# Between land and sea — saline and brackish grasslands of the Baltic Sea coast

data usability, characterisation and conservation

**Ricarda Pätsch** 





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Hildesheim 2019

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### Between land and sea saline and brackish grasslands of the Baltic Sea coast data usability, characterisation and conservation

Dissertation for the award of the degree 'Doctor rerum naturalium' (Dr. rer. nat.)

of the University of Hildesheim Area of specialisation: Biology

Submitted by:

Ricarda Pätsch from Herne (DE) Date of oral defence: 19. August 2019

In my thesis I investigate the vegetation and phytodiversity of Baltic Sea saline and brackish grasslands, focussing on methodological, ecological and nature conservation aspects. My co-authors and I conduct analyses based on my own data and compiled historical and current data, which we propose to transform to make them applicable for further analyses (Pätsch et al. accepted a). We jointly describe the Baltic Sea coastal grasslands along the entire coastline in relation to their ecology, littoral placement, geographic patterns, phytogeography and assignment to North-west European salt grasslands. We further review their conservation aspects (Pätsch et al. accepted b). Based on analyses of characteristic species of low-growing coastal grasslands in relation to *Elytrigia repens*, we elaborate a proposal for assessing the quality of coastal grassland vegetation (Pätsch et al. 2019).

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# **Keywords**

- I Baltic Sea coast
- I Coastal grasslands
- I Database
- I Data comparability
- I Data transformation
- I Development and handling of large databases
- I European cultural landscapes
- I Fennoscandia
- I Grassland management
- I Grassland monitoring
- I Habitat typologies
- I Indicator species
- I Monitoring
- I Natura 2000 habitat types
- I Nature conservation
- Non-tidal brackish grasslands
- Northern Europe
- I Plant communities
- I Phytogeography
- I Quality assessments
- I Red List species
- I Saline and brackish grasslands
- I Semi-natural grasslands
- 1 Structural and abiotic patterns in plant communities
- I Supra-regional patterns in plant communities
- I Threatened habitats
- I Vegetation analysis
- I Vegetation classification
- I Vegetation types

# Glossary

Accumulative abundance	sum of all species cover abundances	
Admixture of species	relative occurrence of species	
Bodden	coastal indentation	
EVS	European Vegetation Survey	
Fennoscandia	includes Norway, Sweden, Finland and the North Europear	
	of Russia (comprising Republic of Karelia, Karelian Isthmus,	
	Murmansk Region).	
Fjærd-coast	broad, rather flattened coast developed through glacial erosion	
Fjord-coast	narrow, rather steep coast developed through glacial erosion	
Frequency	number of all occurring species within the plot	
Glycophytic vegetation	freshwater influenced vegetation	
Gyttja	sapropelic mud	
Grade	category; degree	
Hypersaline	salinity is strongly increased	
Littoral	shore area (including the intertidal zone; for an overview o	
	littoral zones see Fig. 1-1)	
Micro-tidal	small tidal fluctuation; here: maximum 30 cm	
Peat	water-saturated soil with proportions of more or less	
	decomposed organic tissue	
Plant strategy types (following	Grime 1979):	
ΙC	strong competitors	
ιS	stress tolerators	
I R	ruderals	
ppt	parts per thousand	
Salinity (following Scherfose 1	990):	
ı oligohaline	salinity = 0 ppt < 3 ppt	
ι [α to β] mesohaline	salinity > 3 ppt < 10 ppt	
ı euhaline	salinity > 10 ppt < 16.5 ppt	
ı polyhaline	salinity > 16.5 ppt < 22 ppt	
Simplified coast	coastal area where cliffs undergo erosion caused by the wash of	
	the waves and resultant sediments deposit and build-up a straight	
	line (e.g. Bay of Gdansk)	
Skerry	small rugged island shaped by glacial ice	
Sociability of species	degree of aggregation of species	
Species-plot data	(phytosociological) relevés	
Subsaline	somewhat salty; moderately saline or salty	
Quaternary	geologic age 2 58–0 million years ago	
	Scologio age, 2100 o minion years age	

Abbreviations (used in the studies 1–3) are summarised at the beginning of each related chapter. They are not included in the glossary.

### **Summary**

The study of vegetation-plot data on a broad geographical scale is of increasing importance in vegetation science. It significantly contributes to the transnational characterisation of vegetation types as well as the better understanding of their large-scale patterns and to habitat typologies, which are important for decision-making processes in European nature conservation.

I examined semi-natural, saline and brackish Baltic Sea grasslands which occur on sedimentary flats at the transition between land and sea. Their diverse vegetation is dependent on low intensity grazing (Dijkema 1990). This valuable part of the European cultural landscape (Küster 2004), which is recognized as Annex I priority habitat type (Natura 2000; European Commission 2013), underwent an overall decrease in quality and quantity within the last 150 years, which is frequently related to abandonment. Thus, the coastal grasslands of the Baltic Sea have been assessed as Endangered in the European Red List of Habitats (Janssen et al. 2016).

Within this thesis I (i) developed a proposal to integrate vegetation data using non-standard scales into general vegetation analyses, (ii) characterised the vegetation of Baltic Sea grasslands on transnational level, (iii) regarded them from a North-west European perspective, (iv) discussed their nature conservation aspects on European scale, (v) investigated changes in their plant species composition and discussed its possible relation to cessation of grazing and (vi) formulated a monitoring concept important for management planning in nature conservation.

Study 1: Phytosociological data are generally based on detailed recordings of the relative importance of each species, commonly described by grades of species-quantity scales. During the historical development of vegetation science in Europe, especially in Northern Europe (Fennoscandia), different scales were developed, which are now largely forgotten and often misinterpreted. To adapt records using these scales to a format appropriate for general vegetation analyses and to enable their use for subsequent surveys of saline and brackish grasslands of the Baltic Sea, my co-authors and I searched for the most frequently used species-quantity scales of Fennoscandia, which we identified as the Norrlin, Hult-Sernander and Drude scales (Pätsch et al. accepted a). We successfully elaborated a proposal on the standardised transformation of their scale grades to percentage values, by conducting a comprehensive literature survey and by calculating hypothetical percentage species covers for the individual grades of the Norrlin scale. We identified six and three commonly used variants of the Hult-Sernander scale and the Drude scale, respectively, which were distinctive in the number of grades. The results of this study contribute to an increased international availability and understanding of (historical) quantitative vegetation-plot data and enable a standardised use of copious data from Fennoscandia. They considerably increased the amount of data for study 2.

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**Study 2:** To examine the vegetation of Baltic Sea saline and brackish grasslands, my co-authors and I classified vegetation-plot data of the entire Baltic Sea coast, resulting in 33 vegetation types with most of them belonging to the classes of *Juncetea maritimi* and *Molinio-Arrhenatheretea* (Pätsch et al. accepted b). We determined that abiotic factors such as soil salinity, moisture and nutrient availability strongly relate to their separation within the littoral zones (height above sea level), whereas the geographic distribution of vegetation types relates to phytogeographical patterns, sea water salinity, differences in tidal range and climatic conditions. Our results revealed that grassland communities of the Baltic Sea coast are either most similar to North-west European or Arctic communities or are unique. Our findings contribute to an improved transnational perspective on Baltic Sea coastal grasslands and to the refinement of Natura 2000 habitat type descriptions (European Commission 2013), which are substantial for decision-making processes in nature conservation.

**Study 3**: My co-authors and I surveyed the relation of *Elytrigia repens* (couch grass) to species generally characteristic for the low-growing vegetation types of the southern Baltic Sea coast (Pätsch et al. 2019). We revealed that a high cover of *Elytrigia repens*, which goes along with additional strongly competitive plants, significantly relates to a low incidence of characteristic salt grassland species and differences in abiotic factors. We developed a monitoring method based on a regular record of the abundance of *Elytrigia repens*, which may contribute to improved decision-making in grazing management and hence to the conservation of Baltic Sea coastal grasslands.

**Future perspectives: Study 1:** The improved data availability can support the development of a sufficiently detailed and uniform syntaxonomic concept on further Fennoscandian vegetation types. Information given on the interpretation of the Drude scale can be used additionally outside the scope of the study. **Study 2:** The transnational characterisation of Baltic Sea saline and brackish grasslands can serve as a basis for further surveys on the small-scale spatial placement (e.g. micro relief; ecological niches) of vegetation types and thus, can contribute to estimate climate change-induced alteration in Baltic Sea coastal grassland habitats expected in the future. **Study 3:** There is evidence, that the proposed monitoring method for Baltic Sea coastal grasslands may be transferred to other regions.

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## Zusammenfassung

Die Untersuchung plot-basierter vegetationskundlicher Daten innerhalb eines geographisch weitgefassten Gebietes ist in der vegetationskundlichen Forschung von zunehmender Bedeutung. Sie trägt erheblich zur transnationalen Charakterisierung von Pflanzengesellschaften, zum Verständnis über großräumige Vegetationsmuster und zur Charakterisierung von Habitattypen (European Commission 2013), die für Entscheidungsprozesse im europäischen Naturschutz von Bedeutung sind, bei.

Ich untersuchte die Salzgrasländer der Ostseeküste, die auf Sedimentflächen am Übergang zwischen Land und Meer vorkommen. Die von komplexen abiotischen Faktoren beeinflusste, facettenreiche Vegetation ist stark abhängig von einer präzise gesteuerten, extensiven Beweidung (Dijkema 1990). Innerhalb der letzten 150 Jahre sind diese kulturell wertvollen Grasländer (Küster 2004), die als prioritärer Lebensraumtyp des Anhangs I (Natura 2000; European Commission 2013) anerkannt sind, stark im Rückgang begriffen. Dies steht in Zusammenhang mit ihrer Nutzungsaufgabe. Demzufolge wurden die Salzgrasländer der Ostseeküste in der europäischen Roten Liste der Lebensräume als gefährdet eingestuft (Janssen et al. 2016).

In meiner Arbeit habe ich (i) einen Vorschlag zur möglichen Nutzung von bisher übergangenen fennoskandischen Vegetationsdaten erarbeitet, die auf wenig bekannten Artmengen-Skalen beruhen, (ii) die Vegetation der Ostseesalzgrasländer auf transnationaler Ebene charakterisiert, (iii) sie aus einer nord-west-europäischen Perspektive betrachtet, (iv) auf europäischer Ebene relevante naturschutzfachliche Aspekte diskutiert, (v) Veränderungen in der Zusammensetzung der Pflanzenarten untersucht und deren möglichen Zusammenhang zur Beweidungsaufgabe diskutiert und (vi) eine Empfehlung für ein naturschutzrelevantes Monitoring von Salzgrasländern konzipiert.

Studie 1: Vegetationskundliche Daten beruhen im Allgemeinen auf detaillierten Aufnahmen der relativen Bedeutung aller Pflanzenarten innerhalb einer begrenzten Fläche. Die relative Bedeutung wird durch grad-basierte (kategoriale) Artmengen-Skalen beschrieben. Im Zuge der Entwicklung vegetationskundlicher Forschung in Europa wurden insbesondere in Nordeuropa (Fennoskandien) unterschiedliche Skalen entwickelt, die heute wenig bekannt sind und oft fehlerhaft interpretiert werden. Um auf diesen Skalen beruhende Daten für vegetationskundliche Analysen nutzbar zu machen, haben meine Mitautoren und ich die folgenden in Fennoskandien gängigsten (historischen) Artmengen-Skalen identifiziert: Norrlin-Skala, Hult-Sernander-Skala und Drude-Skala (Pätsch et al. accepted a). Um einen Vorschlag für die standardisierte Transformation ihrer Skalengrade zu Prozentwerten auszuarbeiten, haben wir eine umfassende Literaturrecherche durchgeführt und für die Norrlin-Skala hypothetische prozentuale Deckungsgrade der Arten berechnet. Für die Hult-Sernander Skala und die Drude-Skala konnten wir sechs bzw. drei häufig genutzte Varianten

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ermitteln, die sich in Bezug auf die Anzahl ihrer Grade unterscheiden. Die Ergebnisse dieser Studie tragen zu einer erhöhten internationalen Verfügbarkeit und einem besseren Verständnis über (historische) quantitative Vegetationsdaten bei und ermöglichen eine standardisierte Verwendung zahlreicher, bisher unbeachteter, Datensätze aus Fennoskandien. Die Datengrundlage für die zweite Studie konnte dadurch erheblich verbessert werden.

**Studie 2:** Im Vordergrund dieser Studie stand die vegetationskundliche Klassifizierung und Charakterisierung von Salzgrasländern der Ostseeküste auf transnationaler Ebene (Pätsch et al. accepted b). Es ergaben sich 33 verschiedene Pflanzengesellschaften, die überwiegend den Klassen *Juncetea maritimi* und *Molinio-Arrhenatheretea* zuzuordnen sind. Ihre Differenzierung innerhalb der litoralen Zonen (Höhen über Normalnull) steht in Zusammenhang mit den abiotischen Faktoren Bodensalzgehalt, Bodenfeuchte und Nährstoffverfügbarkeit, während sich die großräumige Verbreitung der Pflanzengesellschaften auf phytogeographische Muster, auf den Salzgehalt des Meerwassers sowie auf Unterschiede im Tidenhub und in klimatischen Bedingungen bezieht. Die Pflanzengesellschaften der Ostseeküste sind meist denen der nord-west-europäischen Gesellschaften, einige auch denen der arktischen Gesellschaften, zuzuordnen. Manche haben einen einzigartigen Charakter. Auf Grundlage unserer Ergebisse, schlagen wir eine Anpassung relevanter Natura 2000-Lebensraumtypen (H1330, H1639; European Commission 2013) vor.

**Studie 3:** In dieser Studie haben meine Mitautoren und ich das Vorkommen von *Elytrigia repens* (Gewöhnliche Quecke) in Relation zu charakteristischen Arten der niedrigwüchsigen Salzgraslandvegetation der südlichen Ostsee untersucht (Pätsch et al. 2019). Unsere Ergebnisse zeigen, dass eine hohe Deckung von *Elytrigia repens*, die zusammen mit weiteren konkurrenzstarken Arten vorkommt, signifikant mit einem reduzierten Auftreten charakteristischer Arten des Salzgraslandes zusammenhängt und mit veränderten Ausprägungen abiotischer Faktoren einhergeht. Basierend auf einer regelmäßig durchgeführten Deckungserfassung von *Elytrigia repens*, haben wir ein Monitoring-Konzept entwickelt, das zu einer verbesserten Entscheidungsfindung im Weidemanagement und somit zum Erhalt wertvoller Grasländer der Ostseeküste beitragen kann.

#### Zukunftsperspektiven

**Studie 1:** Die verbesserte Datenverfügbarkeit kann die Entwicklung eines ausreichend detaillierten und einheitlichen syntaxonomischen Konzepts weiterer Vegetationstypen in Nordeuropa unterstützen. Die hier erarbeiteten Interpretationen der Drude-Skala und ihrer Varianten können auch außerhalb Fennoskandiens genutzt werden. **Studie 2:** Die transnationale Charakterisierung von Salzgrasländern der Ostsee kann als Grundlage für Erhebungen über kleinräumige Variationen innerhalb von Vegetationstypen dienen und somit das Abschätzen der für den Ostseeraum zu erwartenden, vom Klimawandel induzierten, Veränderungen verbessern. **Studie 3:** Es wird erwartet, dass die vorgeschlagene Monitoring-Methode auch auf weitere Regionen übertragbar ist.

## Introduction

# Phytosociology in Central and Northern Europe – Diverse approaches led to diverse data

### Brief overview of the historic development of phytosociology

In Europe, the study of vegetation aiming to describe recurring vegetation patterns observed on a landscape level, has a long tradition. Whereas prior to the 20th century, the examination of vegetation was conducted using varying methodological approaches (Ellenberg 1956), in Central Europe since the beginning of the 20th century the concept of phytosociology and its related methods gained acceptance and were increasingly applied (Dierschke 1994). This concept is still known as the Zürich-Montpellier or the Braun-Blanquet School (Westhoff & van der Maarel 1973). The botanists and plant phytosociologists Reinhold Tüxen, Heinz Ellenberg, Erich Oberdorfer and many others were strongly involved in the development and dissemination of this school and worked on the standardisation of applied methods (Whittaker 1973; Dierschke 1994).

However, in Northern Europe, including Denmark, Finland, Norway, European Russia and Sweden, the common concept of phytosociology broke apart into several approaches and schools. The development of the manifold approaches and schools, in summary the so called 'northern tradition', was significantly influenced by the works of the Swedish geologist Hampus von Post, the Finnish botanist Johan Petter Norrlin, the Swedish botanists Ragnar Hult, Rutger Sernander and Gustaf Einar Du Rietz and the Finnish forest scientist and geobotanist Aimo Kaarlo Cajander. All of them are known as pioneers of phytosociology in Fennoscandia but also many others were involved (Du Rietz 1921; Rübel 1922; Frey 1973; Trass & Malmer 1973).

The core objective of the phytosociological schools was to derive a comprehensible typology and classification of so called 'basic vegetation units' from the records of observed vegetation patterns. The magnitude of the works carried out since the end of the 19th century in Central and Northern Europe was described as 'one of the striking features of the history of ecology' (Trass & Malmer 1973). Researchers developing the concepts and methods underlying the Central and North European schools were consistently connected and influenced each other in their work, which is still noticeable through the general similarities in basic ideas and methods.

With the objective to comprehensively describe observed vegetation patterns, climate, abiotic soil conditions, physiognomy (plant growth-forms, life-forms) and structure (vegetation layers) of vegetation were used as criteria in different research approaches (Whittaker 1973; van der Maarel 1975; Lawesson 2000). Although their importance is undeniable, phytosociology focusses on plant species composition as the most crucial aspect for studying vegetation patterns

(Tüxen 1984). Phytosociological data underlying North and Central European vegetation descriptions were generally based on detailed recording of species composition (phytosociological relevé) within a clearly defined area called a plot. This plot is considered representative for the larger vegetation unit in which it is placed. The selection of a suitable plot commonly included the criteria of floristic and/or structural (physiognomic) homogeneity (Lawesson 2000), resulting in a higher homogeneity in the surface area of the plot than in the examined vegetation pattern (Trass & Malmer 1973).

# Phytosociological vegetation analyses – Limits in the application of common vegetation-plot data based on diverse species-quantity scales

Differences between plot-based methods applied in North and Central Europe are mostly related to variations in the placement of plots (Lawesson 2000) and plot size. Beyond the survey of vegetation dominated by herbaceous plants, differences also relate to the separate survey of several vertical layers (Whittaker 1973), not further discussed in this work. Pivotal differences relate to the recording or estimation of the relative importance for each species found within the plot using varying forms of species-quantity scales. Until today this is a major impediment for the comparability of plot-based vegetation data from within Northern Europe and with Central European data.

In Central Europe, phytosociological relevés are commonly conducted using the well-known original Braun-Blanquet scale or its later, more detailed variants (Ellenberg 1956; Barkman et al. 1964; Braun-Blanquet 1964). In contrast a multitude of species-quantity scales were used in Northern Europe, based on grades, which either describe the abundance, cover, density and/or admixture of species (Drude 1890a; Gams 1918; Rübel 1922; Pakarinen 1984; Rabotnov 1984; Lawesson 2000). At times the sociability of species was additively given.

A frequently used method to make varying scales comparable and usable for vegetation analyses is the transformation of scale grades to mid-percentage values. There is a predominant agreement on the transformation of scale grades of the Braun-Blanquet scale, although slightly differing interpretations exist for the transformation of the lowest scale grades (Barkman et al. 1964; Westhoff & van der Maarel 1973; standardised transformation in TURBOVEG 2, Hennekens & Schaminée 2001). However, the transformation of grades from the numerous scales applied in Northern Europe is generally hindered due to a lack of knowledge about those scales and poor documentation especially regarding the exact quantitative meaning of scale grades. The interpretation of the scale grades therefore often remains ambiguous. Thus, there is an urgent need to make data using different species-quantity scales mutually comparable by approximation of their quantitative meaning and thus, available for phytosociological vegetation analyses.

### The present-day availability of vegetation-plot data

Owed to diverse initiatives aiming to make vegetation-plot data available for analyses, present day availability of vegetation-plot data is remarkably high in Europe (Schaminée et al. 2009). The initiatives resulted in the establishment of manifold European databases holding enormous amounts of phytosociological relevés. A large proportion is retrievable via the data repository EVA (European Vegetation Archive; Chytrý et al. 2016), which was initiated by the International Association for Vegetation Science (IAVS) working group 'European Vegetation Survey' (EVS) and is stored and managed in the database management system TURBOVEG (Hennekens & Schaminée 2001). Here, for reasons of comparability, species-quantity information is available in percentage values (additional to the original scale grades).

However, the availability of data from Northern Europe is still limited by (i) the reduced interest in phytosociological research in Northern Europe in recent decades, (ii) the sporadic contact between Central and North European researchers (Lawesson 2003) and (iii) the limitations for implementing many North European vegetation data into common databases and vegetation analyses because of above discussed reasons. Hence, vegetation-plot data from North European countries are often disregarded. The data from Northern Europe that are available via EVA are used with unstandardised transformation of their scales. Considering the uncertainty in the interpretation of scale grades, this adds unintentional heterogeneity to the datasets or results in the loss of important quantitative information due to the transformation of scale grades to presence-absence information (Peterka et al. 2015). To facilitate the availability of North European vegetation data, we need to make great efforts to understand Fennoscandian species-quantity scales and to elaborate a protocol suggesting standardised methods for scale-grade conversions to percentage values.

### The present-day need and state of phytosociological research

Present-day large-scale (transnational) vegetation analyses are of high relevance to increase our understanding of vegetation patterns and to find answers for arising questions within the scope of global environmental changes (Biurrun et al. 2019). Phytosociological studies serve as a major basis for European habitat typologies (Schaminée et al. 2016; Rodwell et al. 2018), are important for the development of reasonable and beneficial tools such as concepts for monitoring, quality assessments (Janssen et al. 2016; Tsiripidis et al. 2018) and land-use planning and for decision-making processes in European nature conservation (Chytrý et al. 2019). Enabled by the present day amplified data availability, which constitutes an irreplaceable source of information (Schaminée et. al 2009), a thoroughly conducted study using findings from manifold previously conducted phytosociological works resulted in an extensive syntaxonomical overview of diverse vegetation units of Europe (Mucina et al. 2016). Furthermore, recently conducted transnational studies predominantly conducted on Atlantic, Central and Southern European vegetation

contributed important findings such as refined characterisation of syntaxonomical units, the identification of floristic patterns and main driving factors of species composition (Rodríguez-Rojo et al. 2017; Willner et al. 2017, 2019; Marcenò et al. 2018).

