil                                 |
| <i>Montia fontana</i> L.  | -                               | -                              | -                              | 0                             | 2                                | -                    | -  |
| <i>Epilobium angustifolium</i> L.<br>[ <i>Chamaenerion angustifolium</i> (L.) Scop.]  | -                               | -                              | Onagraceae                     | 0                             | 0                                | -                    | dunes  |
| <i>Epilobium hirsutum</i> L.  | -                               | -                              | -                              | 0                             | 0                                | -                    | -  |
| <i>Epilobium palustre</i> L.  | -                               | N1H: 12                        | -                              | 0                             | 0                                | -                    | -  |
| <i>Oenothera biennis</i> L.   | -                               | -                              | -                              | 0                             | 0                                | -                    | disturbed ground / dunes                       |
| <i>Euphrasia botanica</i> Kihlm.  | -                               | -                              | Orobanchaceae                  | 6                             | 0                                | -                    | -  |
| <i>Euphrasia micrantha</i> Rchb.  | -                               | -                              | -                              | 0                             | 0                                | -                    | -  |
| <i>Euphrasia nemorosa</i> (Pers.) Wallr.  | -                               | -                              | -                              | 0                             | 1                                | -                    | -  |
| <i>Euphrasia officinalis</i> L.   | -                               | -                              | -                              | 0                             | 0                                | -                    | undisturbed grassy places                      |
| <i>Euphrasia stricta</i> J.P.Wolff ex J.E.Lehm.   | -                               | -                              | -                              | 0                             | 1                                | -                    | -  |
| <i>Euphrasia wettsteinii</i> G.L.Gusarova   | -                               | -                              | -                              | 1                             | 0                                | -                    | -  |
| <i>Melampyrum arvense</i> L.  | -                               | -                              | -                              | 0                             | 0                                | -                    | -  |
| <i>Melampyrum pratense</i> L.   | N1F: 24.9                       | N1F:56                         | -                              | 0                             | 0                                | -                    | -  |
| <i>Odonites litoralis</i> (Fr.) Fr.   | -                               | -                              | -                              | 0                             | 10                               | -                    | -  |
| <i>Odonites vernus</i> (Bellard) Dumort.  | -                               | -                              | -                              | 0                             | 3                                | machair              | disturbed ground                               |
| <i>Odonites vulgaris</i> Moench   | -                               | MA232: 14                      | -                              | 0                             | 2                                | -                    | -  |
| <i>Rhinanthus major</i> L.<br>[ <i>Rhinanthus angustifolius</i> C.C.Gmel.]<br>[ <i>Rhinanthus serotinus</i> (Schönh.) Oborny] | -                               | -                              | -                              | 0                             | 1                                | -                    | grassland                                      |
| <i>Rhinanthus minor</i> L.  | -                               | -                              | -                              | 0                             | 1                                | machair              | undisturbed meadows / stabilized dunes         |
| <i>Fumaria officinalis</i> L.   | -                               | -                              | Papaveraceae                   | 0                             | 0                                | -                    | drained arable soils                           |
| <i>Glaucium flavum</i> Crantz   | -                               | -                              | -                              | 7                             | 0                                | shingle              | shingle beach                                  |
| <i>Pseudofumaria lutea</i> (L.) Borkh.  | -                               | -                              | -                              | 2                             | 0                                | -                    | -  |
| <i>Callitriche hermaphroditica</i> L.   | -                               | -                              | Plantaginaceae                 | 0                             | 4                                | -                    | -  |