Therefore, it is legitimate to conclude that there is an urgent need for comprehensive and transnational studies on the vegetation of Northern Europe (Fennoscandia), where we lack sufficiently detailed syntaxonomical concepts (Dierßen & Dierßen 1996; Lawesson 2000). Even though Mucina et al. (2016) included descriptions of Nordic vegetation units, the reduced availability of (high quality) data from Fennoscandia led so far to the evaluation of Northern European vegetation from a Central European rather than a holistic European perspective.

### Saline and brackish grasslands of the Baltic Sea coast

### A valuable part of the European cultural open landscape

The open landscapes in Europe are mostly of anthropogenic origin (Poschlod et al. 2009; Leuschner & Ellenberg 2017). With a great diversity in structure, form and colour, changing over the course of the year, its (non-intensively managed) grasslands hold an intrinsic aesthetic value which improves the quality of human life (Dierschke & Briemle 2002). Related to their current extent, the importance of European grasslands for plant and animal species diversity is disproportionally high (Dierschke & Briemle 2002; Carboni et al. 2015; Dengler & Tischew 2018).

As a valuable part of the European cultural open landscape, saline and moist coastal (marshlands and) grasslands are recognized as habitats of community importance (European Commission 2013). As such they are beneficial for the biotic diversity of adjoining ecosystems (Boormann 2003) and incorporate further environmental and varying economic and cultural values.

They are distributed from the Mediterranean up to the (Sub)Arctic and occur on varying kinds of alluvial and sedentary flats in more or less sheltered conditions (Dierßen & Dierßen 1996; Doody 2008). Due to their placement at the transition between land and sea, their ecosystem structure and functioning are determined by terrestrial and marine factors (Strandmark et al. 2015), making them a complex object to study. Although they occur along tidal coasts under natural conditions, they are seriously altered and extended by anthropogenic utilisation, mostly by mowing or grazing (Dierßen & Dierßen 1996; Dengler & Tischew 2018).

Unlike the large marshes and grasslands along the North-west European tidal sea coastline, saline and brackish vegetation of the micro-tidal and structurally rich Baltic Sea coast occurs naturally only rarely and on a spatially small scale. These natural patches of saline and brackish vegetation have been expanded by non-intensive mowing but mainly by low-intensive grazing of adjacent reed beds, forb stands and wet meadows to create the large areas of coastal grassland that now shape the Baltic Sea coastline. The utilisation facilitated the build-up of coastal peat, characterised by varying amounts of sand, loam, silt, gyttja and high proportions of organic matter from terrestrial plants (Gillner 1960). Although information given in the literature differs in the exact date and time, it is proven that they have been utilised by humans for hundreds of years (Dahlbeck 1945; Gillner 1960; Siira 1970; Dijkema 1990; Dierßen & Dierßen 1996; Zerbe 2009). They have been mown, but mostly grazed by sheep or cattle (Scherfose 1993; Rannap et al. 2004). That way, long-term resilient extensive littoral meadows persisted as an integrative part of the coastal landscape.

### What do we know about their vegetation and ecology?

There are many phytosociological studies which have classified and described Baltic Sea saline and brackish grassland vegetation (see introduction of study 2). Their majority were examined at the local level (including one or few study sites), with a focus on the southern Baltic Sea coast. In a few studies or books (Tyler 1969a; Dierßen & Dierßen 1996; Wanner 2009; Leuschner & Ellenberg 2017), where authors aimed to present a broader view of Baltic Sea coastal grasslands, either investigations on geographically widely separated areas were conducted or results of varying local studies were summarised (e.g. as synoptic tables; Dierßen & Dierßen 1996).

Until now we have lacked a reproducible and spatially comprehensive (plot-based) vegetation classification of Baltic Sea saline and brackish grasslands providing an interpretation on a broad geographical level. Nevertheless, by summarising the existing body of studies one can derive the general distribution of saline and coastal grasslands and review detailed insights of local characteristics, important to understand the littoral zonation, vegetation and ecology of Baltic Sea coastal grasslands and the effects of management on the vegetation.

Saline and brackish grasslands of the Baltic Sea occur in shallow and relatively sheltered situations, where fine-grained sandy, loamy or silty sediments allow for their development (Gillner 1960; Dierßen & Dierßen 1996). They are embedded between adjacent (hyper-)saline to oligohaline plant communities including grasses, herbs, forbs or occasionally shrubs and trees (Dierßen & Dierßen 1996; Lehtomaa et al. 2018). Seawards, brackish reeds and occasionally small-scale glasswort flats occur around the border of the eulittoral (hydrolittoral) to the supralittoral (geolittoral). Depending on the sea water salinity and dynamic stress by the wash of the waves, brackish reeds consisting of *Phragmites australis, Bolboschoenus maritimus* and/or *Schoenoplectus tabernaemontani* (Leuschner & Ellenberg 2017). Above the high water line saline and brackish grasslands are bordered by diverse glycophytic or some salt-spray influenced, often grass-dominated, plant communities.

Saline and brackish grasslands are situated between the upper limit of the eulittoral and the lower epilittoral of the Baltic Sea coast (Fig. I). Vegetation patterns are linked to soil salinity, soil moisture, nutrient availability and soil base content (Gillner 1960; Siira 1970; Dierßen & Dierßen 1996; Burnside et al. 2007; Hulisz et al. 2016). The mechanical effects of wind and waves as well as those of banking-up ice (Aavik et al. 2009), which may cause severe damage to the sward (Siira 1970; Dijkema 1990) especially in the Gulf of Bothnia and Finland, are co-responsible for the dynamic in patterns of vegetation (Ericson & Wallentinus 1979).



Fig. I Schematic overview on the littoral zones and coastal grassland positioning following information given in Dierßen & Dierßen (1996). The dotted line indicates the littoral placement of saline and brackish grasslands. In comparison to the less known concept suggested for the Baltic Sea, the mean low-water line corresponds to the low water line, the mean high-water line to the average water line and the mean high-water spring tide line to the high water line.

Vegetation types of saline and brackish Baltic Sea grasslands consist of halophytes as well as more or less halotolerant glycophytes. Directly above the average water line where grasslands are regularly exposed to sea water (Fig. I), dense swards occur on more or less saline soil, distinctive from the open-structured pioneer vegetation of the eulittoral. Towards the middle supralittoral, where flooding is decreased, *Agrostis stolonifera* and *Juncus gerardi* gain in importance as abundant species in varying vegetation types. Towards the upper supralittoral up to the low epilittoral where *Festuca rubra* and *Scorzoneroides autumnalis* are frequently abundant, only irregular flooding by sea water occurs. Here, the influence of adjoining glycophytic vegetation types is visible (Gillner 1960; Härdtle 1984; Dijkema 1990; Dierßen & Dierßen 1996; Vestergaard 2002; Leuschner & Ellenberg 2017).

Baltic Sea coastal grasslands developed mainly through non-intensive grazing. Present day coastal grasslands are predominantly maintained by nature conservation management (Poschlod et al. 2009) aiming to preserve their diversity (Köster et al. 2004) by continuing grazing related to the traditional way of utilisation. Grazing facilitates the diversity of grasslands by changing the vegetation composition through selective grazing or through the decrease of grazing sensitive plant species (Scherfose 1993). Grazing-related grassland alterations

additionally go along with decreasing intraspecific competition (Härdtle 1984), shifts in proportions of species life-forms and species growth-types (Scherfose 1993), decreasing heights and the opening of the sward (Scherfose 1993), which alters micro-climatic conditions (Irmler & Heydemann 1986) and facilitates soil salinization through increased evapotranspiration (Schmeisky 1977a; Westhoff & Sykora 1979; Siira 1985). It also affects abiotic soil conditions (Scherfose 1993; Dierßen & Dierßen 1996) and contributes to patterned soil compaction which for instance leads to a decreased decomposition of organic matter (Scherfose 1993). That way, grazing is crucial for the development and the long-term stable preservation of the soil (peat) and facilitates the diversity of vegetation structure, plant species and vegetation types of Baltic Sea saline and brackish grasslands.

Notwithstanding the above, poorly adapted or unbalanced grazing may lead to the deterioration of saline and brackish coastal grasslands (Rebassoo 1975; Dijkema 1990; Dierßen & Dierßen 1996; Sammul et al. 2012), most apparent through structural equalization of vegetation (Bakker 1987; Scherfose 1993), reduced trampling effects (Dijkema 1990; Scherfose 1993), the decrease of species diversity (Bakker 1987) and the increase of intraspecific competition (Dahlbeck 1945; Kiehl 1997) and strong competitors (Sammul et al. 2012). With total cessation of grazing, valuable characteristic plant communities (Jeschke 1987) and associated species (Amiaud et al. 2008) of saline and brackish grasslands may get lost. At the same time strong competitors such as *Phragmites australis* in the lower supralittoral and *Elytrigia repens* in the middle and high supralittoral (up to the epilittoral; Kauppi 1967; Schmeisky 1977a; Jeschke 1987; Dijkema 1990; Burnside et al. 2007; Rŭsina 2017) spatially extent up-respectively downwards and may form one-species phytocoenoses (Jeschke 1987; Dierßen & Dierßen 1996; Sammul et al. 2012). Northwards coastal grassland vegetation occasionally may also get overgrown by trees (Kauppi 1967).

# Nature conservation – Aspects on saline and brackish grasslands of the Baltic Sea coast

#### Their value and their assessment on habitat level

The structural diverse coastal grasslands are particularly important as foraging, wintering, stop-over, breeding and resting sites for numerous migratory and sedentary birds (Janssen et al. 2016; Dengler & Tischew 2018) such as waterfowl, wading birds, geese or cranes (van Eerden et al. 2005; van der Graaf et al. 2007; Doody 2008; Aavik et al. 2009). Thus, Baltic Sea coastal grasslands are important habitats for diverse bird species listed in Annex I of the European Birds Directive (Doody 2008). They further serve as an important habitat for endangered amphibians as for instance the natterjack toad or the green toad and for a diverse invertebrate fauna such as numerous species of carabid beetles and spiders, of which some are highly

specialised on saline and brackish grasslands (Andresen et al. 1990; Rannap et al. 2007; Doody 2008; Ford et al. 2013).

Baltic Sea coastal grasslands are embedded in varying halophilous and freshwater influenced habitats of the Baltic Sea coastal landscape. These habitats, just like the Baltic Sea coastal grasslands from which 95 % occur within the European Union, are recognized as Annex I priority habitat types of the European Habitats Directive and its nature conservation network Natura 2000 (European Commission 2013). The recognition of the importance of Baltic Sea coastal grasslands on European scale is also reflected through their assessment as endangered habitat in the recently published European Red List of Habitats (Janssen et al. 2016).

### A threatened habitat - are there ways to preserve its diversity?

Saline and brackish grasslands from the Baltic Sea coast undergo an overall decrease in quality and quantity; their area loss during the last 100–150 years is assumed to be 60–90 % (Janssen et al. 2016). The latter is in accordance with the worldwide trend of coastal grasslands surface area loss (Köster et al. 2004), and assumed to be co-responsible for the continuing loss of biodiversity (Normander et al. 2009). Diverse factors have been examined that may lead to unfavourable conditions in Baltic Sea coastal grasslands. Above all they result in three major problems which were recognized as being responsible for a considerable proportion of the overall surface area loss of coastal wetlands: building development, eutrophication and abandonment.

The ongoing trend of urbanisation, residential and economic development of coastal areas results in the loss of surface area for any grassland plant species (except species that grow in strongly human influenced, urban areas). By contrast, embanked areas resulting from coastal protection measures (Boormann 2003; Janssen et al. 2016) still provide a suitable habitat for grasslands. But with increasing heights and positioning tending seawards, dike constructions prevent natural flood dynamics (Boormann 2003; Zerbe 2009) and thus, facilitate the establishment of glycophytic, mesophilous grasslands (Wanner et al. 2007) on the former saline and brackish grassland areas.

Eutrophication and abandonment were found to adversely affect Baltic Sea coastal grassland vegetation and are both known as major threats of wet grassland habitats in general (Dengler & Tischew 2018). Eutrophication, but especially abandonment was reported to alter plant species composition and provoke biomass accumulation and a notable decrease in the diversity and quality of Baltic Sea coastal grasslands (Jeschke 1987; Dijkema 1990; Jutila 2001, 2017; Boormann 2003; Köster et al. 2004; Janssen et al. 2016). Driven by the reduced economic value (Zerbe 2009) traditional grazing rapidly decreased during the 20th century (Köster et al. 2004).

To re-establish diversity of saline and brackish grasslands and to counteract effects of abandonment (and eutrophication), the reintroduction of grazing management is of major importance. On a grazed site, too low stocking rates or the permanent unequal distribution of cattle may lead to effects of partial abandonment. Thus, there is a particular need of a precise management to benefit from grazing effects (Bakker 1987; Scherfose 1993). As the appropriate stocking rate varies between sites according to abiotic factors (Hulisz et al. 2016), monitoring on site (Normander et al. 2009) or even plot level is of general importance as basis for decision making in nature conservation. In relation to the possible unequal livestock distribution, indirect monitoring of the suitability of grazing may be preferred over the direct recording of stocking rates.

# The study area – The development of coastal formations and present-day characteristics of the Baltic Sea (coast)

The semi-enclosed Baltic Sea is a vast intra-continental shelf sea and is one of the largest brackish waters of the world (Tyler 1969a; Schiewer 2008; Schwarzer et al. 2008). It has a north-south and west-east extent of more than 1000 km each. The coastline spreads along Central, Eastern and Northern Europe, including parts of European Russia. It contains a large number of islands, most of them aggregated in the Archipelago Sea and the West Estonian Archipelago. The study object of Baltic Sea saline and brackish coastal grasslands is intrinsically tied with the diverse geomorphological, abiotic and climatic factors of the Baltic Sea shoreline.

The origin of the present-day geomorphological shape of the Baltic Sea shoreline can be traced back to Pleistocene glacial and post-glacial period times (Willers 1987; Schwarzer et al. 2008). The retreat of glacial ice went along with transgressions and regressions of the Baltic Sea, isostatic processes, strong fluctuation in sea-water salinity and eustatic sea-level fluctuation. The present day transition to the North Sea was formed about 7,000 years ago, where the shape of the current Baltic Sea (coast) was already recognizable. Subsequently the water level fluctuation stagnated and sedimentary processes such as the re-deposition of sediments, the erosion of cliff coasts, the built up of islands and of semi-enclosed lagoons and backwaters occurred (Schiewer 2008; Schwarzer et al. 2008; Leuschner & Ellenberg 2017).

The present-day Central and East European Baltic Sea coast is characterised by Bodden and simplified coasts with Quaternary and recent sediments. Cliff coasts occur scattered along the eastern Baltic Sea coast. Hard rock formations, which only occasionally occur in the south of the Baltic Sea, such as the Fjord coasts or Fjærd coasts, dominate the North European coastlines (Tyler 1969a; Willers 1988; Schubert & Blindow 2004; Schiewer 2008). Within the skerry coasts of the Archipelago between the Bothnian Bay and the southern part of the Gulf of Bothnia, the Archipelago Sea, the southern coast of Finland and the Estonian Archipelago, fine-grained

sediments occur in numerous spatially limited zones of stagnant water (Willers 1988; Dijkema 1990). Overall, sedimentary flat areas, the basis of coastal grassland development, decrease in number and size towards north. However, the extended sedimentation basins in the (emerging) flats of for instance the Liminka Bay (Bothnian Bay, Fig. II) or around Pori (south-west Finland) constitute exceptions of that standard principle (Siira 1985; Willers 1987; Dijkema 1990).

Caused by the glacial rebound there is still a land-upheaval in the northern part of the Baltic Sea coast, ranging from 9 mm/year at the northernmost parts (Bothnian Bay) to 0 mm/year in the areas of the southern tip of Sweden, St. Petersburg and Estonia. Southwards, the Baltic Sea coast sinks between < 0 mm/year to -2 mm/year (Tyler 1969a; Willers 1987; Schiewer 2008; Schwarzer et al. 2008). The isostatic movement has until today an influence on the zonal placement of coastal grassland vegetation patterns.

Through the narrow connection to the North Sea (Fig. II, transitional area), where a deep saline water current flows towards the Baltic Sea (Gillner 1960), a pronounced gradient in salinity (HELCOM Map and Data Service 2008) and tidal fluctuation can be detected, which ranges from  $\sim$  30 ppt (salinity) and 10–30 cm (tidal fluctuation) in the south-west to < 2 ppt (salinity) and a hardly recognizable tidal movement in the Bothnian Bay (Tyler 1969a; Dijkema 1990). The overall gradient in decreasing soil salinity of coastal grasslands towards east and north is discontinuous through the occurrence of ascending relic brine (Bosiacka 2011; Bosiacka et al. 2011). Within the transition zone between the North and the Baltic Sea pronounced spatial and temporal changes in coastal soil salinity occur (Dijkema 1990). Considerable water-level fluctuations at the shoreline, which are driven by wind, differences in air pressure and high river water inputs and supported by the shallow shores of the Baltic Sea coast, reach heights above 1 m (to maximum 4 m). They are strongest in autumn and early winter (Dijkema 1990; Schiewer 2008).



**Fig. II Study area.** The total extent of the Baltic Sea (light grey) coastline and indicated sub-basins follow information given by HELCOM Map and Data Service (2012, 2018). x = Archipelago Sea

o = West Estonian Archipelago

The climate ranges from subcontinental temperate to nemoral conditions (Dierßen & Dierßen 1996). A continental climatic influence is visible in the eastern and northern parts of the Baltic Sea coast (Schiewer 2008; Karger et al. 2017). Related to the boreal climate and the continental climatic influence, parts of the Baltic Sea are regularly covered by ice during winter. For example, the northernmost part (Bothnian Bay) can be covered by ice stretching from January to April, while the ice in the Gulf of Finland and along the Estonian coastline persists for a much shorter period (Jönsson et al. 2003).

The mean annual precipitation ranges from 520 mm/year to 698 mm/year and the mean annual temperature ranges from 9.1 °C in the south to 2.2 °C in the northernmost part of the Bothnian Bay (Karger et al. 2017). While the yearly period of plant growth lasts over 200 days in the southern parts, it is reduced to about 140 days at the northernmost end of the study area (Dierßen & Dierßen 1996).

Sea-water salinity, coastal flooding and banking-up ice as well as climatic conditions influence the growth of the coastal grassland vegetation.

### **Data and methods**

The studies are based on my own vegetation-plot data, taken in 2014 (vegetation-plot records, Braun-Blanquet method [Braun-Blanquet 1964]), as well as on vegetation-plot data requested from international vegetation databases and through individual contact to colleagues.

Data included information on the quantity of species, their date of recording and their locality. Due to the inconsistency in the recording of further related data, information on vegetation structure was only used for a limited set of data in study 3.

The first study was based on a review of literature, methods and data. The vegetation-plot datasets which we examined in the second and third study consisted of 3,732 relevés including 556 taxa and 109 relevés including 124 taxa, respectively.

Taxonomic references relate to the Euro+Med Plantbase (2006-2019), except for names given in Appendix S2-3 (Table S2-3-1). References of higher syntaxa relate to Mucina et al. (2016).

We combined proven and reliable methods, commonly used in vegetation science, with cutting-edge approaches of processing and analysing data from large databases. Detailed descriptions of each method are given in the respective studies. The following lists provide an overview on applied methods and programs.

### Data handling

- Study 1–3:
  - GIS-based data handling (general functions; handling and allocation of climatic data [following Karger et al. 2017]; spatial analyst tools)

### - Study 2 and 3:

- compilation and processing of large datasets (data requests, digitizing, input, transformation [related to study 1]; taxonomic work)
- data interpretation (unweighted mean Ellenberg values [Ellenberg et al. 2001]; weighted life-forms, life-spans, strategy types [Grime 1979; Klotz et al. 2002])
- Study 2:
  - data classification (modified TWINSPAN [Roleček et al. 2009]; Silhouette graphics [Rousseeuw 1987])
  - univariate and multivariate statistical analyses (DCA [Detrended Correspondence Analysis]; permutation test; test of significance)
- Study 3:
  - univariate and multivariate statistical analyses (linear models; NMDS [Non Metric Multidimensional Scaling]; permutation test; rank abundance calculation; test of correlation; test of significance)

### Applied scientific and subject-specific software

### - Studies 1-3:

- ArcGis (ArcGis 1999–2015 version 10.3.1.4959; Esri Inc. version 10.3.1.4959) for GIS-based data selection, analysis and presentation
- TURBOVEG 2 (Hennekens & Schaminée 2001) and TURBOVEG 3 (prototype) for storing and handling of vegetation-plot data in large databases
- Studies 2 and 3:
  - JUICE (version 7.0.213; Tichý 2002), for handling and editing large compilations of vegetation-plot data, for data exploration, manipulation and classification
  - R Studio (version 2.9.0–3.3.1; R Core Team 2009-2016), for statistical computing and graphics (packages: *goeveg* [Goral & Schellenberg 2017]; *psych* [Revelle 2018]; *vegan* [Oksanen et al. 2018])

### **Objectives and thesis outline**

The main objective of this thesis was to characterise the vegetation of Baltic Sea coastal grasslands and to contribute to their transnational interpretation. Therefor I elaborated three studies, resulting in three scientific articles. I led the development process and writing of all articles, which were elaborated together with differing teams of co-authors.

The relations between the research topic 'Baltic Sea coastal grasslands', the factors influencing it and the main structure of the thesis, are depicted in Fig. III. Fig. IV gives a schematic outline with particular focus on the three conducted studies.

In **study 1** (Pätsch et al. accepted a) my co-authors and I aimed to make (historic) North European vegetation-plot data compatible with data from Central Europe, to increase the availability of Fennoscandian data for broad-scale vegetation analyses in general and for the analyses of Baltic Sea saline and brackish grasslands (Pätsch et al. accepted b; study 2) in particular. In order to best capture the subject, in this study the investigation area was set to the entire scope of Fennoscandia (coastal and inland).

My co-authors and I conducted a comprehensive literature and metadata (EVA) survey in search for the most frequently applied species-quantity scales in Fennoscandia and to understand how they have been applied. We made an attempt to develop a proposal for their transformation to percentage values, by incorporating calculations to approximate assumed percentage species-cover values or by reviewing their definitions and applications applied in the literature. To present the widespread use of differing species-quantity scales, we intended to summarise related studies in a GIS-based approach (Fig. 1-1; Appendix S1-1).



**Fig. III Schematic overview of relations** between the research topic, its surveyed and/or discussed influencing factors and the structure of the conducted studies. Grey font = background information not surveyed; 1, 2, 3 = part of study 1, 2 and 3 respectively.

In **study 2** (Pätsch et al. accepted b) we investigated the floristic diversity, ecological characteristics and distribution patterns of Baltic Sea saline and brackish grasslands to contribute to their enhanced interpretation on European scale. To ensure a high data quality and enable target-oriented analyses, we reduced the compilation of 9,562 relevés to 3,732 relevés (including 556 taxa) with regard to species composition and abundances (Appendix S2-2), to the documentation of locality and to plot-size variability (1 m<sup>2</sup>–80 m<sup>2</sup>).

To answer the questions which plant community types can be found and where they occur, we used a modified TWINSPAN clustering, a proven method in vegetation analyses (Roleček et al. 2009). We examined and discussed identified distribution patterns in terms of habitat availability, phytogeography and complex abiotic gradients such as climate, flooding or sea-water salinity. In order to interpret patterns in diversity, vegetation structure, abiotic and climatic conditions, we studied the relationship of plants with differing life-spans or ecological strategies, of soil abiotic factors and of raster-based climate data to plant communities. We aimed to regard the investigated vegetation types from a geographically broad, North-west European perspective and to discuss conservation aspects important on regional as well as on European scale.

In study 3 (Pätsch et al. 2019) we examined the incidence of the competitive stoloniferous grass species *Elytrigia repens* and characteristic species of low-growing grasslands of the southern Baltic Sea coast. The latter were defined as chiefly character or differential taxa of the class *Juncetea maritimi*. We hypothesized that, if *E. repens* increases due to abandonment or other causes, characteristic species will decrease. We subdivided the plot-based dataset in groups of plots comprising *E. repens* with a cover above (group A) or below (group B) five percent or without any occurrence of *E. repens* (group C). We investigated the relation between *E. repens* and the accumulative abundance (= sum of all species cover abundances) and frequency (= number of all occurring species) of characteristic species and structural, functional and abiotic conditions. To strengthen the results, we calculated the explanatory power of *E. repens* cover abundances for the accumulative abundance and frequency of characteristic species by calculating a linear model. To investigate the species composition where the cover of *E. repens* was high, we calculated species ranks.

Applying the basic assumption that *E. repens* increases after cessation of grazing, we discussed our findings in relation to grassland abandonment, on which we lack appropriate data on plot scale. We aimed to develop a monitoring concept that, if applied, indirectly determines the quality of coastal grasslands and directly contributes to the future protection of valuable Baltic Sea coastal grassland vegetation.

Conducted work		Main studies	
Installation of a vegetation-plot database:			
Majaje Jos	fieldwork		
]↔?	database queries	Study 1: Making them visible and usable –	
$\bigcirc$	transformation of (so far overlooked) data	vegetation-plot observations from Fennoscandia based on historic species-quantity scales	
→ 🔲 veg	getation-plot database as basis for f	urther studies	
Classification and ch	naracterisation of vegetation:		
h	Numerical classification		
<u>Make Ma</u>	<ul> <li>Characterisation</li> <li>abiotic, biotic and structural factors</li> <li>climate</li> <li>distribution</li> </ul>	Study 2: Between land and sea – a classification of saline and brackish grasslands of the Baltic Sea coast	
₩≠₩	North-west European perspective		
S	Nature conservation – Natura 2000 habitat types – Red List species		
<i>Elytrigia repens,</i> cha conservation mana	aracteristic species and gement:		
	<ul> <li>Analyses of <i>Elytrigia repens</i> in relation to <ul> <li>characteristic plant species</li> <li>plant strategy types</li> <li>species composition</li> <li>soil abiotic conditions</li> </ul> </li> </ul>	Study 3: <i>Elytrigia repens</i> co-occurs with glycophytes rather than characteristic halophytes in low-growing salt meadows on the southern Baltic Sea coast	
	Nature conservation <ul> <li>grazing management</li> <li>quality assessment</li> </ul>		

### Main research topic: Baltic Sea saline and brackish grasslands

### Fig. IV Schematic outline of the thesis with particular focus on studies 1–3.

Pictograms are partly constructed using icons retrievable via icons8 (https://icons8.de/).
# Making them visible and usable – vegetation-plot observations from Fennoscandia based on historical species-quantity scales

# **Technical information**

**Contents of this chapter are accepted for publication**: Pätsch R, Jašková A, Chytrý M, Kucherov IB, Schaminée JHJ, Bergmeier E, Janssen JAM accepted a. Making them visible and usable – vegetation-plot observations from Fennoscandia based on historical species-quantity scales. *Applied Vegetation Science*. The conduction of this article and the writing was led by myself; all co-authors contributed scientifically to this study.

**Keywords:** cover-abundance scales; data standardisation; Drude scale; European vegetation; Hult-Sernander scale; Norrlin scale; North European countries; phytosociology; plant density measures; scale transformation; species abundance; vegetation records

#### Supplementary material:

- I Appendix S1-1: Literature sources.
- Appendix S1-2: Transformation of the Norrlin scale.
- Appendix S1-3: Original description of the Drude scale.

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# Abstract

Aims: Present-day large-scale and plot-based vegetation analyses contribute to the transnational characterisation and interpretation of biodiversity patterns and to habitat typologies, which are important for planning, monitoring and decision making in nature conservation. Many historical vegetation surveys applied cover-abundance, relative occurrence or density scales (species-quantity scales) that are nowadays poorly known and consequently disregarded or misinterpreted. Therefore, it is worthwhile to put effort into making them compatible with the datasets sampled using mainstream methods. Within Europe, this especially applies to historical data from Fennoscandia. Here we aim to propose how to transform the species-quantity scales frequently used in Fennoscandia into percentage-cover scales, based on the conversion of their individual grades.

**Study area:** Fennoscandia, including Norway, Sweden, Finland and the Fennoscandian part of Russia (Republic of Karelia, Karelian Isthmus, Murmansk Region).

**Methods and results:** We inventoried Fennoscandian vegetation-plot studies and identified that the most frequently applied species-quantity scales were those of Norrlin, Hult-Sernander and Drude. We reviewed the definitions and applications of these scales in the literature and, if not available, calculated hypothetical species covers to approximate realistic conversions to the percentage scale. As a result, we propose alternative ways of conversion of the individual scale grades to mid-percentage-cover values.

**Conclusion:** Historical vegetation-plot data from Fennoscandia can be used as quantitative information for vegetation research if their grades are consistently transformed into percentage-cover values using the proposals presented in this paper.

# Introduction

Present-day vegetation science contributes considerably to comprehensive classifications of plant communities and standardised regional or transnational vegetation analyses (Chytrý et al. 2019), which is enabled by the increasing availability of vegetation-plot data in electronic databases. The resulting vegetation types facilitate the identification of geographic patterns and main driving factors of species composition (e.g. Rodríguez-Rojo et al. 2017; Willner et al. 2017, 2019; Marcenò et al. 2018). Vegetation classification studies have played a major role in the development of transnational European habitat typologies (Schaminée et al. 2016; Rodwell et al. 2018; Biurrun et al. 2019) and their quality assessment (e.g. Janssen et al. 2016; Tsiripidis et al. 2018), which is an important basis for decision-making processes in nature conservation. Given that historical data are included in the databases, also studies on temporal vegetation changes are conceivable (Kapfer et al. 2016).

The concept of phytosociology, in which plant composition was recognized as a key factor for the definition and characterisation of recurring vegetation patterns observed at the landscape scale (Tüxen 1984), rapidly spread over Central Europe in the first half of the 20<sup>th</sup> century (Knapp 1971;

Dierschke 1994). While the Central European (Braun-Blanquet) school derived from several scientific concepts and merged into one approach (Trass & Malmer 1973), in Fennoscandia, the idea of phytosociology diverged into several distinct approaches known as the schools of the 'northern tradition'. Nevertheless, in phytosociology a floristic-taxonomic view of recurring uniform vegetation patterns has prevailed over time in most of the European phytosociological schools. These recurring vegetation patterns are commonly surveyed on a uniformly structured, homogeneous area (vegetation plot or phytosociological relevé; Du Rietz 1921, 1929; Braun-Blanquet 1928; Lawesson 2000) representative for, but smaller than the surveyed vegetation pattern.

Next to evaluations of plant frequency, the use of cover-abundance, relative occurrence (admixture) or density-based scales on the plot level (Rübel 1922; Lawesson 2000) became a common practice to estimate the relative importance of each plant species within a plant community (Drude 1890a; Vestal 1943) and their sociability (= degree of aggregation; Gams 1918, Braun-Blanquet 1928). The use of species-quantity scales as fixed standards, instead of direct percentage estimations, facilitated the cover measures and supported the objectivity of the conducted visual estimations. Schools of the 'northern tradition' have always been connected and compared with the Braun-Blanquet school, including the comparisons and conversions of species quantity estimations (Rübel 1922, Barkman et al. 1964; Westhoff & van der Maarel 1973; van der Maarel 1979; Rabotnov 1984; Oksanen 1990; Lawesson 2000; Sorokin & Golub 2007).

Enabled by the use of common methods and concepts a multitude of local, regional and transnational classifications in Western, Central and Southern Europe recently resulted in a well-elaborated syntaxonomical description of manifold vegetation units (Mucina et al. 2016). By contrast, sufficiently detailed and unified syntaxonomic concepts are lacking in Fennoscandia (Dierßen & Dierßen 1996; Lawesson 2000). Next to some differences in vegetation recording (Dengler et al. 2006), not discussed in this paper, this is also attributed to the nowadays poorly known Fennoscandian cover, abundance, relative occurrence or density scales (henceforth species-quantity scales). They involve considerable uncertainty in interpreting the scale grades (Barkman et al. 1964), partly because of the lacking documentation of their exact quantitative meaning. Hence, they have been used inconsistently in the literature, and historical vegetation-plot data using these scales are difficult to incorporate into current databases and often disregarded.

There have been promising initiatives to strengthen the previously limited collaboration in vegetation survey between Fennoscandian and other European countries and between Fennoscandian countries themselves. These include the Nordic Vegetation Survey network (Lawesson et al. 1997, Lawesson 2003), which was active in the late 1990s and early 2000s, and the European Vegetation Survey (EVS 2019) with its EVA database (Chytrý et al. 2016), which

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includes several vegetation-plot databases storing Fennoscandian data (e.g. EU-00-002, Nordic-Baltic Grassland Vegetation Database, Dengler et al. 2006; 00-00-004, Vegetation Database of Eurasian Tundra, Virtanen 2012; EU-00-018, The Nordic Vegetation Database; EU-00-22, European Mire Vegetation Database, Peterka et al. 2015; EU-00-027, European Boreal Forest Vegetation Database, Jašková et al. submitted). Although a considerable amount of Fennoscandian data are already available in EVA databases, the transformation of scales is partly inconsistent and adds unintentional heterogeneity to the datasets. In order to avoid inaccuracies, quantitative information on species abundance was sometimes converted to presence-absence of species when data were digitized (e.g. Peterka et al. 2015). Thus, essential information on species abundances is unnecessarily lost.

Present-day vegetation studies and resulting recommendations for nature conservation practice clearly benefit from the availability of datasets that are as little as possible biased against the data that were collected using different sampling methods. Therefore, it is worthwhile to put effort into making Fennoscandian data compatible with the data sampled by the mainstream methods. Here, we evaluate the species-quantity scales that were most frequently used in Fennoscandia. We present how they have been applied and recommend conversions of their grades to mid-percentage values. We hope this contribution can increase collaboration between vegetation scientists with different backgrounds.

# Methods

We inventoried historical and more recently published literature sources and metadata from the European Vegetation Archive (EVA; Chytrý et al. 2016) using different species-quantity scales applied in sampling Fennoscandian vegetation plots. Based on this, we identified the most common species-quantity scales, which proved to be the Norrlin, Hult-Sernander and Drude scales, and their frequently used variants. For each scale we generated distribution maps of the inventoried studies (ArcGis 1999–2015 version 10.3.1.4959, Esri Inc. 2011 version 10.3.1.4959; Fig. 1-1a-c).

In search of the most applicable transformation of the individual scale grades to mid-percentage values, we assembled information on how these scales were applied and, if conducted, how they were converted to percentage-cover values including the limits of the scale's grades. We reviewed the literature for studies that applied the selected species-quantity scales and additionally the following methodological works and handbooks: Drude (1890a, 1890b), Gams (1918), Rübel (1920, 1922), Du Rietz (1921, 1932), Braun-Blanquet (1928), Vestal (1943), Barkman et al. (1964), Knapp (1971), Trass & Malmer (1973), Oksanen (1976, 1984, 1990), van der Maarel (1979), Pakarinen (1984), Rabotnov (1984) and Dierschke (1994). Thereafter we used this information to propose the most plausible transformation of the scale grades into percentage values.



We elaborated the transformation of the Hult-Sernander scale, the Drude scale and their variants by applying the most appropriate transformations of, for the most part, arithmetic mid-percentage values given in the literature; if preferable because it was always applied that way, we considered also geometric mid-percentage values or values slightly differing from the grade's arithmetic mean. To approximate the conversion of the Norrlin scale, we calculated hypothetical species minimum, mean and maximum relative cover values (relative cover = species cover/plot, henceforth cover) for each grade. Information on low species abundance, indicated for example as '+' or r. (rare), was specified additionally to the scale grades; we converted these terms in relation to the general structure of each individual scale. We rounded all mid-percentage values < 1 % to the first decimal place and values > 1% to the nearest whole number.

Fig. 1-1a-c Geographic distribution of the compiled Fennoscandian studies using different scales, summarized in Appendix S1-1. Local studies are indicated by black circles. Works with an extended geographical scope are indicated by grey triangles at their approximate midpoints; studies 42, 68, 69 and 72 were conducted in two or more separate areas (with some of the areas outside the scope of our study and thus not shown in the map). For supra-regional studies stretching along the coastline (indicated by underlined study numbers), grey triangles indicate their limits connected by a grey line. Study 8, based on the Norrlin scale, includes several study sites along the Baltic Sea coast and is not shown in the map.

# **Results and discussion**

As a result of the literature and database search, the Norrlin scale, Hult-Sernander scale and Drude scale were identified as commonly applied in historical (and current) studies from Fennoscandia (Appendix S1-1). The Norrlin scale was used in the Russian parts of Fennoscandia and both the Norrlin and the Hult-Sernander scales came into use in Finland and Sweden, the latter also in Norway. The Drude scale was frequently applied in Russian parts of Fennoscandia and additionally in some Finnish studies (Fig. 1-1a–c).

The proposed transformations of the Norrlin, Hult-Sernander and Drude scales to mid-percentage values are given in Table 1-1, including their commonly used (above described) variants. All variants of the considered scales have a progressive character, which means that the width of the individual grades increases with increasing cover values (Table 1-1).

#### **Norrlin scale**

The ten-grade Norrlin scale is named after the Finnish botanist and lichenologist Johan Petter Norrlin, who was substantially involved in the advancement of vegetation science around 1900 in Finland and Sweden (Palmgren 1912; this work was supervised by Norrlin). The first seven grades (1, 2 = sparse; 3, 4 = scattered; 5, 6, 7 = abundant/plenty) of the ten-grade scale are based on distance measures (= density) between the individuals of each species. The distances given in the literature overall range from > 914.4 cm (= grade 1) to 2.54 cm (= grade 7). Originally they were specified in foot/inch (Palmgren 1912; Häyrén 1914-1915), and they slightly differ in Rübel (1922), who rounded them to cm/m.

The upper three grades (8–10) relate to the admixture of other species, overall between 7.5 species (= grade 8) and one species (= grade 10; Palmgren 1912; Häyrén 1914-1915; Du Rietz 1932; Barkman et al. 1964; Pakarinen 1984). These grades describe species which frequently overlap or form densely-vegetated areas (Vestal 1943), but when applied in the field, these grades are hardly used (Gams 1918). The application of the Norrlin scale on plots smaller than 100 m<sup>2</sup>, for example while studying small vegetation patches, leads to the general disuse of the upper grades (Palmgren 1912). Additional information, such as '+' = *sporadic*, *r.* = *rare* or *rr.* = *rarissimo*, relates to species which are present with the lowest density (Palmgren 1912; Rübel 1920).

In order to approximate the transformation of '+', r., rr., and the Norrlin scale's grades 1–7, we separately calculated means of hypothetical species covers for each of the grades, assuming that plant individuals are equally distributed and have a circular shape with a diameter of 3 cm, 20 cm, 50 cm and 100 cm, respectively (Appendix S1-2). Distance measurements were taken from the edge of each hypothetical plant individual. The calculation is based on a 100 m<sup>2</sup> plot. The first calculation (diameter of a hypothetical circular species = 3 cm) resulted in very low percentage-cover values (maximum percentage value of grade 7  $\approx$  23 %), not meaningful in relation to plot-based vegetation surveys; we excluded it from further counting. Calculations of

species cover with hypothetical circular species of 20 cm, 50 cm and 100 cm diameter resulted in maximum species cover values of  $\approx$  61 % to  $\approx$  71 % (= maximum percentage value of grade 7). For each grade of the Norrlin scale, we calculated the minimum (= lower grade limit), mean (= mid-percentage value) and maximum (= upper grade limit) species cover as a mean of the respective results of each of the three above-mentioned calculations (based on the diameter of hypothetical circular species = 20 cm, 50 cm and 100 cm). Due to their similarity, we summarised the grades 1 and 2 of the (transformed) Norrlin scale to one grade.

Considering the rare use of grades 8–10, we transformed them jointly to 83 % (= mid-percentage value; Table 1-1). We refrained from a more refined transformation, because we considered finer divisions as unreliable.

Still, uncertainties remain when transforming the Norrlin scale. As the variance of distances between individuals of a certain species increases with decreasing equal distribution (increasing sociability), the Norrlin scale depends on species distribution patterns on a plot level (Pakarinen 1984). Hence, it is rather unusable for recording lichens and bryophytes, which typically grow in patches within sampling plots. We could not find any information on how researchers handled the occurrence of plants with pronounced, patchy ground cover such as typically in clonal plants, tussocks or mat-forming procumbent plants.

It also remains unclear if the distance measures relate to the centres of each plant individual or to its margins. In the latter case, the scale's grades could be considered as abundance values (Barkman et al. 1964). As the Norrlin scale was often used as an alternative to cover scales, for example in dense herb and shrub layers of forests, and in the past it was preferred over cover scales by Finnish researchers (Du Rietz 1932), we assume that it was rather used to estimate species abundance.

By proposing the transformation of the Norrlin scale grades we aim to support the use of the collected historical plot data based on this scale, especially numerous Finnish data (Fig. 1-1a–c). Due to the remaining uncertainties regarding the application of the Norrlin scale in the field, we suggest to carefully read the methods of the concerned studies before applying the transformation proposed here.

#### **Hult-Sernander scale**

The Hult-Sernander (also known as the Hult-Sernander-Du Rietz) scale was inspired by the Norrlin scale (Rübel 1920) and developed as an abundance scale by the Finnish botanist and plant geographer Ragnar Hult (1881, cited after Gams 1918; Du Rietz 1921; Rübel 1922; Pakarinen 1984) and afterwards (1890) converted into a cover scale by the Swedish botanist and geologist Rutger Sernander (cited after Du Rietz 1921, 1932; Trass & Malmer 1973; Pakarinen 1984). In its development, the initially twelve scale grades (*r.* [*rare,* single], *rr.* [*rarissime,* sporadic] & numbers 1–10), were merged to five grades, which were first expressed in general terms describing the abundance of species (*rr.* - *r.* = enstaka = single; 1-2 = spridda/tunnsådd = sparse; <math>3-4 = strödda

= scattered; 5-7 = [copiosa] rikliga = plenty; 8-10 = [sociales] ymniga-täckande = area-wide/comprehensive; Hult 1881; Sernander 1912; Gams 1918; Du Rietz 1921; Rübel 1922); these terms were later on renamed to scale numbers ranging from 1 (single) to 5 (area-wide/comprehensive; Du Rietz 1921). The scale was developed into a geometric series (mean values = 1/32, 3/32, 6/32, 12/32, 24/32; Barkman et al. 1964; Trass & Malmer 1974), which means that the width of the grades increases uniformly in a progressive way; here, information on the abundance of individuals was no more given. Limits of the grades were clearly defined for estimating percentage plant cover (e.g. range borders = 0-1/16, 1/16-1/8, 1/8-1/4, 1/4-1/2, 1/2-1; Du Rietz 1921; Braun-Blanquet 1928; Malmer et al. 1978). We identified the following six variants of the Hult-Sernander scale (Table 1-1):

- Variant A: A five-grade scale based on a geometric series (Du Rietz 1921; Whittaker 1973; applied e.g. by Larsson 1967; Nylander 1972; Malmer et al. 1978).
- Variant B: A six-grade scale similar to variant A, but the grade 1 is subdivided into two grades ('x'/'+', 1; applied e.g. by Gillner 1960); the lower grade specifies (very) sparse occurrences of plants which we converted to 1 % cover.
- Variant C: A six-grade scale similar to variant A, but the grade 5 is subdivided into two grades with equal extents (1/2–3/4, 3/4–1); this series is no longer geometric (applied e.g. by Fransson 1963, 1972; Losvik 1991).
- Variant D: As variant A, but the grade 1 is subdivided into three grades (s. [single] = 0–1%,
  u. [unic] = 1–3.125 %, 1 = 3.125–6.25 %). This variant was only applied additionally to variant
  C (e.g. by Moen 1990) and therefore results in an eight-grade scale.
- Variant E: As variant B, applied additionally to variant C. This results in a seven-grade scale (applied e.g. by Tyler 1971; Losvik 1993).
- Variant F: ten-grade scale, where the original grade 1 is divided into six grades. This extended conversion of the Hult-Sernander scale was first defined as a twelve-grade strictly geometric scale (Oksanen 1976) and later applied as described here (e.g. Oksanen & Virtanen 1995; Virtanen et al. 2016; Vuorinen et al. 2017). Variant E has always been applied on the basis of the geometric mean of values, which we follow.