Continued

Table S1. Continued

| Species   | EUNIS<br>diagnostici <sup>c</sup> | EUNIS<br>constant <sup>1</sup> | EUNIS<br>dominant <sup>1</sup> | SE sea<br>shores <sup>2</sup> | SE shore<br>meadows <sup>2</sup> | GB NPMS <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>             |
|---|-----------------------------------|--------------------------------|--------------------------------|-------------------------------|----------------------------------|----------------------|--|
| <i>Cymbalaria muralis</i> G.Gaertn., B.Mey. & Scherb.               | -                                 | -                              | -                              | 0                             | 0                                | -                    | rocks / shingle                            |
| <i>Hippuris lanceolata</i> Retz.                                    | -                                 | -                              | -                              | 0                             | 10                               | -                    | -  |
| <i>Hippuris tetraphylla</i> L.f.                                    | -                                 | -                              | -                              | 0                             | 10                               | -                    | -  |
| <i>Linaria loeselii</i> Schweigg.                                   | -                                 | -                              | -                              | -                             | -                                | -                    | -  |
| <i>Linaria vulgaris</i> Mill.                                       | -                                 | -                              | -                              | 2                             | 0                                | -                    | dry grassland / roadsides                  |
| <i>Littorella uniflora</i> (L.) Asch [ <i>Plantago uniflora</i> L.] | -                                 | -                              | -                              | 0                             | 2                                | -                    | -  |
| <i>Plantago coronopus</i> L.  | N31: 16.9<br>N34: 25.4            | N31: 38; N34: 57               | -                              | 5                             | 5                                | dunes / shingle      | grassland / disturbed ground / rocky sites |
| <i>Plantago lanceolata</i> L.                                       | -                                 | N1A: 12; N1H: 12<br>N34: 33    | -                              | 0                             | 1                                | shingle / machair    | dunes / cliffs                             |
| <i>Plantago major</i> L.  | -                                 | MA232: 17                      | -                              | 1                             | 1                                | -                    | disturbed grassland                        |
| <i>Plantago maritima</i> L.   | MA232: 21.8                       | MA232: 47<br>N31: 18; N34: 18  | -                              | 3                             | 4                                | saltmarsh / cliffs   | saltmarsh / cliffs                         |
| <i>Plantago media</i> L.  | -                                 | -                              | -                              | 0                             | 1                                | -                    | -  |
| <i>Veronica arvensis</i> L.   | -                                 | -                              | -                              | 0                             | 0                                | -                    | dunes                                      |
| <i>Veronica beccabunga</i> L.                                       | -                                 | -                              | -                              | 0                             | 0                                | -                    | -  |
| <i>Veronica longifolia</i> L.                                       | -                                 | -                              | -                              | 1                             | 2                                | -                    | -  |
| <i>Veronica officinalis</i> L.                                      | -                                 | N1A: 18                        | -                              | 0                             | 0                                | -                    | -  |
| <i>Veronica scutellata</i> L.                                       | -                                 | -                              | -                              | 0                             | 1                                | -                    | -  |