The authors of most studies either simply name the Hult-Sernander scale or they refer to Du Rietz (1921) as the original literature source. The scale was applied quite uniformly in the way that all variants (A–F) separate given grades but do not shift previously defined borders (Table 1-1); if information on extended versions (Variants B–F) of the original scale (Variant A) was given, they were mostly underpinned by numerical values (arithmetic or geometric means of the new defined grades or values of their lower and upper limits).

The meaning of '+' is ambiguous; it either refers to a sparse presence of a species (e.g. Gillner 1960) within the examined area (plot), its presence outside (e.g. Galten 1987; Singsaas 1989; Moen 1990) or an occurrence recorded without specified cover value. If applied

as sparse presence, we interpreting it as 1 %. Scale grades supplemented with '+' (or '-') were sometimes also applied to indicate cover values somewhat higher (or lower) than the mean of the particular grade (Du Rietz 1921, 1932). Because we considered the refinement of the mid-percentage grade values as unreliable in this case, we refrained from proposing a transformation of these finer grades.

The quite broad definition of the last grade '5' (used in all the variants except C and E; Table 1-1) was criticized (Braun-Blanquet 1928; Barkman et al. 1964; Dierschke 1994). Still, mid-percentage values of individual grades provide a suitable basis for most quantitative vegetation analyses, supported by the more or less narrow grade partitions within the lower parts of the scale, which are of ecological importance (Knapp 1971; Dierschke 1994). The division of the grade 5 into four degrees was rarely used (applied in 1963 by Gaare, unpublished [cited after Moen 1990]).

A few researchers used the Hult-Sernander scale as an abundance scale and estimated plant cover independently (applied e.g. by Aarrestad 2000), but most vegetation scientists used it as a cover scale.

#### **Drude scale**

The Drude scale, named after the German geobotanist Oscar Drude, was published in 1890 (Drude 1890a; Appendix S1-3). The five grades of the scale go back to Grisebach (1884). They are based on the indication of species abundance and cover (*sol. = plantae solitariae*/single plant; *sp. = sparsae, sporadice intermixtae*/sparse-sporadic; *cop. = copiose intermixtae*/copious, numerous; *gr. = plantae gregariae*/growing gregariously; *soc. = plantae sociales*/plants of high sociability, the definition of *soc.* includes species with 100 % cover, for example a full canopy closure (Drude 1890a). For the grades *sp.* and *cop.* information on the distribution (admixture) of speces is given, which still can be interpreted as information on species abundance. The fourth grade 'gregariae' of the original Drude scale (Drude 1890a; Du Rietz 1921) was never used as an abundance-based grade but was applied as an indication of a patchy (gregarious) occurrence of the species (Drude 1890a; Gams 1918) and could be applied additionally to the given abundance scale grades (Rübel 1922). The partition of the grade '*cop.*' was recommended (Drude 1890a; Du Rietz 1921), resulting in a six-grade basic scale (*sol., sp., cop.*<sup>1</sup>, *cop.*<sup>2</sup>, *cop.*<sup>3</sup>, *soc.*; Rübel 1922). Additionally quoted '+' and *un. = unicum* indicate lowest abundance values and single or few (*rr.*) individuals, respectively.

There is some uncertainty as to whether the Drude scale was mainly used in its original sense as an abundance (and relative-occurrence [admixture of species] based) scale, or whether if it was rather applied as if it were a percentage-cover scale. Unlike the Hult-Sernander scale, the Drude scale never developed into a clearly defined cover scale, although Bykov (1978) demonstrated the relation of the Drude scale to certain percentage-cover values (see Variant C below). The use of the Drude scale as a cover scale was confirmed for Ukraine by Yakov P. Didukh (personal communication 2018). Most of the literature sources relate this scale to abundance estimations (e.g. Sukachev 1928, 1931; Ponyatovskaya 1964; Dylis 1974; Mirkin et al. 1989; Volkov 2008). However, considering the application of an abundance scale in the field, we think that, if the researcher is not trained to distinguish between cover and abundance in a right way, the estimation of the cover is always additionally taken into account.

Different studies describing the abundance or cover of plants interpreted the Drude scale differently. If the scale was transformed to mid-percentage-cover values, the numerical values corresponding to the individual grades varied. The structure of the surveyed vegetation type influenced the interpretation of the scale grades: In a scarce, open vegetation with a total vegetation cover of ~20 %, the scale grades *soc.*, *sp.*, *cop.*<sup>1</sup> and *cop.*<sup>2</sup> were usually distributed across the total vegetation cover range of 0-20 %. However, in a dense, possibly also multi-dominant vegetation, the same grades were distributed across a range of 0-~~50 %, which leads to a much broader interpretation of the individual scale grades. We identified three main variants of the Drude scale with different numbers of grades and different interpretations of these grades in terms of their transformation to percentage values (Table 1-1).

- Variant A: A 12-grade scale, using *rr*. in the lowest parts and intermediate grades between each of the originally defined grades (e.g. *sp.-cop<sup>-1</sup>*; Kucherov 2018). For reasons of practicability during fieldwork, the percentage values given for *sol., cop.<sup>1</sup>* and *cop.<sup>2</sup>* slightly differ from the arithmetic means of individual grades (by 1–3%). For all other grades the arithmetic mean is given. This variant was developed for dwarfshrub and moss-lichen layers and is most appropriate for boreal vegetation like forests, mires and heathlands.
- Variant B: A seven-grade scale (applied in IBIS, Zverev 2007) similar to variant A in the lower cover grades. The upper cover grades *cop*.<sup>3</sup> and *soc*. are lower than those in variant A. If the upper grades seem to be overestimated when applying variant A, variant B is recommended for the transformation of species data. As the mean values were given for each grade, their limits were calculated accordingly. This variant is similar, but not equal to the transformation suggested by Tikhodeyeva & Lebedeva (2015).
- Variant C: This six-grade scale is transformed to the lowest percentage values for the scale grades *soc.*, *sp.*, *cop.*<sup>1</sup> and *cop.*<sup>2</sup> (Bykov 1978). If these grades seem to be overestimated when applying variant A or B, variant C is recommended for the transformation of species-quantity data. As the grade limits were given by Bykov (1978), we calculated the mid-percentage values of each grade. This variant is most appropriate for scarce vegetation (e.g. xeric vegetation such as dry steppes, chasmophytic vascular plant communities or open structured aquatic vegetation).

We cannot say in which sense the Drude scale was applied in each single study. This means that data probably can be transformed by each of the proposed transformation types, regardless of the number of applied grades (12, 7, 6 or any other [less frequently used]). As an example this does not mean that any six-grade scale should be transformed as proposed in variant C; but could

be also converted based on each proposed type of transformation. However, which type of transformation is best suitable for the given data can be estimated by calculating the sum of all individual species covers per plot on the basis of each of the here proposed transformation types, which reflect the variety of interpretations used. The over- or underestimation is indicated if these sums are much higher or lower than the total cover of the studied vegetation. When applying the three transformation types used in variant A, B or C to approximate the best fitting transformation of scale grades, we suggest to convert grades *un., rr.* or *rr.-sol.* always to values  $\leq 1$  %.

Caution should be made when dealing with forest data in which *soc*. is applied to tree species. According to the original explanation (Drude 1890a; Appendix S1-3), *soc*. is given for (a) one tree if it is abundant, (b) one tree species if it is not abundant but stands out high or (c) for several tree species if they show high sociability amongst themselves, which means that they are jointly abundant and aggregated.

Emerging from the critique of its wide ranges for higher grades (Rabotnov 1984), the Drude scale was further developed in various ways. Six or ten-grade abundance scales, not anymore known as Drude scale, were used between 1940 and 1970 in Russian forest surveys (Ponyatovskaya 1964). Another proposed variant of the Drude scale, based on distance measures between plant individuals (Rabotnov 1984), hardly came into use.

#### **Additional remarks**

In some studies, layers were recorded separately and two different species-quantity scales were used (e.g. Linkola 1929; Lumiala 1937; Ruuhijärvi 1960; Eurola 1962; Koponen 1967); the tree layer was estimated on the basis of one of the above discussed scales, while the herb and/or cryptogam layer were estimated as direct or categorical percentage values. In this case, particular attention is needed, especially when combining species cover values across different layers (Fischer 2015) for the purpose of analyses.

Due to the wide influence of the well-known Braun-Blanquet school, the Braun-Blanquet scale has also been used in some Fennoscandian studies, either in its original sense (Braun-Blanquet 1928; Tüxen 1984) or as variants with different transformations to (mid-)percentage values. Additionally, cover estimations based on percentage values, with progressively structured or decimal-based categories were increasingly used from the 1970s onwards, and largely replaced the formerly used species-quantity scales in Fennoscandia (Pakarinen 1984; Lawesson 2000).

Table 1-1: Transformation of scale grades to mid-percentage values of the Norrlin, Hult-Sernander and Drude scales and their frequently used variants. The well-known Braun-Blanquet scale is displayed as a reference, with mid-percentages of the grades following the transformation given in TURBOVEG 2. We rounded all mid-percentage values < 1 % to the first decimal place and values > 1 % to the nearest whole number. Mid-percentage values of the grades are based on the arithmetic mean except for variant F of the Hult-Sernander scale, which is based on geometric mean percentage values, and variant A of the Drude scale; here, the values given for sol., cop.1 and cop.2 slightly differ from the true mean values (by about 1–3 %). The y-axis is stretched below 5 % and again below 1 % cover. Names of columns follow the description in the text.

S	even grade	Norrlin		Hult-Serna	inder scale	Drude scale					
Bra	un-Blanquet scale	scale	Variant A	Variant B & E	Variant C & D	Variant F	Variant A	Variant B	Variant C		
0 -		+, <i>r., rr.</i> =0.2% 1,2 = 0.5%			s. =0.5%	1 =0.1% 2 =0.3% 3 = 0.5%	rr.= 0.1%	un.=0.5%	sp. = 0.5%	- 0	
1 -	r = 1% + = 2%	3 = 3%	1 = 3%	x/+ = 1%	u. = 2%	4 = 1% 5 = 2%	rr sol. =1% sol.=3%	sol.=3%	cop!=2%	- 1	
- 5 - -			1 - 570	1 5%	1 = 5%	6 =5%	sol sp. =5%			- 5	
10 -		4 = 8%	2 =9%	2 =9%	2 =9%	7 = 9%	sp.=10%	sp.=10%	cop?=12%	- 10	
20 -	2 =15%	5 = 16%	3 =19%	3 = 19%	3 = 19%	8 = 18%	sp cop: =15% cop! = 20%	cop: <sup>1</sup> =20%		- 20	
/ plot		6 = 31%				9 = 35%	<i>cop</i> <sup>1</sup> - <i>cop</i> <sup>2</sup> = 30%			- 30	
[%] ដ <sup>40</sup>	3 = 38%		4 = 38%	4 = 38%	4 =38%	5-55%	3 100/	<i>cop</i> ?=38%		- 40	
U C O C O							<i>cop</i> : = 40%				
		7 =52%								-	
60-	4 =63%			<u>5 =63%</u>	5 =63%		<i>cop? - cop?</i> =60%	<i>cop</i> .³=63%	cop:³=60%	- 60	
1 70 -						10 =71%				- 70	
80-		8, 9, 10 = 82%	5 =75%	-5=75%		-	cop <sup>3</sup> =80%			- 80	
90	5 = 88%			<u>6 =88%</u>	6 =88%			soc.=88%		- - 90	
100							<i>soc</i> .=95%		-soc.=100%-	L L L 100	

# Conclusion

Vegetation science has a long tradition in Fennoscandia. However, during the last decades, there has been little focus on phytosociological research in this region (Dierßen & Dierßen 1996; Lawesson 1998; Peterka et al. 2015). In many Fennoscandian regions historical vegetation data are the only available records describing certain vegetation types. As these data fill important gaps in the data volume on European vegetation databases, transformations to make them compatible with other datasets are very important, especially in large-scale studies on biodiversity patterns.

With our suggestions on transforming the three species-quantity scales of Norrlin, Hult-Sernander and Drude, we hope to contribute to their comprehensibility and application and to the preservation of a substantial volume of historical quantitative information on Fennoscandian vegetation. An example of a geographically broad-scale study in which Nordic vegetation-plot data recorded with different species-quantity scales were specifically transformed and used, is the survey of salt-marsh vegetation of the Baltic Sea shores (Pätsch et al. accepted b).

Our proposed transformations of species-quantity scales have been implemented as a standardised species cover-abundance scale in the database-management program TURBOVEG 2 (Hennekens & Schaminée 2001).

# Between land and sea – a classification of saline and brackish grasslands of the Baltic Sea coast

# **Technical information**

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**The following abbreviations are used:** BKØ (Belt Sea-Kattegat-Øresund area including the south-western Swedish coast and the German Sea coast); BP (Baltic Proper); BS (Baltic Sea); GeB (German Bight); GB (Great Britain); H (when leading a 4-digit code, European Union Habitats Directive Annex I habitat type); nBS (northern Baltic Sea including the Gulfs of Finland and Bothnia); NL (The Netherlands); var. (variant).

# Supplementary material:

- I Appendix S2-1: Data sources.
- Appendix S2-2: Data selection and reduction.
- Appendix S2-3: Nomenclature particularities.
- Appendix S2-4: Shifts in synoptic tables.
- I Appendix S2-5: Synoptic tables.
- Appendix S2-6: Evaluation of structural, abiotic and climatic factors.
- Appendix S2-7: Analogues in literature.

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# Abstract

Aims: Baltic Sea coastal grasslands are influenced by saline or brackish sea water, a narrow tidal range and non-intensive land use. At least since they have been listed as Natura 2000 habitat types (EU Habitats Directive), they have become an important conservation issue at European scale. So far, only little supra-regional research has been conducted on their floristic and ecological diversity, syntaxonomy and geographic variation. We aim to survey the geographical distribution and syntaxonomical variation of saline and brackish grasslands on a transnational perspective to highlight large-scale gradients in species composition and underlying climatic and other abiotic factors. We discuss the resulting vegetation types in the light of a wider North-west European perspective and review conservation aspects.

Study area: Baltic Sea coast

**Methods:** We compiled an overall plot-based vegetation dataset for the Baltic Sea coast and subsequently selected relevés by species composition and plot size. We classified 3,732 relevés, using modified TWINSPAN, identified differential species and syntaxa, and performed a DCA with *post-hoc* fitted intrinsic and climatic variables. We tested main differences in relevant factors for significance.

**Results:** The classification resulted in 33 vegetation types widely differing in distribution range and area size and mainly belonging to the classes *Juncetea maritimi* and *Molinio-Arrhenatheretea*, and a few to the *Phragmito-Magnocaricetea*, *Cakiletea maritimae*, *Saginetea maritimae*, *Scheuchzerio palustris-Caricetea fuscae* and *Koelerio-Corynephoretea canescentis*. Baltic Sea coastal grasslands vary in soil salinity and moisture and to a lesser extent in nutrient availability and base content.

**Conclusions:** Variation in plant communities generally reflects regional phytogeographical patterns. Communities most similar to north-west European coastal grassland types are characterised by euhaline to  $\alpha$ -mesohaline site conditions. Designations of the Natura 2000 habitat types H1330 and H1630 require revision. Many Baltic Sea coastal grassland plant communities include species threatened on national level.

### Introduction

The Baltic Sea coast has played an eminent role in European cultural history for many centuries (Küster 2004) and constitutes an important yet vulnerable part of the European landscape diversity (Dijkema 1990). Under natural conditions, littoral grasslands occur only at a small scale and/or temporarily on newly formed terrain. Extended through mowing and grazing since hundreds of years (Dijkema 1990; Dierßen & Dierßen 1996), large-scaled, resilient and persistent coastal grasslands occur almost throughout the Baltic Sea coast.

Baltic coastal meadows are listed as habitat types (H1330: Atlantic salt meadows; H1630: Boreal Baltic coastal meadows), the latter priority-rated, in Annex I of the European Union Habitats Directive (European Commission 2013), and have been assessed as Endangered in the European Red List of habitats (Janssen et al. 2016). Associated halophytic habitats such as drift-lines (H1210) and sandy flats (part of H1310), as well as landward glycophytic habitats such as *Molinia* meadows (H6410) and hydrophilous tall herb fringes (H6430), are also listed in the Directive's Annex I (European Commission 2013). The overall decrease of Baltic Sea coastal grasslands is a result of abandonment (Janssen et al. 2016; Lehtomaa et al. 2018), prevention of flooding dynamic (LUNG 2011), agricultural intensification (Siira 1985; Helsinki Commission 2013), eutrophication (Jutila 2017), water pollution (Rautiainen et al. 2007), building development and barrier constructions (Dierßen & Dierßen 1996; European Commission 2013).

Coastal saline and brackish grasslands (henceforth coastal grasslands) are transitional habitats of the semi-enclosed Baltic Sea, growing on shallow coasts with fine-grained sandy to silty sediments. They range from the intertidal zone (eulittoral) to above the mean high water line (supralittoral) up to just above the high water spring tide line (epilittoral; Tyler 1969a; Dierßen & Dierßen 1996; Jutila 2001; Leuschner & Ellenberg 2017). Patterned by local factors, such as micro-topography (Ward et al. 2016), salinity, water saturation, nutrient availability and base content, these grasslands are inhabited by halophytes as well as by more or less halotolerant glycophytes (Adam 1981; Jeschke 1987).

Numerous descriptions and classifications of coastal grasslands along the Baltic Sea coast have been published, but mostly with a local or regional scope, or referring to particular vegetation types (e.g. Dahlbeck 1945; Gillner 1960; Fukarek 1961; Siira & Haapala 1969; Siira 1970; Krisch 1974, 1990; Schmeisky 1974; Rebassoo 1975; Härdtle 1984; Siira & Merilä 1985; Jeschke 1987; Willers 1988; Wolfram 1996; Vestergaard 1998; Jutila 2001; Czyż et al. 2003; Berg et al. 2004; Burnside et al. 2007; Bosiacka 2011; Hulisz et al. 2016; Ward et al. 2016). The works of Wanner (2009), Dijkema (1990), Dierßen & Dierßen (1996), Leuschner & Ellenberg (2017) and Tyler (1969a) refer to a larger geographical extent. They include own investigations or summarize further regional studies but do not provide a reproducible and/or spatially comprehensive classification of vegetation. Thus, we lack an overall view of Baltic Sea saline and brackish grasslands, based on cutting-edge classification methods and transnational data, an important component for European habitat typologies and decision-making processes in European nature conservation.

To contribute to a better transnational interpretation of European vegetation and habitats, our study presents a survey of Baltic Sea coastal grasslands, feasible by means of today's amplified data availability. Main emphasis is given to their floristic diversity, ecological characteristics and distribution. The following research questions are addressed: (i) Which plant community types

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can be found and (ii) where do they occur? (iii) Which diversity patterns, vegetation structure, abiotic and climatic factors characterise the observed vegetation types? We regard the classified coastal grassland vegetation types from a wider geographical perspective and discuss important conservation issues including management, Red List species and Natura 2000 habitat types.

Fig. 2-1 Geographic distribution of all relevés in the dataset. Dense occurrences of relevés along the German Sea coast partly refer to a spatially unbalanced data compilation. Regions within the study area are separated related to phytosociological and phytogeographical patterns (source: HELCOM Map and Data Service 2012, modified). Data from Willers 1988, marked with x, are distributed along the entire Finnish Sea coast; single relevés could not be allocated to a certain location.

# **Study Area**

Relevés reflected in this study are located along the mainland and insular coasts such as the Archipelago Sea and the West Estonian Archipelago of the Baltic Sea (BS; Fig. 2-1). The study area includes coastlines characterised by pre-glacial and glacial sediments in the Belt Sea-Kattegat-Øresund region (BKØ) and the southern part of the Baltic Proper (BP) as well as more diverse landforms in the northern Baltic Sea (nBS, Gulfs of Bothnia and Finland) and the eastern part of the study area where land masses are rising (postglacial rebound; Schiewer 2008; Schwarzer et al. 2008).

Differences in annual temperatures (temperature seasonality) are most pronounced towards the eastern and northern parts of the study area, driven by continental climatic influences and the transition from a nemoral to a boreal temperature regime. Increasing temperature seasonality is related to decreasing annual mean temperatures. Average minimum temperatures range from -25.1 in the north to -5.2 °C in the south of the study area. The period of plant growth in the boreal zone is approximately a third of the one in the south (Dijkema 1990). Generally higher annual precipitations in the eastern part of the study area (most pronounced along the west coast of Lithuania and Latvia) occur mainly in the warmest quarter of the year. The annual

precipitation in the study area varies between 520 mm and 698 mm (interquartile range; according to Karger et al. 2017).

Baltic Sea coastal grasslands develop under slightly saline (oligohaline) to strongly saline (euhaline, occasionally hypersaline) conditions, ranging from 30 ‰ salt content in the BKØ where the tidal range usually amounts up to 30 cm, to a brackishness as low as 2 ‰ in the Bothnian Gulf where tidal fluctuation hardly exists (Tyler 1969a). While grasslands of the eulittoral and supralittoral are directly influenced by seawater, the epilittoral is affected only at irregular high tides and during inshore storms (Vartiainen 1980; Dijkema 1990). Soil salinity is further influenced by ascending relic salt solution from the Mesozoic (Bosiacka 2011; Bosiacka et al. 2011; Lehtomaa et al. 2018). Salt accumulation and water saturation (fresh- and seawater) vary greatly. East of the transition area to the North Sea seasonal flooding affects coastal grasslands more than tidal fluctuation. The flooding is mainly driven by river flood water, wind and inlets (Dijkema 1990; Dierßen & Dierßen 1996). Mean seasonal fluctuations within the growing season can account for up to 20 cm difference in water level (Tyler 1969a; Dijkema 1990) but occurs predominantly in autumn and early winter with ranges from 70-180 cm height up to severe level differences of 180-300 cm height (Dijkema 1990).

# Methods

#### **Data collection**

Focusing on the total extent of the BS coastline (HELCOM Map and Data Service 2018), we compiled a plot-based vegetation dataset of 9,562 relevés of coastal grasslands (stored in Turboveg, Hennekens & Schaminée 2001), considering own data as well as databases from the European Vegetation Archive (EVA, Chytrý et al. 2016) and further non-published and published data (Appendix S2-1). Data without locality indication were omitted. We reduced our selection to relevés of the vegetation class *Juncetea maritimi* and associated grassland communities, based on species composition and abundances (Appendix S2-2). As an example, relevés dominated by annual *Salicornia* and *Suaeda* were excluded, which in effect excludes communities of the class *Thero-Salicornietea*.

Vast variance in plot-size (0.25-9,782 m<sup>2</sup>) was constrained to 1-80 m<sup>2</sup>. As we found no evidence of negative effects of geographically non-stratified relevé sampling (by means of preliminary classification), we refrained from stratifying relevés geographically. Bryophytes were excluded because of their limited consideration in the dataset; besides, they play a marginal role in these ecosystems. The original taxonomy was checked for synonyms, subspecies and varieties of unclear or inconsistent status that had to be integrated or pooled, respectively (Appendix S2-3). The final dataset ready for analysis comprised 3,732 relevés collected over the last ninety-seven years. Cover scale values were translated to their respective mean percentage values.

#### Classification

We calculated a hierarchical modified TWINSPAN (Roleček et al. 2009) in the program JUICE (Tichý 2002), conducted with pseudo-species cut levels 0, 5, 25, ensuring compatibility of various used cover abundance scales (distance measure: Whittaker's beta-diversity). If modified TWINSPAN did not result in clusters with ecologically meaningful differential species, we refrained from further hierarchical subdivision (Tsiripidis et al. 2009). Subsequently we improved the resulting table by re-allocation of 85 relevés. Re-allocations were made only if (i) the differentiation of the cluster by differential species constancy values was improved and (ii) the silhouette value (JUICE, Silhouette function) of clusters remained consistent or was enhanced (Appendix S2-4; Rousseeuw 1987). Thirty-two relevés of five clusters turned out to be geographical outliers lacking differential species of the respective clusters; as they could not be re-allocated to other clusters they were removed from the dataset (Appendix S2-4).

To facilitate overall comparison at the level of alliances, orders and classes, we followed the syntaxonomic conspectus by Mucina et al. (2016), even if deviating from the original authors' choice of syntaxa. For further allocation to association level or below, we consulted chiefly the following works: Almquist (1929); Dahlbeck (1945); Gillner (1960); Fukarek (1961); Siira & Haapala (1969); Tyler (1969a, 1969b); Krisch (1974, 1990); Rebassoo (1975); Adam (1981); Härdtle (1984); Siira & Merilä (1985); Willers (1988); Preising et al. (1990); Rodwell et al. (1991, 2000); Dierßen & Dierßen (1996); Sýkora et al. (1996); Wolfram (1996); Zuidhoff et al. (1996); Dierschke (1997, 2012); Schaminée et al. (1998); Westhoff et al. (1998); Jutila (2001); Berg et al. (2004).

#### **Data interpretation**

We calculated unweighted mean Ellenberg indicator values (Ellenberg et al. 2001) per relevé and DVA (Grime 1979, C [strong competitors], S [stress tolerators], R [ruderals]; Klotz et al. 2002); intermediary CSR-strategy types were treated as own classes. Taxa assigned to more than one lifeform were considered more than once. For a multiple comparison of groups of higher classification levels we calculated Mann-Whitney-U tests for the above named variables, using a *post-hoc* Bonferroni adjustment to correct *p* values for different group sizes.

We assigned BIOCLIM data (Karger et al. 2017) to each relevé (spatial analyst tool; ArcGis 1999-2015 Esri Inc., version 10.3.1.4959). A DCA (Detrended Correspondence Analysis) was computed (function: decorana) to examine relations of above-named variables and climatic factors to plant communities. The variables were fitted *post-hoc* (function: envfit, package: *vegan*; Oksanen et al. 2018; R Development Core Team 2009, version 2.9.0). To increase clarity in the plotted DCA, we generated groups of correlated climatic vectors (Pearson correlation > 0.8, function: pairs.panels/cor.plot, package: psych; Revelle 2018; R Development Core Team

2009, version 2.9.0). Abiotic factors and structural variables were tested for significance by a permutation test with 999 permutations. We generated distribution maps of all clusters (ArcGis 1999-2015, Esri Inc. version 10.3.1.4959).

# Results

The relevés included a total of 556 taxa (species and additional subspecies). The classification resulted in three main clusters (M), each subdivided into two, five and six groups (G), respectively. We further divided each group into two to five sub-groups (S [= cluster]). The sub-groups of each group have a similar species composition, ecology and/or syntaxonomically close relationship. In total, we distinguished 33 sub-groups (Fig. 2-2).



Fig. 2-2 Classification tree of the modified TWINSPAN (Roleček et al. 2009) analysis resulting in 33 sub-groups (clusters). If a sub-group did not hold ecologically meaningful negative or positive differential species following the differential species concept of Tsiripidis et al. (2009), we refrained from further divisions towards lower hierarchical levels. Colours indicate their allocation to the main groups (blue = M1; green = M2; yellow-red = M3) and groups (following floristic similarities and syntaxonomical allocation; see Table 2-4) of each part of the dataset: light = M1G1, dark = M1G2; light = M2G1, bright = M2G2, dark = M2G3, cyan = M2G4, moss-green = M2G5; orange = M3G1, dark yellow = M3G2, bright red = M3G3, light yellow = M3G4, dark red = M3G5, pink = M3G6. Colours go along with those used in Table 2-4 and Fig. 2-3 and 2-5.



Fig. 2-3 Relation of groups M1G1-M3G6 within DCA axes 1 and 2 (length of axes 1: 5.98, 2: 4.76; Eigenvalue of axes 1: 0.58, 2: 0.38). Main clusters of the dataset are reflected in intermediate (M1) light (M2) and dark grey (M3) respectively. Groups are shown as "spider"-graphs; its grey shades follow Fig. 2-4. The positions of group numbers indicate group centroids; their colours indicate their allocation to the main groups (blue = M1; green = M2; yellow-red = M3) and groups (following floristic similarities and syntaxonomical allocation; see Table 2-4) of each part of the dataset: light = M1G1, dark = M1G2; light = M2G1, bright = M2G2, dark = M2G3, cyan = M2G4, moss-green = M2G5; orange = M3G1, dark yellow = M3G2, bright red = M3G3, light yellow = M3G4, dark red = M3G5, pink = M3G6. Colours go along with those used in Table 2-4 and Fig. 2-2 and 2-5. Ellenberg indicator values, life-forms, mean number of species and climatic variables (Karger et al. 2017) are plotted *post-hoc*. Selected variables provide a significance of  $p \le 0.001$  and  $r^2 > 0.1$  (Appendix S2-6). Correlating climatic variables, providing an equal direction within DCA axes one and two, have been aggregated; the vector which correlates best with the ordination is shown: climate-a: annual mean temperature (minimum temperature of the coldest month, mean temperature of the driest, wettest, warmest and coldest quarter; correlation < 0.8: precipitation of driest and coldest quarter and of driest month); climate-b: temperature seasonality (mean diurnal temperature range, temperature annual range; correlation < 0.8: precipitation seasonality).

#### Ordination

The first two axes of the DCA diagram have a length of 5.98 and 4.76, respectively (Fig. 2-3). Soil salinity, moisture and base content correlate with the ordination with  $r^2 > 0.5$ , weighted sums of strong competitors and stress tolerators and species numbers correlate with  $r^2 > 0.4$  (Appendix S2-6). With little overlap, the three main clusters were clearly separated by species composition along the first axis. From M1 towards M3, the cover of stress tolerators decreases along with likewise decreasing soil salinity. Species numbers are highest in M3 vegetation types (axis 1). Within each main cluster M, the groups (G) were distributed along the second axis. This

axis is characterised by a gradient of increasingly wet site conditions and, with only weak correlation to the ordination axis, a southern to middle boreal climate with a slight continental character (climate-b) in the upper part, and a temperate climate (climate-a) and nutrient-rich site conditions in the lower part of the diagram. Climate-b is characterised by a more pronounced



temperature seasonality, diurnal range and, to a lesser extent, precipitation seasonality, whereas climate-a is related to generally increased temperatures (Appendix S2-6).

Fig. 2-4 Whisker-plots of main clusters M1-3 for Ellenberg indicator values, life-forms, life-span, plant strategy types and mean numbers of species, showing striking patterns (Ellenberg indicator values: differences  $\geq$  one category; Cover abundance: differences  $\geq$  20 %) and significant differences ( $p \leq 0.001$ ; Appendix S2-6). Width of whisker-plots refers to the number of relevés within each main cluster (M1-3); grey shades go along with "spider"graphs of Fig. 2-3: M1 = medium grey; M2 = light grey; M3 = dark grey.

#### Plant community classification and characterisation

The descriptions of plant communities refer to Tables 1-3 (M1-3; Appendix S2-5) and Figs. 3 and 4 (Appendix S2-6). Analogoues communities found in literature are listed in Appendix S2-7.

Striking patterns in Ellenberg indicator values (mean of plot-based unweighted mean [%]/sub-group), CSR-strategists and species life-forms (mean of plot-based weighted sum [%]/sub-group) and mean numbers of species are mentioned for each group. Information other than that derived from own data was taken from the indicated literature sources where descriptions of the respective vegetation types are provided. Information on the littoral zonal placement of sub-groups and their position relative to certain landscape structures (e.g. along rivers, in depressions) is always derived from the given literature sources. For Natura 2000 habitat types see European Commission (2013), for those of soil salinity terminology see Scherfose (1990).

Table 2-1 Shortened combined synoptic table of classified saline and brackish plots (relevés) of the first main cluster (M1). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009).

Group - Sub-group	G1S1	G1S2	G1S3	G1S4	G1S5	G2S6	G2S7	G2S8
Number of relevés	24	64	125	40	109	48	15	120
Average species number	8.8	6.7	9.6	4.6	6.8	7.1	8.7	8.0
Limonium vulgare	<b>75</b> <sup>73</sup>	5	17 <sup>5.5</sup>	0	0	0	0	0
Armeria maritima	<b>67</b> <sup>63</sup>	0	22 <sup>11</sup>	0	2	0	7	0
Parapholis strigosa	<b>54</b> <sup>65</sup>	0	2	0	0	0	7	0
Halimione pedunculata	33 <sup>45</sup>	11 <sup>8.4</sup>	1	0	1	0	0	0
Suaeda maritima	8	<b>39</b> <sup>34</sup>	12 <sup>1.4</sup>	10	0	0	0	18 <sup>8.1</sup>
Glaux maritima	<b>50</b> <sup>1.4</sup>	31	<b>88</b> <sup>30</sup>	35	<b>50</b> <sup>1.8</sup>	42	47	42
Festuca rubra	17 <sup>8.8</sup>	3	<b>35</b> <sup>32</sup>	3	$11^{1.6}$	2	7	1
Juncus ranarius	0	0	6 <sup>1</sup>	0	1	29 <sup>38</sup>	0	10 <sup>6.8</sup>
Puccinellia phryganodes	0	0	0	0	0	0	<b>80</b> 88	0
Triglochin palustris	0	0	2	0	15 <sup>0.3</sup>	21 <sup>6.9</sup>	<b>67</b> <sup>56</sup>	11
Juncus bufonius	4	3	0	0	0	10 <sup>8.3</sup>	13 <sup>13</sup>	13 <sup>12</sup>
Atriplex prostrata	4	31 <sup>2.6</sup>	<b>39</b> <sup>9.3</sup>	18	32 <sup>3.3</sup>	21	20	<b>60</b> <sup>27</sup>
Phragmites australis	4	2	6	10	21 <sup>10</sup>	10	$13^{1.1}$	33 <sup>23</sup>
Argentina anserina subsp. anserina	0	0	2	0	5	0	13 <sup>14</sup>	20 <sup>26</sup>
Triglochin maritima	46	<b>56</b> <sup>5.7</sup>	<b>70</b> <sup>16</sup>	<b>85</b> <sup>28</sup>	42	35	33	22
Bolboschoenus maritimus	4	9	27 <sup>0.8</sup>	<b>50</b> <sup>20</sup>	<b>65</b> <sup>33</sup>	10	0	<b>44</b> <sup>15</sup>
Puccinellia distans	13	27	20	13	1	<b>98</b> 45	<b>87</b> <sup>36</sup>	<b>64</b> <sup>19</sup>
Plantago major	0	2	2	0	1	25 <sup>29</sup>	0	22 <sup>23</sup>
Spergularia media	<b>71</b> <sup>42</sup>	<b>66</b> <sup>38</sup>	<b>40</b> <sup>15</sup>	0	8	0	0	3
Puccinellia maritima	<b>88</b> <sup>31</sup>	<b>84</b> <sup>29</sup>	<b>86</b> <sup>29</sup>	8	<b>85</b> <sup>29</sup>	8	0	16
Salicornia europaea	<b>67</b> <sup>23</sup>	<b>67</b> <sup>23</sup>	<b>55</b> <sup>14</sup>	0	15	6	<b>67</b> <sup>23</sup>	22
Plantago maritima	<b>71</b> <sup>22</sup>	<b>50</b> <sup>6.4</sup>	<b>87</b> <sup>35</sup>	10	16	38	<b>53</b> <sup>8.9</sup>	9
Juncus gerardi	<b>88</b> <sup>29</sup>	20	<b>84</b> <sup>26</sup>	15	41	<b>58</b> <sup>6.5</sup>	<b>73</b> <sup>18</sup>	18
Spergularia marina	13	53	<b>59</b> <sup>4.1</sup>	10	39	<b>83</b> <sup>22</sup>	<b>80</b> <sup>20</sup>	<b>94</b> <sup>31</sup>
Agrostis stolonifera	17	14	<b>62</b> <sup>7.7</sup>	35	<b>83</b> <sup>23</sup>	<b>67</b> <sup>11</sup>	<b>73</b> <sup>16</sup>	<b>67</b> <sup>11</sup>
Tripolium pannonicum subsp. tripolium	<b>67</b> <sup>2.9</sup>	<b>83</b> <sup>16</sup>	<b>80</b> <sup>13</sup>	<b>95</b> <sup>25</sup>	<b>83</b> <sup>15</sup>	31	0	<b>66</b> <sup>2.2</sup>

Table 2-2 Shortened combined synoptic table of classified saline and brackish plots (relevés) of the second main cluster (M2). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009).

Group - Sub-group	G1S1	G1S2	G2S3	G2S4	G3S5	G3S6	G3S7	G3S8	G4S9	G4S10	G4S11	G5S12	G5S13
Number of relevés	87	54	163	548	24	250	50	42	272	73	107	38	91
Average species number	8.0	9.6	7.6	8.0	11.6	11.9	12.3	12.1	10.0	15.0	10.1	10.9	11.8
Elytrigia repens	<b>87</b> <sup>59.2</sup>	6	1	11	0	28 <sup>11.1</sup>	26 <sup>9.2</sup>	14	11	0	6	0	1
Cochlearia anglica	22 34.6	11 <sup>15.3</sup>	1	1	0	0	0	0	0	0	0	0	0
Limonium vulgare	5	<b>81</b> <sup>83</sup>	5	1	0	2	0	0	0	0	0	0	0
Puccinellia maritima	0	31 <sup>37.6</sup>	18 <sup>19.4</sup>	4	0	2	0	0	1	0	1	0	0
Spergularia media	6 <sup>3.9</sup>	22 <sup>30.4</sup>	12 14.4	3	0	1	0	0	0	0	0	0	0
Sagina maritima	1	2	1	2	<b>83</b> <sup>84.7</sup>	3	0	2	0	0	0	0	0
Carex extensa	1	7	7	12 1.2	<b>83</b> <sup>68.7</sup>	5	4	0	2	14 3.1	1	0	0
Centaurium pulchellum	0	0	9	4	<b>79</b> <sup>69.6</sup>	5	6	0	1	7	3	0	5
Plantago coronopus	0	0	1	2	<b>71</b> <sup>75.9</sup>	5	4	0	1	0	0	0	0
Juncus maritimus	2	6	1	5	8	2	<b>70</b> <sup>64.2</sup>	0	4	8	2	0	0
Oenanthe lachenalii	6	0	0	5	0	6	<b>68</b> <sup>62.7</sup>	0	3	10 1.4	9 <sup>1.2</sup>	0	0
Schedonorus arundinaceus	9 <sup>4.7</sup>	0	1	3	4	15 <sup>12.3</sup>	22 <sup>21</sup>	2	7 <sup>1.9</sup>	1	1	0	4
Inula britannica	1	0	1	0	0	2	22 <sup>32.6</sup>	0	1	11 <sup>13.7</sup>	0	0	0
Molinia caerulea	0	0	0	1	0	1	0	<b>48</b> <sup>65.5</sup>	1	0	1	0	0
Carex panicea	0	0	0	1	0	2	0	<b>43</b> <sup>51.5</sup>	1	16 <sup>15.8</sup>	0	0	0
Taraxacum sect. Taraxacum	0	0	0	0	4 1	4 0.1	0	<b>36</b> <sup>50.3</sup>	1	1	0	0	0
Trifolium pratense	0	0	1	1	0	5 0.5	10 7	<b>36</b> <sup>41.7</sup>	4	7 2.8	0	0	0
Carex flacca	0	0	0	0	0	2 0.3	0	21 41.8	1	0	0	0	0
Peucedanum palustre	0	0	1	0	0	0	4 <sup>2</sup>	21 <sup>32.1</sup>	0	0	0	8 8.7	3 <sup>0.7</sup>
Blysmopsis rufa	0	0	1	2	13 <sup>3.3</sup>	3	0	5	6	<b>81</b> <sup>71.7</sup>	2	5	2
Poa humilis	0	0	2	1	0	15 <sup>12.7</sup>	4	0	12 <sup>8.3</sup>	27 28.4	1	0	7 <sup>1.7</sup>
Schoenoplectus tabernaemontani	1	0	0	3	0	2	6 <sup>0</sup>	0	5	11 <sup>6.1</sup>	<b>36</b> <sup>37.1</sup>	13 <sup>8.8</sup>	0
Samolus valerandi	0	0	0	2	0	1	0	0	2	1	28 44.5	0	1
Carex mackenziei	0	0	0	1	0	2	0	0	0	4	6	<b>74</b> <sup>76.3</sup>	3
Carex halophila	0	0	1	1	0	0	0	0	1	5 <sup>2.8</sup>	1	<b>37</b> <sup>50.9</sup>	3
Carex glareosa	0	0	4	2	0	3	0	0	1	8 4.1	0	26 <sup>28</sup>	22 <sup>22.2</sup>
Carex paleacea	0	0	1	2	0	1	0	0	1	0	0	29 44.1	7 6.1