| <i>Veronica spicata</i> L.  | -                                 | -                              | -                              | 0                             | 0                                | -                    | -  |
| <b>Plumbaginaceae</b>   |                                   |                                |                                |                               |                                  |                      |  |
| <i>Armeria maritima</i> (Mill.) Willd.                              | N31: 28.8<br>N34: 44.1            | N31: 51; N34: 77               | N34: 32                        | 4                             | 3                                | saltmarsh / cliffs   | cliffs / saltmarsh                         |
| <i>Limonium humile</i> Mill.  | -                                 | -                              | -                              | 0                             | 10                               | saltmarsh            | saltmarsh                                  |
| <i>Limonium vulgare</i> Mill.                                       | -                                 | -                              | -                              | 0                             | 10                               | saltmarsh            | saltmarsh                                  |
| <b>Polygalaceae</b>   |                                   |                                |                                |                               |                                  |                      |  |
| <i>Polygala serpyllifolia</i> Hosé                                  | -                                 | -                              | -                              | 0                             | 0                                | cliffs               | -  |
| <b>Polygonaceae</b>   |                                   |                                |                                |                               |                                  |                      |  |
| <i>Persicaria amphibia</i> (L.) Delarbre                            | -                                 | -                              | -                              | 0                             | 0                                | -                    | -  |
| <i>Persicaria hydropiper</i> (L.) Delarbre                          | -                                 | -                              | -                              | 0                             | 2                                | -                    | -  |
| <i>Persicaria lapathifolia</i> (L.) Delarbre                        | -                                 | -                              | -                              | 1                             | 3                                | -                    | -  |
| <i>Polygonum aviculare</i> L.                                       | -                                 | -                              | -                              | 1                             | 1                                | -                    | bare soil                                  |
| <i>Polygonum oxyspermum</i> C.A.Mey. & Bunge                        | -                                 | -                              | -                              | 10                            | 0                                | -                    | sand beach / shingle beach                 |
| <i>Rumex acetosa</i> L.   | -                                 | -                              | -                              | 0                             | 0                                | -                    | shingle / meadow                           |
| <i>Rumex acetosella</i> L.  | -                                 | N15: 18                        | -                              | 0                             | 0                                | dunes / machair      | shingle beach / short grassland            |
| <i>Rumex conglomeratus</i> Murray                                   | -                                 | -                              | -                              | 0                             | 0                                | -                    | damp meadows / beside tracks               |
| <i>Rumex crispus</i> L.   | -                                 | N21: 26                        | -                              | 2                             | 2                                | shingle              | meadows / dunes / strandlines              |
| <i>Rumex hydrolapathum</i> Huds.                                    | -                                 | -                              | -                              | 0                             | 0                                | -                    | -  |