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Lysimachia thyrsiflora	0	0	1	0	0	0	0	0	0	0	0	24 <sup>44.2</sup>	2 <sup>0.3</sup>
Eriophorum angustifolium	0	0	1	1	0	0	0	0	1	0	0	24 <sup>43.5</sup>	2 0.2
Argentina anserina subsp. groenlandica	0	0	2	7 5.1	0	0	0	0	1	0	2	24 <sup>32.4</sup>	9 <sup>8.6</sup>
Parnassia palustris	0	0	0	2	0	4	0	0	1	4	0	13 10.2	<b>45</b> <sup>51.5</sup>
Pedicularis palustris	0	0	0	1	0	1	0	0	0	0	0	16 18.2	32 42.6
Artemisia maritima	<b>43</b> <sup>33.9</sup>	<b>61</b> <sup>52.6</sup>	2	2	4	3	2	0	0	0	0	0	0
Atriplex prostrata	<b>59</b> <sup>35.8</sup>	24 <sup>7.7</sup>	2	15 <sup>0.5</sup>	8	8	24 <sup>7.6</sup>	0	9	5	30 12.4	3	3
Bolboschoenus maritimus	30 16.9	0	10	16 <sup>4.5</sup>	8	10	8	2	9	8	<b>46</b> <sup>31.4</sup>	0	0
Lotus tenuis	0	0	6	3	0	25 <sup>22.5</sup>	30 28.8	0	7 <sup>1.5</sup>	8 2.5	1	0	0
Odontites litoralis	0	2	6	7	0	18 <sup>6</sup>	6	<b>48</b> <sup>32.2</sup>	7	$14^{1.8}$	0	8	<b>37</b> <sup>23</sup>
Juncus articulatus	0	0	0	3	4	4	0	5	10 <sup>3.5</sup>	<b>40</b> <sup>36.5</sup>	22 17.1	0	4
Carex nigra	0	0	1	1	0	4	0	19 <sup>9.1</sup>	8	<b>36</b> <sup>25.2</sup>	3	<b>37</b> <sup>26.4</sup>	18 <sup>7.7</sup>
Calamagrostis stricta	0	0	5	7	0	2	0	0	2	3	1	<b>84</b> <sup>56</sup>	<b>91</b> 61.6
Armeria maritima	9	<b>63</b> <sup>44.5</sup>	33 <sup>18.3</sup>	6	25 11.1	14 <sup>1.8</sup>	8	0	0	1	0	0	0
Centaurium littorale	0	0	2	3	<b>42</b> <sup>26.2</sup>	10	12	<b>38</b> <sup>23</sup>	3	<b>44</b> <sup>28.1</sup>	0	0	3
Trifolium repens	0	0	1	4	17 <sup>3.4</sup>	<b>43</b> <sup>26.4</sup>	18 4.6	2	27 12.6	<b>44</b> <sup>27</sup>	4	3	2
Trifolium fragiferum	0	0	4	6	8	28 16.3	8	0	30 <sup>17.9</sup>	<b>48</b> <sup>34.4</sup>	8	0	0
Plantago major	5	0	2	6	17 <sup>7.4</sup>	16 6.7	8	0	21 11.3	23 <sup>14</sup>	21 12.2	0	1
Carex distans	0	0	1	3	<b>38</b> <sup>19.5</sup>	17 <sup>2.7</sup>	34 <sup>16.6</sup>	<b>38</b> <sup>20</sup>	2	<b>47</b> <sup>27.1</sup>	3	0	0
Scorzoneroides autumnalis	5	2	12	10	8	<b>74</b> <sup>31.6</sup>	<b>38</b> <sup>7.7</sup>	<b>69</b> <sup>28.1</sup>	31 <sup>3</sup>	<b>48</b> <sup>14.2</sup>	4	3	<b>37</b> <sup>7.3</sup>
Galium palustre	1	0	2	3	0	8	24 <sup>7.5</sup>	26 <sup>9.3</sup>	6	21 <sup>4.7</sup>	27 <sup>10</sup>	32 <sup>13.6</sup>	<b>43</b> <sup>22.8</sup>
Eleocharis uniglumis	0	0	6	7	0	10	0	0	<b>39</b> <sup>10.9</sup>	52 <sup>19.8</sup>	<b>72</b> <sup>33.5</sup>	<b>66</b> <sup>29.3</sup>	<b>49</b> <sup>18.1</sup>
Triglochin palustris	0	0	1	5	4	8	0	0	28 <sup>9.7</sup>	<b>44</b> <sup>22.7</sup>	32 <sup>13.1</sup>	<b>50</b> <sup>27.6</sup>	30 11.4
Tripolium pannonicum subsp. tripolium	53 <sup>18.9</sup>	<b>72</b> <sup>31.9</sup>	<b>49</b> <sup>16.4</sup>	<b>41</b> <sup>11</sup>	8	11	34 <sup>6.3</sup>	0	7	0	<b>45</b> <sup>13.6</sup>	0	0
Plantago maritima	28	<b>93</b> <sup>20.5</sup>	<b>99</b> <sup>24.4</sup>	<b>61</b> <sup>2.1</sup>	42	<b>82</b> <sup>14.3</sup>	<b>72</b> <sup>8.4</sup>	<b>95</b> <sup>22</sup>	31	<b>66</b> <sup>4.8</sup>	3	13	<b>64</b> <sup>3.6</sup>
Phragmites australis	23	2	5	<b>35</b> <sup>0.7</sup>	29	<b>38</b> <sup>2.4</sup>	<b>58</b> <sup>14.6</sup>	10	<b>41</b> <sup>4.1</sup>	<b>38</b> <sup>2.6</sup>	<b>59</b> <sup>15.1</sup>	<b>45</b> <sup>6.5</sup>	<b>60</b> <sup>16.1</sup>
Triglochin maritima	17	<b>78</b> <sup>9.8</sup>	<b>67</b> <sup>3.7</sup>	57	17	<b>70</b> <sup>5.5</sup>	46	<b>90</b> <sup>17.4</sup>	<b>78</b> <sup>10.2</sup>	<b>89</b> <sup>16.5</sup>	<b>71</b> <sup>5.8</sup>	<b>76</b> <sup>9</sup>	37
Argentina anserina subsp. anserina	33	0	2	12	33	<b>67</b> <sup>16.5</sup>	<b>66</b> <sup>16</sup>	<b>52</b> <sup>7.9</sup>	<b>63</b> <sup>14.1</sup>	<b>78</b> <sup>23.1</sup>	<b>53</b> <sup>8.5</sup>	3	<b>44</b> <sup>2.9</sup>
Festuca rubra	<b>85</b> <sup>10.3</sup>	<b>96</b> <sup>17.3</sup>	<b>71</b> <sup>1.3</sup>	61	<b>96</b> <sup>17</sup>	<b>96</b> <sup>16.9</sup>	<b>90</b> <sup>13.4</sup>	<b>90</b> <sup>13.7</sup>	53	58	12	21	60
Glaux maritima	56	<b>74</b> <sup>2.4</sup>	<b>83</b> <sup>8.3</sup>	<b>83</b> <sup>8.2</sup>	<b>79</b> <sup>5.6</sup>	<b>83</b> <sup>8.2</sup>	<b>84</b> <sup>8.7</sup>	<b>71</b> <sup>0.7</sup>	<b>71</b> <sup>0.4</sup>	<b>88</b> <sup>11</sup>	56	11	<b>74</b> <sup>2.1</sup>
Agrostis stolonifera	62	<b>81</b> <sup>0.5</sup>	64	<b>89</b> <sup>6</sup>	<b>88</b> <sup>4.9</sup>	<b>89</b> <sup>5.8</sup>	<b>90</b> <sup>6.7</sup>	67	<b>95</b> <sup>10.5</sup>	<b>93</b> <sup>9</sup>	<b>87</b> <sup>4.5</sup>	61	<b>86</b> <sup>3.6</sup>
Juncus gerardi	57	<b>91</b> 5.5	<b>96</b> <sup>9.8</sup>	<b>92</b> <sup>6.4</sup>	<b>88</b> <sup>2.9</sup>	<b>94</b> <sup>8.3</sup>	64	67	<b>96</b> <sup>9.3</sup>	<b>95</b> <sup>8.4</sup>	53	<b>97</b> <sup>10.7</sup>	<b>99</b> <sup>11.9</sup>

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Table 2-3 Shortened combined synoptic table of classified saline and brackish plots (relevés) of the third main cluster (M3). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009).

Group - Sub-group	G1S1	G1S2	G2S3	G2S4	G3S5	G3S6	G4S7	G4S8	G5S9	G5S10	G6S11	G6S12
Number of relevés	68	66	277	56	55	121	44	58	76	135	170	230
Average species number	18.4	17.1	15	16.3	13	11.4	14.3	15.3	14.4	20.4	20.3	18.4
Filipendula ulmaria	<b>79</b> <sup>69.1</sup>	18 <sup>8</sup>	1	0	4	0	0	9	0	7	0	4
Parnassia palustris	<b>60</b> 66.9	15 <sup>10.9</sup>	1	0	0	0	0	0	0	0	0	0
Lathyrus palustris	<b>54</b> <sup>71.5</sup>	0	1	0	0	0	0	0	0	1	0	0
Poa humilis	<b>53</b> <sup>34.7</sup>	18 <sup>4.1</sup>	22 <sup>7.5</sup>	20 5.4	4	1	14 <sup>0.1</sup>	9	7	13	1	3
Calamagrostis stricta	<b>46</b> <sup>57</sup>	6 1.7	1	0	4	0	0	2	0	0	0	0
Angelica sylvestris	<b>43</b> <sup>59.7</sup>	2	1	0	0	0	0	2	0	1	0	0
Rhinanthus serotinus	<b>38</b> <sup>52</sup>	8 5.3	1	2	0	0	0	0	0	1	0	0
Eriophorum angustifolium	29 <sup>45.4</sup>	8 7.7	1	0	0	0	0	0	0	0	0	0
Valeriana excelsa	24 <sup>44.5</sup>	2	1	0	0	0	0	0	0	0	0	0
Comarum palustre	21 40.4	3 <sup>2.3</sup>	0	0	0	0	0	0	0	0	0	0
Odontites litoralis	21 <sup>20.5</sup>	8 <sup>3</sup>	16 <sup>14.7</sup>	0	2	1	5	0	9 <sup>5.2</sup>	3	0	0
Carex panicea	3	30 34.6	10 6.4	0	0	0	0	2	0	15 <sup>13.3</sup>	1	1
Galium uliginosum	4 <sup>2</sup>	20 <sup>27.9</sup>	2	0	0	0	76	0	0	5 <sup>3.3</sup>	0	1
Lotus pedunculatus	0	20 22.6	9 <sup>6.3</sup>	0	0	1	0	9 <sup>6.3</sup>	0	9 <sup>6.7</sup>	1	5 <sup>1.2</sup>
Molinia caerulea	0	21 <sup>32.3</sup>	3	0	0	0	0	7 6.9	0	5 <sup>3.9</sup>	0	0
Carex distans	0	3	24 <sup>22.9</sup>	16 <sup>13</sup>	2	1	0	12 <sup>7.9</sup>	8 <sup>2.5</sup>	4	0	2
Hordeum secalinum	0	0	0	<b>66</b> <sup>77.8</sup>	0	0	0	0	0	3	0	1
Inula britannica	0	0	7	<b>41</b> <sup>33.7</sup>	9 0.1	5	14 <sup>4.9</sup>	14 <sup>5</sup>	1	16 <sup>6.9</sup>	1	1
Bolboschoenus maritimus	0	2	6	5	27 18.2	15 <sup>5.5</sup>	20 11.2	3	1	2	16 <sup>6.5</sup>	16 <sup>6.7</sup>
Spergularia marina	0	0	2	4	24 <sup>30.8</sup>	8 6.8	0	0	1	1	0	7 4.1
Artemisia maritima	0	0	2	2	2	24 <sup>35.2</sup>	0	2	8 7.9	0	0	0
Atriplex littoralis	1	0	0	0	4 <sup>3</sup>	20 <sup>36.4</sup>	0	0	1	0	0	0
Persicaria amphibia	1	6 <sup>1.9</sup>	1	4	4	1	23 <sup>25.5</sup>	3	0	3	0	12 <sup>9.9</sup>
Angelica archangelica subsp. litoralis	0	2	1	0	0	2	20 <sup>35</sup>	2	0	2	0	1
Carex vulpina	0	0	5 <sup>0.6</sup>	11 <sup>8.8</sup>	4	3	20 22.8	0	0	0	0	12 <sup>10.9</sup>
Festuca rubra	<b>97</b> <sup>11.5</sup>	<b>91</b> <sup>6.6</sup>	<b>89</b> <sup>4.9</sup>	<b>91</b> <sup>6.7</sup>	60	<b>87</b> <sup>3.3</sup>	77	<b>98</b> <sup>12.5</sup>	<b>92</b> <sup>7.5</sup>	<b>89</b> <sup>5</sup>	81	39
Oenanthe lachenalii	0	3	8 <sup>0.5</sup>	7	5	7	16 10.2	34 <sup>31.9</sup>	0	5	0	1
Valeriana officinalis	0	8 6.8	3	0	0	0	0	29 <sup>42.6</sup>	0	1	0	0
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Agrostis gigantea	9 <sup>3.4</sup>	6	5	2	0	5	7 <sup>0.9</sup>	26 <sup>24.9</sup>	1	10 4.5	1	3
Galium verum	0	5	4	0	4	3	7 <sup>1.3</sup>	22 <sup>21.5</sup>	13 <sup>9.5</sup>	11 <sup>6.9</sup>	0	0
Armeria maritima	0	0	15 <sup>8.7</sup>	7	4	3	0	0	<b>57</b> <sup>57.1</sup>	2	0	0
Cerastium semidecandrum	0	0	1	0	4	2	0	0	<b>39</b> 55	1	0	0
Bupleurum tenuissimum	0	0	5 <sup>3.4</sup>	0	2	2	0	0	25 <sup>40.3</sup>	0	0	0
Rumex acetosella	1	0	1	0	0	0	0	0	25 <sup>37.6</sup>	8 8.6	2	1
Cochlearia danica	0	0	1	0	0	2	5 <sup>3.8</sup>	0	22 <sup>38</sup>	0	0	0
Bromus hordeaceus	0	0	1	4	2	1	2	0	20 25.4	7 5.8	0	9 <sup>7.8</sup>
Plantago lanceolata	0	9 <sup>0.4</sup>	4	2	4	2	2	2	20 11.7	<b>44</b> <sup>38.1</sup>	4	13 <sup>5</sup>
Rumex acetosa	12 <sup>4.7</sup>	11 <sup>3.4</sup>	1	9 <sup>1.5</sup>	2	0	0	3	5	33 <sup>29.2</sup>	1	14 <sup>7.6</sup>
Anthoxanthum odoratum	6	12 <sup>6.1</sup>	6	9 <sup>2.3</sup>	0	0	0	2	9 <sup>2.6</sup>	32 <sup>29.5</sup>	0	8 <sup>1</sup>
Dactylis glomerata	0	2	0	0	2	1	2	3	4	25 <sup>30.3</sup>	0	14 <sup>14.5</sup>
Galium mollugo aggr.	0	2	1	0	0	0	0	5 <sup>4</sup>	4 1.8	23 <sup>35.7</sup>	0	1
Potentilla reptans	0	0	4	4	4	7 <sup>1.7</sup>	14 <sup>9.4</sup>	14 <sup>9.6</sup>	0	22 <sup>20.2</sup>	0	5
Stellaria graminea	3	5 <sup>1.7</sup>	1	2	2	1	0	0	8 7.1	20 <sup>26.9</sup>	0	2
Lathyrus pratensis	0	9 <sup>6.7</sup>	2	0	0	1	11 <sup>10</sup>	7 <sup>3.5</sup>	0	20 22.6	0	4
Schedonorus pratensis	0	15	6	13	0	1	11	7	0	33 <sup>13.9</sup>	<b>90</b> <sup>60.1</sup>	20 <sup>3</sup>
Juncus articulatus	0	14	10	7	2	0	0	2	0	1	<b>98</b> <sup>72.9</sup>	<b>35</b> <sup>18.1</sup>
Phleum pratense	1	3	1	2	4	0	0	2	0	12 <sup>0.7</sup>	<b>88</b> <sup>73.9</sup>	21 <sup>9.7</sup>
Juncus bufonius	4	0	1	4	7	2	0	2	0	0	<b>81</b> <sup>74.4</sup>	11 <sup>1.6</sup>
Juncus effusus	0	8	2	5	2	1	0	3	0	7	<b>76</b> <sup>63.5</sup>	27 <sup>15.2</sup>
Juncus conglomeratus	0	8 <sup>1.6</sup>	1	2	0	0	0	3	0	6	<b>52</b> <sup>56.7</sup>	3
Lolium multiflorum	0	0	0	0	0	0	0	0	1	1	<b>51</b> <sup>66.5</sup>	2
Eleocharis uniglumis	12 <sup>3.6</sup>	12 <sup>4</sup>	16 <sup>8.5</sup>	0	4	1	2	0	0	0	<b>36</b> <sup>29.8</sup>	18 <sup>10.7</sup>
Juncus compressus	0	0	5 <sup>1.9</sup>	0	2	0	2	0	0	1	29 <sup>40.3</sup>	7 <sup>4.3</sup>
Glyceria declinata	0	0	0	0	0	0	0	0	0	0	29 <sup>50.4</sup>	2
Persicaria maculosa	0	0	0	0	2	0	0	0	0	0	24 <sup>40.9</sup>	4 <sup>3.6</sup>
Trifolium hybridum	0	0	0	0	2	0	0	0	0	1	24 <sup>43.2</sup>	1
Sagina procumbens	7 <sup>2.6</sup>	5	8 <sup>2.9</sup>	0	2	2	0	0	9 <sup>5</sup>	1	21 <sup>20.2</sup>	11 <sup>7.2</sup>
Bellis perennis	0	2	8 <sup>2.4</sup>	16 <sup>13.3</sup>	7 <sup>2</sup>	2	2	0	7 <sup>1.1</sup>	4	0	22 <sup>20.7</sup>
Galium palustre	<b>66</b> <sup>37.9</sup>	<b>70</b> <sup>40.7</sup>	6	4	7	2	20 <sup>2</sup>	24 4.9	0	5	2	9
Peucedanum palustre	<b>35</b> <sup>33.3</sup>	18 <sup>13.2</sup>	2	0	0	0	0	28 <sup>24.2</sup>	0	1	0	0
Ophioglossum vulgatum	10 4	20 15.1	4	0	0	2	7	22 <sup>18.4</sup>	4	14 <sup>8.5</sup>	0	0
Deschampsia cespitosa	21 <sup>9.7</sup>	24 <sup>13.3</sup>	3	20 <sup>8.8</sup>	7	1	2	5	4	30 <sup>18.5</sup>	1	10

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Atriplex prostrata	1	0	4	7	<b>35</b> <sup>19.6</sup>	<b>61</b> <sup>43.6</sup>	14 <sup>0.7</sup>	10	8	6	0	8
Tripolium pannonicum subsp. tripoliun	n 0	0	5	4	20 16.7	30 <sup>28.6</sup>	14 <sup>8.8</sup>	2	1	0	0	3
Sonchus arvensis	10 <sup>0.5</sup>	5	8	0	9	18 <sup>8.4</sup>	25 <sup>15.3</sup>	<b>36</b> <sup>26.7</sup>	1	6	0	0
Centaurea jacea	0	6	7	20 7.4	0	0	11	<b>59</b> <sup>43.9</sup>	4	33 <sup>20.2</sup>	0	1
Trifolium pratense	7	29 <sup>7.3</sup>	25 <sup>4.4</sup>	21 <sup>1.7</sup>	13	1	9	26 <sup>5.1</sup>	7	<b>46</b> <sup>20.4</sup>	34 <sup>11.4</sup>	13
Poa trivialis	0	6	4	25 <sup>4.7</sup>	5	2	20 <sup>1.2</sup>	2	5	12	<b>88</b> <sup>52.9</sup>	<b>57</b> <sup>29</sup>
Alopecurus geniculatus	3	3	6	13	18 <sup>1.7</sup>	1	0	0	1	2	<b>86</b> <sup>57.2</sup>	<b>61</b> <sup>36.7</sup>
Ranunculus repens	6	11	4	5	5	2	20 4.6	0	1	13	<b>60</b> <sup>37.9</sup>	<b>53</b> <sup>31.7</sup>
Polygonum aviculare aggr.	1	0	1	2	11 <sup>5</sup>	7	5	0	8 <sup>1.3</sup>	4	23 <sup>19.4</sup>	20 15.4
Carex nigra	<b>93</b> <sup>52.2</sup>	<b>73</b> <sup>37.6</sup>	18	2	0	0	5	7	0	19	33 <sup>8.4</sup>	10
Agrostis stolonifera	<b>91</b> <sup>13.8</sup>	<b>79</b> <sup>5.7</sup>	82 <sup>8</sup>	<b>93</b> <sup>14.9</sup>	<b>95</b> <sup>16</sup>	54	57	50	34	69	60	<b>79</b> <sup>5.9</sup>
Agrostis capillaris	<b>43</b> <sup>24.7</sup>	6	5	5	2	3	2	2	<b>50</b> <sup>31.1</sup>	<b>36</b> <sup>18.6</sup>	1	15 <sup>1</sup>
Triglochin maritima	10	30 <sup>13.7</sup>	<b>35</b> <sup>17.5</sup>	<b>41</b> <sup>23</sup>	11	3	18 <sup>3.3</sup>	16 <sup>1</sup>	1	1	1	5
Glaux maritima	9	27 <sup>10.7</sup>	<b>38</b> <sup>20</sup>	21 <sup>5.7</sup>	27 <sup>10.7</sup>	20 4.3	16 <sup>1</sup>	10	3	0	1	4
Plantago maritima	24 <sup>1.6</sup>	27 <sup>4.3</sup>	<b>61</b> <sup>29.1</sup>	<b>46</b> <sup>18.4</sup>	11	21 <sup>0.1</sup>	2	16	33 <sup>8.4</sup>	13	0	2
Lotus tenuis	0	3	30 16.1	18 <sup>5.1</sup>	24 <sup>10.3</sup>	4	0	7	7	16 <sup>3.6</sup>	34 <sup>20</sup>	6
Holcus lanatus	0	17	16	<b>50</b> <sup>19.3</sup>	2	7	14	17	16	<b>74</b> <sup>36.5</sup>	12	<b>53</b> <sup>21.2</sup>
Plantago major	7	11	29 <sup>1</sup>	<b>39</b> <sup>8.3</sup>	29 <sup>1.4</sup>	24	16	9	3	15	<b>92</b> <sup>43.9</sup>	<b>53</b> <sup>17.3</sup>
Schedonorus arundinaceus	<b>37</b> <sup>0.9</sup>	8	18	<b>39</b> <sup>2.5</sup>	35	<b>47</b> <sup>7.4</sup>	<b>95</b> <sup>37.9</sup>	<b>78</b> <sup>26.7</sup>	13	40 <sup>3</sup>	0	14
Cirsium arvense	3	0	6	21 <sup>3</sup>	15	<b>49</b> <sup>24.6</sup>	<b>36</b> <sup>14.8</sup>	24 <sup>5.2</sup>	8	28 <sup>8.3</sup>	2	19 <sup>1.2</sup>
Vicia cracca	15	20	12	7	5	8	<b>41</b> <sup>14.7</sup>	<b>67</b> <sup>34.1</sup>	16	<b>53</b> <sup>23.3</sup>	4	6
Lolium perenne	0	0	9	20 <sup>0.9</sup>	11	3	0	0	34 <sup>12.2</sup>	17	<b>75</b> <sup>44.1</sup>	<b>53</b> <sup>26.5</sup>
Cerastium holosteoides	13	11	15	29 <sup>3.9</sup>	4	17	11	9	<b>67</b> <sup>31.5</sup>	<b>41</b> <sup>13.2</sup>	16	<b>44</b> <sup>15.2</sup>
Ranunculus acris	<b>53</b> <sup>19.4</sup>	<b>41</b> <sup>11</sup>	14	<b>45</b> <sup>13.6</sup>	5	3	20	22	4	<b>59</b> <sup>23.8</sup>	3	30 <sup>3.7</sup>
Phragmites australis	<b>35</b> <sup>3.3</sup>	23	32 <sup>0.9</sup>	29	<b>44</b> <sup>8.7</sup>	29	<b>57</b> <sup>17.4</sup>	<b>69</b> <sup>25.3</sup>	5	27	1	14
Trifolium fragiferum	0	2	<b>47</b> <sup>19.8</sup>	18	31 <sup>8</sup>	2	2	3	12	7	<b>92</b> <sup>53.7</sup>	27 <sup>5.4</sup>
Juncus gerardi	<b>60</b> <sup>18.2</sup>	<b>50</b> <sup>11.6</sup>	<b>74</b> <sup>27.3</sup>	<b>66</b> <sup>22</sup>	<b>49</b> <sup>11</sup>	13	11	17	12	13	1	18
Scorzoneroides autumnalis	<b>60</b> <sup>14.3</sup>	<b>55</b> <sup>10.7</sup>	<b>66</b> <sup>18.1</sup>	<b>64</b> <sup>16.8</sup>	36	6	32	17	<b>43</b> <sup>3.8</sup>	23	10	35
Poa pratensis	10	17	39	<b>66</b> <sup>14.6</sup>	<b>45</b> <sup>2</sup>	28	32	12	<b>68</b> <sup>16</sup>	<b>51</b> <sup>5.4</sup>	<b>75</b> <sup>20.2</sup>	<b>63</b> <sup>12.5</sup>
Achillea millefolium	3	11	16	<b>46</b> <sup>7.8</sup>	13	<b>39</b> <sup>3</sup>	<b>45</b> <sup>7.2</sup>	<b>72</b> <sup>24.3</sup>	<b>62</b> <sup>17.6</sup>	<b>76</b> <sup>26.8</sup>	4	23
Rumex crispus	3	0	3	18	<b>36</b> <sup>7.1</sup>	<b>41</b> <sup>10.5</sup>	<b>64</b> <sup>25.8</sup>	7	16	33 <sup>4.5</sup>	<b>51</b> <sup>17.3</sup>	<b>40</b> <sup>9.9</sup>
Trifolium repens	35	<b>56</b> <sup>2.8</sup>	<b>71</b> <sup>11.9</sup>	<b>68</b> 9.9	47	12	5	10	<b>72</b> <sup>12.6</sup>	<b>56</b> <sup>2.5</sup>	<b>99</b> <sup>28.6</sup>	<b>86</b> <sup>20.6</sup>
Argentina anserina subsp. anserina	<b>79</b> <sup>2.6</sup>	<b>82</b> <sup>4.2</sup>	<b>81</b> <sup>3.8</sup>	<b>96</b> <sup>14.5</sup>	<b>82</b> <sup>4.2</sup>	<b>77</b> <sup>0.8</sup>	<b>93</b> <sup>12.2</sup>	<b>90</b> <sup>9.8</sup>	28	76	59	67
Elytrigia repens	18	15	43	<b>95</b> <sup>17.3</sup>	<b>87</b> <sup>12.5</sup>	<b>93</b> <sup>16.5</sup>	66	<b>97</b> <sup>18.5</sup>	<b>80</b> <sup>8</sup>	<b>77</b> <sup>5.9</sup>	<b>80</b> <sup>7.8</sup>	64

**Main clusters 1-3** are positively differentiated from each other. M1 is characterised by *Tripolium pannonicum* subsp. *tripolium, Spergularia marina, Puccinellia maritima, Salicornia europaea* and *Puccinellia distans,* M2 by *Juncus gerardi* and M3 by *Elytrigia repens, Trifolium repens, Poa pratensis, Trifolium fragiferum* and *Achillea millefolium. Agrostis stolonifera* and *Juncus gerardi* occur frequently in all main clusters; but the latter has a particularly high constancy and abundance in M2.