Continued



Table S1. Continued

| Species   | EUNIS diagnostic <sup>1</sup> | EUNIS constant <sup>1</sup> | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMs <sup>3</sup> | GB, IE, NW Europe <sup>4</sup>                           |
|---|-------------------------------|-----------------------------|-----------------------------|----------------------------|-------------------------------|----------------------|--|
| <i>Rumex longifolius</i> DC.  | -                             | -                           | -                           | 0                          | 0                             | -                    | cliffs / beaches   |
| <i>Rumex maritimus</i> L.   | -                             | -                           | -                           | 0                          | 8                             | -                    | muddy freshwater margins / brackish margins              |
| <i>Rumex obtusifolius</i> L.  | -                             | -                           | -                           | 0                          | 0                             | cliffs               | field margins / disturbed meadows                        |
| <i>Rumex palustris</i> Sm.  | -                             | -                           | -                           | 0                          | 4                             | -                    | -  |
| <i>Rumex pseudonatronatus</i> (Borbás) Murb.  | -                             | -                           | -                           | 7                          | 0                             | -                    | -  |
| <b>Primulaceae</b>  |                               |                             |                             |                            |                               |                      |  |
| <i>Lysimachia arvensis</i> (L.) U.Manns & Anderb.<br>[ <i>Anagallis arvensis</i> L.]    | -                             | -                           | -                           | 0                          | 0                             | -                    | disturbed ground / dunes / machair / cliffs              |
| <i>Lysimachia maritima</i> (L.) Galasso, Banfi & Soldano<br>[ <i>Glaux maritima</i> L.] | MA232: 36.2                   | MA232: 58                   | -                           | 3                          | 7                             | saltmarsh            | upper saltmarsh / wet shingle hollows                    |
| <i>Lysimachia vulgaris</i> L.   | -                             | -                           | -                           | 0                          | 0                             | dunes                | -  |
| <i>Primula nutans</i> Georgi  | -                             | -                           | -                           | 10                         | 0                             | -                    | -  |
| <i>Samolus valerandi</i> L.   | -                             | -                           | -                           | 0                          | 8                             | -                    | dune slacks / lagoons                                    |
| <b>Ranunculaceae</b>  |                               |                             |                             |                            |                               |                      |  |
| <i>Halperstes cymbalaria</i> Greene   | -                             | -                           | -                           | 0                          | 10                            | -                    | -  |
| <i>Pulsatilla pratensis</i> Mill.   | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Ranunculus acris</i> L.  | -                             | NIH: 11                     | -                           | 0                          | 0                             | dunes                | damp meadows / dune grassland                            |
| <i>Ranunculus auricomus</i> L.  | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Ranunculus bulbosus</i> L.   | -                             | -                           | -                           | 0                          | 0                             | machair / cliffs     | dunes / meadows  |
| <i>Ranunculus circinatus</i> Sibth.   | -                             | -                           | -                           | 0                          | 3                             | -                    | -  |
| <i>Ranunculus confervoides</i> (Brid.) Loeske   | -                             | -                           | -                           | 0                          | 3                             | -                    | -  |
| <i>Ranunculus flammula</i> L.   | NIH: 19.5                     | NIH: 24                     | -                           | 0                          | 0                             | -                    | -  |
| <i>Ranunculus peltatus</i> Schrank  | -                             | -                           | -                           | 8                          | 0                             | -                    | -  |
| <i>Ranunculus repens</i> L.   | -                             | NIH: 12                     | -                           | 0                          | 1                             | dunes                | grassland / disturbed ground / dune slacks               |
| <i>Ranunculus sardous</i> Crantz  | -                             | -                           | -                           | 0                          | 0                             | -                    | disturbed soil / trampled ground                         |
| <i>Ranunculus sceleratus</i> L.   | -                             | -                           | -                           | 0                          | 3                             | -                    | pool margins / muddy hollows in marshes                  |
| <i>Thalictrum flavum</i> L.   | -                             | -                           | -                           | 0                          | 1                             | -                    | -  |
| <i>Thalictrum minus</i> L.  | -                             | -                           | -                           | 0                          | 0                             | dunes / machair      | -  |
| <i>Thalictrum simplex</i> L.  | -                             | -                           | -                           | 1                          | 0                             | -                    | -  |
| <b>Resedaceae</b>   |                               |                             |                             |                            |                               |                      |  |
| <i>Reseda lutea</i> L.  | -                             | -                           | -                           | 0                          | 0                             | -                    | dunes / calcareous grassland                             |
| <i>Reseda luteola</i> L.  | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <b>Rosaceae</b>   |                               |                             |                             |                            |                               |                      |  |
| <i>Agrimonia eupatoria</i> L.   | -                             | -                           | -                           | 0                          | 0                             | -                    | -  |
| <i>Aphanes arvensis</i> L.  | -                             | -                           | -                           | 0                          | 0                             | -                    | bare ground on sandy shores / shingle shores / grassland |
| <i>Borkhausenia intermedia</i> (Ehrh.) Sennikov & Kurtto                                | -                             | -                           | -                           | 1                          | 2                             | -                    | -  |
| <i>Comarum palustre</i> L.  | -                             | -                           | -                           | 1                          | 0                             | -                    | -  |

Continued

Table S1. Continued

| Species   | EUNIS diagnostic <sup>c</sup> | EUNIS constant <sup>1</sup>   | EUNIS dominant <sup>1</sup> | SE sea shores <sup>2</sup> | SE shore meadows <sup>2</sup> | GB NPMS <sup>3</sup>      | GB, IE, NW Europe <sup>4</sup> |
|---|-------------------------------|-------------------------------|-----------------------------|----------------------------|-------------------------------|---------------------------|--------------------------------|
| <i>Filipendula ulmaria</i> (L.) Maxim.                              | -                             | -                             | -                           | 0                          | 0                             | -                         | dune slacks / marshes          |
| <i>Hedlundia hybrida</i> (L.) Sennikov & Kurtto                     | -                             | -                             | -                           | 2                          | 0                             | -                         | -                              |
| <i>Potentilla anserina</i> L.                                       | MA232: 26.5                   | MA232: 52<br>NIH: 25; N21: 17 | -                           | 2                          | 0                             | saltmarsh / shingle       | dunes / saltmarsh / grassland  |
| <i>Potentilla erecta</i> (L.) Raeusch.                              | -                             | NIH: 17; NIH: 14              | -                           | 0                          | 0                             | cliffs                    | grasslands                     |
| <i>Potentilla reptans</i> L.  | -                             | -                             | -                           | 1                          | 1                             | dunes                     | grassland / dune slacks        |
| <i>Potentilla sterilis</i> (L.) Garcke                              | -                             | -                             | -                           | 0                          | 0                             | -                         | -                              |
| <i>Sanguisorba minor</i> Scop.<br>[ <i>Poterium sanguisorba</i> L.] | -                             | -                             | -                           | 0                          | 0                             | cliffs                    | -                              |
| <b>Rubiaceae</b>  |                               |                               |                             |                            |                               |                           |                                |
| <i>Galium aparine</i> L.  | -                             | NIA: 16; NID: 34              | -                           | 2                          | 0                             | shingle / machair         | -                              |
| <i>Galium boreale</i> L.  | -                             | -                             | -                           | 0                          | 1                             | -                         | -                              |
| <i>Galium mollugo</i> L.  | -                             | NIA: 28; NID: 13              | -                           | 0                          | 0                             | -                         | -                              |
| <i>Galium palustre</i> L.   | -                             | MA232: 17<br>NIH: 25          | -                           | 0                          | 1                             | -                         | -                              |
| <i>Galium saxatile</i> L.   | -                             | -                             | -                           | 0                          | 0                             | -                         | heaths / grassland             |
| <i>Galium uliginosum</i> L.   | -                             | -                             | -                           | 0                          | 1                             | -                         | -                              |
| <i>Galium verum</i> L.  | -                             | NI5: 19; NIA: 34              | -                           | 0                          | 0                             | machair                   | dry grassland                  |
| <b>Saxifragaceae</b>  |                               |                               |                             |                            |                               |                           |                                |
| <i>Saxifraga tridactylites</i> L.                                   | -                             | -                             | -                           | 0                          | 0                             | -                         | cliffs / dry bare ground       |
| <b>Scrophulariaceae</b>   |                               |                               |                             |                            |                               |                           |                                |
| <i>Verbascum thapsus</i> L.   | -                             | -                             | -                           | 0                          | 0                             | -                         | dry grassy places / roadsides  |
| <b>Solanaceae</b>   |                               |                               |                             |                            |                               |                           |                                |
| <i>Datura stramonium</i> L.   | -                             | -                             | -                           | 3                          | 0                             | -                         | -                              |
| <i>Hyoscyamus niger</i> L.  | -                             | -                             | -                           | 3                          | 0                             | -                         | -                              |
| <i>Solanum dulcamara</i> L.   | -                             | NIA: 20 NID: 17               | -                           | 2                          | 1                             | shingle                   | shingle beach                  |
| <i>Solanum nigrum</i> L.  | -                             | -                             | -                           | 2                          | 0                             | -                         | -                              |
| <i>Solanum villosum</i> Mill.                                       | -                             | -                             | -                           | 3                          | 0                             | -                         | -                              |
| <b>Urticaceae</b>   |                               |                               |                             |                            |                               |                           |                                |
| <i>Urtica dioica</i> L.   | -                             | NIA: 28 NID: 48               | -                           | 0                          | 0                             | dunes / shingle / machair | disturbed soils                |
| <i>Urtica urens</i> L.  | -                             | -                             | -                           | 1                          | 0                             | -                         | -                              |
| <b>Violaceae</b>  |                               |                               |                             |                            |                               |                           |                                |
| <i>Viola canina</i> L.  | -                             | N18: 11                       | -                           | 1                          | 0                             | -                         | -                              |
| <i>Viola pumila</i> Chaix   | -                             | -                             | -                           | 0                          | 4                             | -                         | -                              |
| <i>Viola tricolor</i> L.  | -                             | -                             | -                           | 1                          | 0                             | -                         | dunes                          |