The communities of **M1** hold lowest species numbers (mean species number = 7.5). They have been reported to grow on sandy and muddy soil (Dahlbeck 1945; Krisch 1974) with polyhaline to  $\alpha$ -mesohaline conditions. The vegetation is characterised by annual stress tolerators (weighted sum = 62 %); competitor species and CSR-strategists rarely occur. M1 was divided into two groups (G1 and G2). G1 belongs to the alliances *Festucion maritimae* (= *Puccinellion maritimae*) and *Armerion maritimae*. G2 reflects the alliances *Puccinellio maritimae-Spergularion marinae* and *Puccinellion phryganodis* respectively. Communities of G1 and G2 occur partly in transition to the *Scirpion maritimi*. The vegetation types resemble H1330, including transitions to H1210, while one sub-group belongs to H1630.

Communities of **M2** grow on  $\alpha$ - to  $\beta$ -mesohaline and moist soil. Hemicryptophytes are highly abundant (weighted sum = 98 %). A certain admixture of geophytes (weighted sum = 30 %) occurs. Stress tolerators cover 39 %, strong competitors only 6 %; CSR-strategists account for 20 % (weighted sums). M2 was subdivided into five groups (G1-G5), comprising communities of the *Armerion maritimae*, the *Caricion glareosae*, the *Caricion davallianae*, the *Molinion caeruleae* and the *Loto tenuis-Trifolion fragiferi* partly in transition to the *Saginion maritimae* or the *Scirpion maritimi*. The vegetation types belong to H1330 or H1630 partly in transition to H1310 (restricted to the habitat subtype of the *Saginion maritimae*), H1210, H2190, H6410 and H6450, respectively.

**M3** comprises rather species-rich (mean species number = 16) communities, predominantly on mesic to moist soil with oligohaline or almost non-haline site conditions. The vegetation types of M3 hold a high amount of CSR-strategists (weighted sum = 34 %) and strong-competitive hemicryptophytes (weighted sum = 77 %), while stress tolerators only account for 13 % (weighted sum). M3 was divided into six groups (G1-G6) which represent communities (including transitions) of the alliances *Armerion maritimae*, *Atriplicion littoralis*, *Calthion palustris*, *Filipendulion ulmariae*, *Loto tenuis-Trifolion fragiferi*, *Molinion caeruleae*, *Potentillion anserinae*, *Saginion maritimae* and *Sedo-Cerastion arvensis* and the order *Arrhenatheretalia elatioris*. Transitions to the *Scirpion maritimi* occur. The vegetation types mainly belong to H1330 or H1630, and in minor parts to H1210, H1310 (restricted to the habitat subtype of the *Saginion maritimae*), H2190, H6410, H6430, and H6450, respectively. A slight transition to H91E0 occurs.

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#### Main cluster 1 (Groups 1 and 2)

**M1G1**, chiefly *Festucion maritimae* (= *Puccinellion maritimae*) saltmarsh-grass swards, comprises five sub-groups. S1 belongs to the *Plantagini-Limonietum* while S2, S3 and S5 represent the *Puccinellietum maritimae* and S4 a basal community of the *Festucion maritimae* (Table 2-4). S4 and S5 include species of the *Scirpion maritimi*. They grow on fluctuating, mainly  $\alpha$ -mesohaline (S3-S5) and polyhaline (S1 and S2), moist or wet, nutrient-rich (S1-S3) or moderately rich (S4 and S5) soil in the eulittoral and in shallow depressions and disturbed sites with open swards (S3) in the lower and middle supralittoral (S3 and S5). S2 holds many geophytes (weighted sum = 28 %) and stress tolerators (weighted sum = 107 %), the latter occurs with only low abundance in S4 (weighted sum = 19 %). S1, S2, S3 and S5 occur chiefly in the BKØ but S1 and S3 are moreover scattered in the eastern BP (Estonia); S4 occurs in the entire area except the south-eastern BP (Fig. 2-5).

**M1G1S1** is dominated either by *Limonium vulgare* or by *Juncus gerardi. Plantago coronopus, Sagina maritima* and *Bupleurum tenuissimum* occur sparsely. **M1G1S2** is dominated by *Puccinellia maritima*. The annuals *Suaeda maritima* and *Spergularia marina* are common but with low abundance. **M1G1S3** is also dominated by *Puccinellia maritima* and differentiated by *Glaux maritima* and *Festuca rubra*. It is the most species-rich vegetation type of M1G1 (mean species number = 9.6). **M1G1S4** forms species-poor vegetation (mean species number = 4.6) with a low cover of graminoids and dominant *Triglochin maritima*. *Puccinellia maritima* is restricted to relevés located in Sweden. **M1G1S5** is dominated by *Puccinellia maritima* and lacks positive differential species.

**M1G2** consists of three sub-groups which belong to the *Puccinellietum distantis* (S6 and S8) or the *Puccinellietum phryganodis* (S7) respectively. S8 includes a transition to the *Scirpion maritimi*. They grow on moist, nutrient-poor to moderately rich (S6 and S7) or rich (S8) soil with  $\alpha/\beta$ - to  $\alpha$ -mesohaline conditions. Dierßen & Dierßen (1996) reported pronounced fluctuation in soil salinity and moisture. S6, S7 and S8 occur in the low and upper supralittoral, S7 primarily on the fringes of shallow epilittoral depressions. S6 and S8 are chiefly distributed in the BKØ; S6 additionally occurs in the Gulf of Bothnia. S7 was found in the Liminka Bay (Fig. 2-5).

**M1G2S6** is dominated by *Puccinellia distans* and/or *Spergularia marina*. *Juncus ranarius*, *Plantago major*, *Polygonum aviculare* aggr. and *Ochlopoa annua* are known to be characteristic for trampled (compacted) soil. *Alopecurus geniculatus* has been reported to indicate temporarily water saturated soil (Berg et al. 2004). **M1G2S7** is dominated by *Puccinellia phryganodes* and *Carex glareosa* occurs with low abundance. In **M1G2S8** *Puccinellia distans* mostly occurs with a cover < 25 %. Associates Atriplex littoralis, Oxybasis glauca, Elytrigia repens, described as characteristic taxa of drift-line vegetation, *Ranunculus sceleratus*, known to indicate seasonally flooded sites, and *Plantago major* and *Polygonum aviculare* aggr., indicators for trampling (Berg et al. 2004), all occur with low abundance.

# Main cluster 2 (Groups 1-5)

**M2G1** comprises two sub-groups which belong to the *Artemisietum maritimae* (Table 2-4). S1 includes a transition to the *Scirpion maritimi*. They develop on  $\alpha/\beta$ -mesohaline (S1) or  $\alpha$ -mesohaline to polyhaline (S2), rather moist than mesic, nutrient-poor to moderately rich (S1)

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or pronouncedly nutrient-rich (S2) soil in shallow depressions in the middle and upper supralittoral, where salt accumulates; S1 has been reported to occur also on drift-line deposits (Gillner 1960; Berg et al. 2004). S1 and S2 are distinguished by an increased cover of strong competitors (S1: weighted sum = 66 %) and stress tolerators (S2: weighted sum = 52 %), respectively. S1 and S2 occur chiefly in the BKØ but S2 is furthermore distributed in the south-eastern BP (Fig. 2-5).

**M2G1S1** is dominated by *Artemisia maritima*, *Festuca rubra* or *Agrostis stolonifera*. The species composition of **M2G1S2** is known to indicate slightly sandy soil (Gillner 1960).

**M2G2** comprises two sub-groups which may be considered as basal communities of the *Armerion maritimae*. They grow on  $\alpha/\beta$ -mesohaline (S4) to  $\alpha$ -mesohaline/polyhaline (S3) and moist soil in the lower and middle supralittoral. Geophytes account for 36-38%; stress tolerators cover 52 % (S4) to 89 % (S3; weighted sums). Both sub-groups occur in the entire study area; S3 is missing in the eastern part of the BP (Fig. 2-5).

While comparatively species-poor (mean species number = 7.6), **M2G2S3** is dominated by *Plantago maritima, Juncus gerardi* prevails in **M2G2S4**.

**M2G3**, mainly *Armerion maritimae* saltmarsh rush and similar swards, encompasses four sub-groups. S5 belongs to the *Junco ancipis-Caricetum extensae* and the *Saginion maritimae*, S6 to the *Juncetum gerardi*, S7 to the *Oenantho-lachenalii-Juncetum maritimi* and S8 is transitional between the *Armerion maritimae* and the *Molinion caeruleae*. Abundant associates *Carex distans* and *Scorzoneroides autumnalis* are abundant associates. The vegetation types were found on  $\beta$ - to  $\alpha/\beta$ -mesohaline, rather moist and nutrient-poor to moderately rich soil in the middle and upper supralittoral (S6-S8), in supralittoral and epilittoral open structured turf (S5) or in the vicinity of trenches and depressions with freshwater influence (S7). While S5 and S7 occur in the BKØ, S6 is distributed in the entire study area. S8 chiefly occurs in the nBS, the West Estonian Archipelago (eastern BP) and the province of Södermanland (Sweden, western BP; Fig. 2-5).

M2G3S5 has been reported to occur on sandy soil (Rodwell et al. 2000; Schaminée et al. 1998). M2G3S6 has no dominant species and is rather negatively differentiated. The species composition indicates silty soil (Berg et al. 2004) and includes a certain proportion of glycophytes. The occurrence of *Lotus tenuis* and *Tripolium pannonicum* subsp. *tripolium* is limited to relevés of southerly provenance. M2G3S7 is either dominated by *Juncus maritimus* or *Festuca rubra*. The community has been reported to grow on silty and compacted soil (Härdtle 1984; Westhoff et al. 1998). The species composition of M2G3S8 indicates local freshwater influence. M2G3S7 and M2G3S8 are accompanied by *Ophioglossum vulgatum* with low frequency.

**M2G4 and M2G5** are distinguished from M2G1-G3 by the frequent occurrence of *Eleocharis uniglumis* and *Triglochin palustris*. **M2G4** comprises two sub-groups of the *Loto tenuis*-
Trifolion fragiferi (S9 and S11: Triglochino-Agrostietum stoloniferae); S11 additionally holds characteristics of the Scirpion maritimi. S10 belongs to the Blysmetum rufi of the Armerion maritimae. They grow on  $\beta$ - to  $\alpha/\beta$ -mesohaline, wet soil with temporarily pronounced groundwater influence. CSR-strategists are abundant (weighted sum = 50-67 %). Within S10, geophytes achieve a cover of 50 % (weighted sum). S9 grows in the eulittoral and in depressions of the lower supralittoral, S10 of the middle and upper supralittoral and S11 of the epilittoral. S9 and S11 are distributed in the entire study area; S10 occurs in the BKØ, the western and southern part of the BP and in the Liminka Bay (nBS; Fig. 2-5).

**M2G4S9** is dominated by *Agrostis stolonifera; Argentina anserina* s. str. is low abundant (cover < 25 %). **M2G4S10** encloses relevés frequently dominated by *Blysmopsis rufa* and accompanied by low frequent *Sagina procumbens, Hydrocotyle vulgaris* and *Eleocharis quinqueflora*. **M2G4S11** includes few relevés with dominance stands of *Eleocharis uniglumis* and is reported to occur on inundated loamy or muddy soil (Rebassoo 1975). Associates *Rumex hydrolapathum, Myosotis scorpioides, Mentha aquatica* and *Sium latifolium* are present with low frequency.

Connected by high frequent *Calamagrostis stricta*, **M2G5** comprises two sub-groups belonging to the *Caricetum mackenziei* and the *Triglochino-Agrostietum stoloniferae*, respectively. They include a transition to the *Caricion davallianae*. They grow on  $\beta$ -mesohaline, moist to wet, nutrient-poor to moderately rich soil in middle and upper supralittoral depressions. Geophytes achieve 44 % abundance (weighted sum) in S12, where stress tolerators rarely occur (weighted sum = 14 %). S12 and S13 occur in the nBS; S12 is restricted to the Gulf of Bothnia (Fig. 2-5).

**M2G5S12** includes a variety of accompanying species, some of which indicating slightly acidic soil. The community consists of species of the *Bolboschoenetalia maritimi* and the *Armerion maritimae*. **M2G5S13** is either dominated by *Calamagrostis stricta* or *Agrostis stolonifera*. The community is known to occur on sandy soil (Siira 1970). Both sub-groups incorporate species related to tall-herb-*Salix phylicifolia* communities of shallow peaty dune valleys, including *Salix repens* (Willers 1988, nBS; Dierßen & Dierßen 1996).

### Main cluster 3 (Groups 1-6)

**M3G1**, subsaline wet meadows, encompasses two sub-groups with abundant *Galium palustre* and *Carex nigra*. Both communities belong to the *Calthion palustris* and include species of the *Triglochino-Agrostietum stoloniferae* (Table 2-4). S1 includes a transition to the *Filipendulion ulmariae* while S2 holds some floristic elements of the *Molinion caeruleae*. They grow on fresh to oligohaline, predominantly moist or mesic, nutrient-poor to moderately rich and moderately acidic soil in dune slacks (S2), depressions along dikes and dry polders, limited landward by the highest drift-line (S1). Occasionally stagnant water is known to occur (S1;

Adam 1981). S1 is distributed in the nBS, with single occurrences southwards (BP,  $BK\emptyset$ ). S2 occurs in the entire study area except the Gulf of Bothnia (nBS; Fig. 2-5).

**M3G1S1** comprises a broad assemblage of differential species including a high abundance of tall-herb species. The vegetation type is dominated by *Deschampsia cespitosa*, *Agrostis stolonifera*, *Festuca rubra* and/or *Carex nigra* respectively. **M3G1S2** holds various low-frequent taxa. M3G1S1 and M3G1S2 hold a certain share of species of the *Juncetum gerardi* and the *Molinietalia caeruleae*.

**M3G2**, temporarily wet or flooded subsaline pastures, encompasses two sub-groups which correspond to the *Trifolio fragiferi-Agrostietum stoloniferae* and the *Hordeetum secalini*, respectively. They grow on oligo- (S4) to  $\beta$ -mesohaline (S3), mesic to moist and rarely flooded soil (S4) in shallow depressions and dune slacks of the upper supralittoral. S3 is limited landward by the uppermost drift-line and occurs in the entire study area. S4 occurs in the BKØ and sparsely in the southern BP (Fig. 2-5).

M3G2S3 holds no dominant species. It has been reported to occur on slightly sandy soil (Leuschner & Ellenberg 2010) and is accompanied by low-frequent *Plantago coronopus*, *Triglochin palustris* and *Centaurium littorale*. M3G2S4 is frequently dominated by *Hordeum secalinum*, associated are various species of the *Cynosurion cristati* and *Arrhenatheretalia*.

**M3G3**, subhalophytic nitrophilous vegetation of wash margins, consists of two sub-groups both belonging to the *Atriplicetum littoralis;* S5 includes species of the *Loto tenuis-Trifolion fragiferi* and the *Scirpion maritimi*. They grow on predominantly oligohaline, mesic to moist and moderately nutrient-rich to rich soil in the lower (S5), middle and upper supralittoral. They include frequently *Atriplex prostrata* and *Tripolium pannonicum* subsp. *tripolium* and are known to occur on drift-line deposits, where nutrient availability fluctuates (Krisch 1990). Geophytes achieve 92 % and strong competitors 78 % cover in S6 (weighted sums). They occur in the BKØ, but S5 moreover scattered in the southern BP and the nBS (Fig. 2-5). Rebassoo (1975) reported the sparse occurrence of a similar vegetation type in Estonia.

**M3G3S5** is characterised by several graminoid species; *Schedonorus arundinaceus* is party dominating. *Polygonum aviculare* aggr., *Puccinellia distans* and *Juncus ranarius* occur with low frequency. **M3G3S6** is comparatively species-poor (mean species number = 11.4) compared to other communities of M3.

**M3G4** comprises two sub-groups belonging to the *Potentillo-Festucetum arundinaceae*. They grow on fresh to oligohaline, rather moist than mesic and moderately nutrient-rich (to rich) soil in the lower and upper supralittoral below or next to (shoreline) reeds or along banks of trenches (S7). Both sub-groups hold a high cover of strong competitors (S7: 70 %, S8: 84 %; weighted

sums). Geophytes achieve 30 % cover in S8 (weighted sum). S7 and S8 are distributed in the BK $\emptyset$  and in the southern (S7) and eastern BP; S8 additionally occurs in the Gulf of Finland (Fig. 2-5).

**M3G4S7** is dominated by *Schedonorus arundinaceus* while *Galeopsis bifida*, *Sonchus palustris*, *Cirsium vulgare*, *Calystegia sepium* and *Anthriscus sylvestris* are scattered. S7 includes species of the *Soncho-Archangelicetum littoralis* (Krisch 1990). **M3G4S8** is dominated equally by *Festuca rubra*, *Elytrigia repens* and *Schedonorus arundinaceus*. *Oenanthe lachenalii* predominantly occurs in the BKØ, further differential species increase in frequency in the eastern BP.

**M3G5** includes two sub-groups with *Agrostis capillaris* and *Cerastium holosteoides*. They belong to the *Arrhenatheretalia elatioris*; S9 additionally includes species of the *Saginetalia maritimae* and the *Loto tenuis-Trifolion fragiferi*. They grow on oligohaline to freshwater influenced (S10), mesic (S10) to wet (S9), moderately nutrient-rich and moderately acidic soil in the transition from the supralittoral to the epilittoral (e.g. along dikes, S10). Both sub-groups hold a high cover of strong competitors (S9: 59 %, S10: 67 %; weighted sums). S9 and S10 occur in the BKØ and the southern BP; S10 additionally at the western and eastern coast of the BP and in the Gulf of Finland (Fig. 2-5).

M3G5S9 is formed predominantly by *Agrostis capillaris* and *Festuca rubra*. It includes occasionally species of sand-dune vegetation, *Cynosurion cristati* and *Saginion maritimae*. M3G5S10 is species-rich and formed by *Holcus lanatus*, *Agrostis stolonifera*, *Elytrigia repens*, *Festuca rubra* and further accompanying glycophytes. Both M3G5S9 and S10 include some species of the *Armerion maritimae*.

**M3G6** is constituted of two sub-groups belonging to the *Ranunculo repentis-Alopecuretum geniculati;* S11 additionally includes species of the *Armerion maritimae*. They grow on fresh to oligohaline, wet to moist and moderately acidic soil in depressions, banks of waterbodies and ditches and along dikes in the upper supralittoral and epilittoral. CSR-strategists achieve a cover of 48 % (S11) and 60 % (S12; weighted sums) respectively. S11 and S12 occur in the BKØ; S12 additionally in the southern BP (Fig. 2-5).

M3G6S11 is formed by various graminoids and tall herbs. M3G6S12 is similar to S11 in species composition, but lacks the majority of its differential species. *Bellis perennis* is low-abundant.

**Table 2-4 Synopsis of syntaxa** mentioned in the text, graded at class, order, alliance, association, and subordinate rank (subassociation, type), and syntaxonomic allocation of classified sub-groups (numbers as in the running text). Asterisks indicate transitional clusters or communities assigned to more than one syntaxonomic group. Colours indicate their allocation to the main groups (blue = M1; green = M2; yellow-red = M3) and groups (following floristic similarities and syntaxonomical allocation) of each part of the dataset: light = M1G1, dark = M1G2; light = M2G1, bright = M2G2, dark = M2G3, cyan = M2G4, moss-green = M2G5; orange = M3G1, dark yellow = M3G2, bright red = M3G3, light yellow = M3G4, dark red = M3G5, pink = M3G6. Colours go along with those used in Fig. 2-2, 2-3 and 2-5.

<i>Juncetea maritimi</i> BrBl. in BrBl. et al. 1952	
Puccinellio maritimae-Salicornietalia BrBl. et De Leeuw 1936	
Festucion maritimae Christiansen 1927	
Triglochin maritima-Bolboschoenus maritimus type —————————	M1G1S4*
Plantagini-Limonietum Westhoff et Segal ex Westhoff et Den Held 1969	
Armeria maritima-Parapholis strigosa type————————————	M1G1S1
Puccinellietum maritimae (Warming 1890) Christiansen 1927	
Agrostis stolonifera type——————————————————	M1G1S5*
Glaux maritima-Festuca rubra type ———————————————	M1G1S3*
Suaeda maritima type———————————————————	M1G1S2
Puccinellio maritimae-Spergularion salinae Beeftink 1965	
Puccinellietum distantis Feekes (1934) 1943	
Juncus ranarius-Plantago major type	M1G2S6
Spergularia marina-Atriplex prostrata type————————————	M1G2S8*
Armerion maritimae BrBl. et De Leeuw 1936	
Armeria maritima type ————————————————————	M3G5S9*
Inula britannica type —————————————————————	M3G2S4*
Juncus gerardi type———————————————————	M2G2S4
Molinia caerulae-Carex panicea type——————————————	M2G3S8*
Plantago maritima type ————————————————————	M2G2S3
Artemisietum maritimae BrBl. et De Leeuw 1936	
Elytrigia repens type —————————————————————	M2G1S1*
Limonium vulgare-Armeria maritima type —————————————	M2G1S2
Blysmetum rufi Gillner 1960 ——————————————————	M2G4S10
Juncetum gerardi (Warming 06) Nordhagen 1923	
Plantago maritima-Festuca rubra type——————————————	M1G1S3*
Scorzoneroides autumnalis-Lotus tenuis type———————————	M2G3S6*
Junco ancipis-Caricetum extensae BrBl. & de Leeuw 1936	
Sagina maritima-Carex extensa type —————————————	M2G3S5*
Oenantho lachenalii-Juncetum maritimi Tx. 1937 ————————	M2G3S7
Puccinellietalia phryganodis Hadač 1946	
Caricion glareosae Nordhagen 1954	
Caricetum mackenziei Nordhagen 1954	
Calamagrostis stricta type —————————————————	M2G5S12*
Puccinellion phryganodis Hadač 1946	
Puccinellietum phryganodis Hadač 1946 ———————————	M1G2S7
Molinio-Arrhenatheretea Tx. 1937	
Arrhenatheretalia elatioris Tx. 1931	
Holcus lanatus-Achillea millefolium type ————————————	M3G5S10
Filipendulo ulmariae-Lotetalia uliginosi Passarge 1975	
Filipendulion ulmariae Segal ex Westhoff et Den Held 1969	
Filipendula ulmaria type ————————————————————	M3G1S1*
Molinietalia caeruleae Koch 1926	
Molinion caeruleae Koch 1926	

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continued from previous page	
Carex panicea-Galium palustre type ——————————————	M3G1S2*
Molinia caerulae-Carex panicea type ——————————————	M2G3S8*
Calthion palustris Tx. 1937	
, Carex panicea-Galium palustre type—————————————	M3G1S2*
Filipendula ulmaria type—————————————————	M3G1S1*
Potentillo-Polygonetalia avicularis Tx. 1947	
Loto tenuis-Trifolion fragiferi Westhoff et Den Held ex de Foucault 2009	
Aarostis stolonifera-Speraularia marina type ————————	M3G3S5*
Schedonorus pratensis-Trifolium fragiferum type ———————	M3G6S11*
Scorzoneroides autumnalis-Lotus tenuis type ———————————	M2G3S6*
Hordeetum secalini Krisch 1974 (as Hordeetum nodosi)	
Inula britannica type————————————————	M3G2S4*
Trifolio fragiferi-Agrostietum stoloniferae Sýkora 1982 nom. inv.	
Carex distans-Trifolium repens type ———————————————————	M3G2S3
Trialochino-Aarostietum stoloniferae Konczak 1968	
Aarostis stolonifera type———————————————————	M2G4S9
Bolhoschoenus maritimus type ———————————————————	M2G4S11*
Carex nanicea-Galium nalustre type——————————————	M3G1S2*
Filipendula ulmaria type ————————————————	M3G1S1*
Parnassia nalustris-Calamaarostis stricta type———————————————	M2G5S13*
Potentillion anseringe Tx 1947	11203313
Potentillo-Festucetum grundingcege (Tx 1937) Nordhagen 1940	
Festuca rubra-Elutriaia repens type ——————————————	M3G4S8
Schedonorus arundinaceus-Rumex crispus type	M3G450
Ranunculo renentis-Alonecuretum geniculati Ty 1937 nom conserv propos	10130437
Holeus lanatus-Bellis perennis type	M3G6512
Schedonorus pratensis Trifolium fragiferum type	M3G6S11*
Cakiletea maritimae Ty et Preising in Ty ey Br -Bl et Ty 1952	WISCOSTI
Atriplicetalia littoralis Sissingh in Westhoff et al. 1946	
Atriplican littoralis Nordhagen 1940	
Atriplicatum littaralis Christianson ov Tv. 1027	
Agroctis stolonifera. Speraularia marina type	M2C2S5*
Artemicia maritima. Atripley prostrata type	Macase
Koelerio Corvenhoretea canescentis Klika in Klika et Novák 1941	14120220
Corupenhoratalia canascentis Klika 1924	
Sada Caraction aryansis Sissingh at Tidoman 1960	
Armoria maritima tuno	M2CES0*
Annehu munumu type	10120229
Priruginico-Wugnocuriceteu Kika in Kika et Novak 1941 Rolboschoonatalia maritimi Hoiný in Holub et al. 1067	
Coimion maritimi Dahl at Llada 1041	
Agreetic stelenifere tune	M1C1SE*
Agrostis stolonijelu type	Macase*
Ayrostis stolonijeru-sperguluru murmu type————————————————————————————————————	M2C4S11*
Elutrigia ranges type	M2G4311 M2G1S1*
Eivingia reperis type —	M1C2S9*
Trialachin maritima Balhaschaanus maritimus tupa	M1C1S4*
Saginatag maritimga Westhoff at al. 1062	1110134
Saginetalia maritimae Westhoff et al. 1962	
Saginetana maritimaa Waathoff at al. 1962	
Saginion mantimae westholl et al. 1962	MOCOSE*
Armoria maritima tuno	
Annena manufilma type — — — — — — — — — — — — — — — — — — —	141202234
Caricotalia davalliando Pr. Pl. 1050 nom. concert. propos	
Carician davalliande Klike 1024	
Calamaaroctic stricta type	MOCEC10*
Darnaccia naluetric Calamagractic stricta tuno	
Parnassia palastris-Calarnagrostis stricta type ———————————————	IVI2G2213*

### Discussion

### **Ecology and zonation**

The observed sub-groups satisfactorily encompass the variation of Baltic coastal grasslands at a supra-national scope. They may not, however, reflect the entire floristic and community variation on local level.

The variation in BS plant communities is clearly reflected by ecological variables, with salinity and moisture as the main driving forces. The influence of these variables generally decreases in littoral grasslands with increasing elevation above sea level (Ward et al. 2016). Communities of M1, forming mainly *Juncetea maritimi* swards, show highest salinity, M2 intermediate and M3, mostly *Potentillo-Polygonetalia* wet pastures and meadows, the lowest. Soil moisture varies among sub-groups of each main cluster with driest communities occurring in M3.

Increased evaporation in shallow depressions with short swards locally may lead to euhaline to hypersaline conditions in the otherwise brackish middle and upper supralittoral and epilittoral (Siira 1985; Westhoff et al. 1998). Where sea-water salinity is low (< 2 ‰, Bothnian Bay; Tyler 1969a), this phenomenon leads to a reversed soil salinity gradient (Siira 1970).

The polyhaline to  $\alpha$ -mesohaline *Plantagini-Limonietum* (M1S1; Table 2-4) grows in shallow, naturally disturbed coastal landscapes at the mean low water line just above the open, annual dominated low tidal marsh (*Thero-Salicornietea*). It forms a dense turf on bare, regularly flooded clay or sand-covered silty soil with occasional oxygen deficiency (Gillner 1960; Eber & Brauser 1995; Rodwell et al. 2000; Metzing 2005). Scattered annuals of the low tidal marsh (e.g. *Salicornia europaea, Spergularia marina*) remain casual and establish in each year by occasional seed transport at times of high flood. High salinity prevents the development of less halophytic vegetation (Eber & Brauser 1995). In marked contrast, in open supralittoral depressions with trampling-induced soil compaction,  $\alpha/\beta$ - to  $\alpha$ -mesohaline conditions enable weakly halotolerant species of the *Loto tenuis-Trifolion fragiferi* to spread into communities of the *Puccinellietum maritimae* and the *Puccinellietum distantis* (Härdtle 1984; Westhoff et al. 1998; Rodwell et al. 2000).

Floristically related to the *Puccinellietum distantis*, which grows usually on disturbed sites, the *Puccinellietum phryganodis* (M1G2S7) occurs in moist and saline supralittoral and epilittoral sites. It is confined to the Liminka Bay of the nBS and constitutes the southernmost extent of the otherwise Arctic distributed *Puccinellietum phryganodis*. The latter grows at the mean low water line equivalent to the *Salicornietum herbaceae* and *Puccinellia maritima* dominated swards further south (Siira & Haapala 1969; Thannheiser 1975).

More landward than the *Puccinellietum maritimae*, the *Armerion maritimae* and the *Loto tenuis-Trifolion fragiferi* form patches of varying species composition on sites with increased humus content (Dierßen & Dierßen 1996). They are most widespread in the middle and upper

supralittoral (Rebassoo 1975; Jeschke 1987). The small patch-size of the *Armerion maritimae* and the less saline, freshwater influenced *Loto tenuis-Trifolion fragiferi* relate to the prevalent narrow tidal range (Leuschner & Ellenberg 2017) and to varying abiotic site conditions on micro-topographic scale (Ward et al. 2016).

Middle and upper supralittoral communities in sites with relatively high salinity (*Artemisietum maritimae*, M2G1; Dijkema 1990), low salinity (*Loto tenuis-Trifolion fragiferi*), transitional to dry, sandy flats (*Junco ancipis-Caricetum extensae* with species of the *Saginion maritimae*, M2G3S5) and in brackish, wet sites (*Scirpion maritimi*, M2G4S11) occur in close contact with the *Armerion maritimae* (Table 2-2).

A broad range of more or less freshwater-influenced upper supralittoral and epilittoral grasslands, characterised by considerable interspecific competition (Rautiainen et al. 2007), grow in close contact to *Scorzoneroides autumnalis* and *Festuca rubra* rich communities (Dijkema 1990). The *Hordeetum secalini* is associated on drier sites (Jeschke 1987) with only occasional inundation (Berg et al. 2004). Pastures of the *Potentillion anserinae* (M3G4 and G6; Table 2-3; Dijkema 1990), dependent on more or less permanent freshwater influence, hay-meadows and dry variants of mesic pastures (M3G5S10) are inhabited by numerous glycophytes (Sýkora et al. 1996; Zuidhoff et al. 1996; Dierschke 1997, 2012; Berg et al. 2004). *Molinia* meadows are sometimes separated from brackish grasslands by a narrow shallowly peaty zone, where *Carex nigra* may be abundant (M3G1; Krisch 1990).

Along the Bothnian Sea coastal grasslands with species of the *Calthion palustris* and the *Filipendulion ulmariae* commonly constitute a transition to *Alnus glutinosa* woodlands (northern relevés of M3G1S1, Table 2-3; Jutila 2017; Lehtomaa et al. 2018).

### Grazing

Non-intensive grazing by sheep, cattle or occasionally by horses co-determines the occurrence of variation of littoral plant communities (Jeschke 1987; Andresen et al. 1990; Berg et al. 2004), prevents their deterioration (Rŭsina et al. 2017) and favours the occurrence of characteristic poorly-competitive halophytes (Andresen et al. 1990; Jutila 1999; Pätsch et al. 2019); mowing is overall of minor importance (Andresen et al. 1990). Grazing effects are not always easy to disentangle from abiotic factors (Jutila 1999) and, where drift-line deposits occur, from effects of recurring depositions (Krisch 1974).

Although there is no plot-specific information on grazing management for most of our relevés, corresponding literature of local studies (Dahlbeck 1945; Rebassoo 1975; Härdtle 1984; Siira 1985; Jeschke 1987; Willers 1988; Wolfram 1996; Jutila 2001; Berg et al. 2004; Rautiainen et al. 2007) shows a general consensus on the significance of non-intensive grazing and trampling for many of the observed vegetation types. There appears to be no or little influence in the vegetation types chiefly belonging to the *Festucion maritimae* (M1G1S1-S5), the

*Puccinellion phryganodis* (M1G2S7), the *Armerion maritimae* (M2G1 and G2, M2G3S7 and S8) especially if transitional to the *Scirpion maritimi*), some meadows of the *Loto tenuis-Trifolion fragiferi* (M2G4S11 and G5S13), the *Molinio-Arrhenatheretea* meadows (M3G1S1), and a few of the *Potentillo-Polygonetalia avicularis* grasslands (M3G2, G3 and G4); moderate impact in the vegetation types which mainly belong to the *Armerion maritimae* (M2G2, M2G3S5 and S6, M3G5S9), the *Triglochino-Agrostietum stoloniferae* (M2G4S9), the *Blysmetum rufi* (M2G4S10), the *Caricetum mackenziei* (M2G5S12), *Holcus lanatus-Arrhenatheretalia* meadows (M3G5S10) and some *Potentillo-Polygonetalia avicularis* (M3G6); strong impact in the vegetation types primarily belonging to the *Potentillo-Polygonetalia avicularis* (M3G1S2 and G2S3). Trampling effects are visible in particular in the *Puccinellietum distantis* (M1G2S6 and S8) and the *Sagina maritima-Carex extensa* type of the *Junco ancipis-Caricetum extensae* (M2G3S5).

Low grazing intensity frequently leads to an increase in abundance of *Bolboschoenus maritimus* in wet sites, *Elytrigia repens* and/or *Schedonorus arundinaceus* in drier sites (cf. M2G4S11 of the *Triglochino-Agrostietum stoloniferae*, M3G6S11 of the *Ranunculo repentis-Alopecuretum geniculati*; Jeschke 1987; Krisch 1990; Ward et al. 2016; Rŭsina et al. 2017) and tall herbs (e.g. *Filipendula ulmaria*) and early successional stages of *Alnus glutinosa* woodlands especially in northern epilittoral grasslands (northern relevés of the *Filipendula ulmaria* type of the *Triglochino-Agrostietum stoloniferae* [M3G1S1]; Jutila 2001). The mentioned species strongly increase at the cost of low-competitive halophytic vegetation on abandoned grasslands (Bakker 1987; Burnside et al. 2007, Pätsch et al. 2019). With increasing height above sea-level, the occurrence of characteristic coastal grassland species increasingly depends on grazing (Bakker 1987), which at times leads to deviating statements on the grazing dependence of analogous communities situated at different elevations above sea-level (e.g. the *Plantago maritima* type of the *Armerion maritimae* [M2G2S3]; Dahlbeck 1945; Rebassoo 1975; Willers 1988).

Trampling induced openings with locally exposed sandy soil in supralittoral and epilittoral turf facilitate the growth of sand-dune species (*Junco ancipis-Caricetum extensae* in transition to the *Saginion maritimae* [M2G3S5]; Härdtle 1984; Rodwell et al. 2000; Metzing 2005). Where heavy trampling leads to compacted soil, the *Puccinellietum distantis* typically forms sparse grassland (Härdtle 1984).

### **Geographic distribution**

Coastal grasslands are more or less evenly distributed along the southern BS coast, where preglacial and glacial (Pleistocene) sandy and loamy deposits occur (BKØ, southern BP) in more or less sheltered sites. However, fjord-coasts, coastal moraine gravel deposits (Schiewer 2008), cliff and sand dune coasts (Bosiacka et al. 2011, south-eastern BP) limit the occurrence of coastal grasslands in the eastern BP and the nBS (Fig. 2-1). The observed geographical patterns of plant

communities (Fig. 2-5) are further related to differences in sea-water salinity (HELCOM Map and Data Service 2008), tidal range (Tyler 1969a; Leuschner & Ellenberg 2017) and to a lesser extent to climatic conditions.

A clear geographic pattern is visible for the more pronounced halophytic vegetation, restricted to the BKØ, for brackish communities, which are widespread in the entire study area (e.g. communities of the *Triglochino-Agrostietum stoloniferae* M2G4S9 and S10, the *Agrostis stolonifera-Spergularia marina* type of the *Atriplicetum littoralis* [M3G3S5]), and for more or less freshwater-influenced communities distributed in the nBS, respectively.

Geographical limits of communities in the BKØ (including few occurrences in the south-eastern parts of the BP) are frequently related to range boundaries of coastal species (e.g. Limonium vulgare in the Plantagini-Limonietum [M1G1S1] and the Limonium vulgare-Armeria maritima type of the Artemisietum maritimae [M2G1S2], Puccinellia maritima in the Festucion maritimae [M1G1], Atriplex littoralis in the Artemisia maritima-Atriplex prostrata type of the Atriplicetum littoralis [M3G3S6]) and of characteristic taxa of the Puccinellio maritimae-Salicornietalia and the Molinio-Arrhenatheretea (e.g. Cochlearia anglica [M2G1S1], Lotus tenuis and Oenanthe lachenalii [M2G3S7], Hordeum secalinum [M3G2S4], Schedonorus pratensis and Juncus articulatus [M3G6S11]; Tyler 1969a; Metzing 2005; GBIF 2017). Other community range limits are related to the occurrence of nutrient rich deposits on sandy soil (Ranunculo repentis-Alopecuretum geniculati [M3G6S11 and S12]) and of drift-line deposits on grassland (Spergularia marina-Atriplex prostrata type of the Puccinellietum distantis [M1G2S8], vegetation types of the Loto tenuis-Trifolium fragiferi [M3G2S3, M3G3S5 and S6]). In the eastern BP and nBS, where gravel and scree occur close to the water, the establishment of dense swards is limited. There, drift-line species associated with the Cakiletea maritimae rarely occur in grassland vegetation (Rebassoo 1975; Dierßen & Dierßen 1996).

Some of the aforementioned species occur scattered beyond their main distribution range (GBIF 2017) in sedimentation basins in the West Estonian Archipelago (eastern BP), the Liminka Bay (Bothnian Bay) and the Archipelago Sea (nBS; Fig. 2-1; Rebassoo 1975; Siira 1983; Willers 1988). The latter constitutes a barrier for diaspores (Tyler 1969a) between the temperate BP and the southern-boreal Gulf of Bothnia (nBS); a pronounced vegetation turnover generally occurs.

Geographically restricted vegetation types of the nBS and major parts of the Swedish east coast (*Puccinellietum phryganodis* [M1G2S7], *Caricetum mackenziei* [M2G5S12], *Parnassia palustris-Calamagrostis stricta* type of the *Triglochino-Agrostietum stoloniferae* [M2G5S13]) are frequently characterised by boreal-arctic relic taxa (Siira & Haapala 1969; Tyler 1969a; Siira & Merilä 1985; Willers 1988; Jutila 2001; Rautiainen et al. 2007). Species of the

*Scheuchzerio palustris-Caricetea fuscae* (M2G3S12 and S13) are related to paludification and occur on narrow strips of coastal grassland bounded by steep shores (Willers 1988).

### Baltic Sea coastal grasslands in North-west European perspective

Most of the BS grasslands are slightly less saline but similar to those of Atlantic coastal grasslands. However, some grasslands restricted to the nBS are either related to Arctic coastal plant communities (*Puccinellietum phryganodis, Caricetum mackenziei, Parnassia palustris-Calamagrostis stricta* type of the *Triglochino-Agrostietum stoloniferae*) or are unique (e.g. *Molinia caerulea-Carex panicea* type of the *Armerion maritimae* [M2G3S8], *Filipendula ulmaria* type of the *Triglochino-Agrostietum stoloniferae* [M3G1S1]). The latter have not yet been described according to formal syntaxonomic standards and may deserve syntaxonomical recognition.

The more saline BS grasslands in the BKØ resemble north-west European (Atlantic) coastal grasslands, although some widespread Atlantic saltmarsh species hardly reach the BS and are absent in our dataset (e.g. Elytrigia atherica [~0.1 % frequency], Halimione portulacoides, Spartina anglica, Spartina townsendii). North-west European coastal grasslands chiefly correspond to BS variants of the Plantagini-Limonietum, the Puccinellietum maritimae and of the polyhaline or  $\alpha$ -mesohaline types of the Armerion maritimae (e.g. M2G1S2, G3S5 and G4S10, Table 2-2; cf. Westhoff et al. 1998, NL), particularly owing to joint occurrences of Armeria maritima, Halimione pedunculata, Limonium vulgare, Parapholis strigosa, Salicornia europaea and Suaeda maritima. The  $\alpha/\beta$ - to  $\alpha$ -mesohaline Puccinellietum distantis of the BS coast (M1G2S6 and S8) has only limited overall floristic similarity with the corresponding north-west European community, which is more close to the Puccinellietum maritimae (Table 2-1.; cf. Adam 1981, GB; cf. Westhoff et al. 1998, NL; cf. Rodwell et al. 2000, GB). Some brackish British coastal grasslands comparable  $\alpha/\beta$ -mesohaline are to Triglochino-Agrostietum stoloniferae communities of the BS coast (e.g. M2G4S9; M3G1, Table 2-2 and 2-3; Rodwell et al. 2000, GB).

Freshwater influenced vegetation of the BS coast is apparently less separated in species composition from brackish supralittoral grasslands than that of the Atlantic coast. Notwithstanding, the Atlantic coastal grasslands reflect the same pattern found in our dataset: a close floristic link to the *Armerion maritimae* vegetation within the north-west European equivalents of communities of the *Hordeetum secalini* and the *Trifolio fragiferi-Agrostietum stoloniferae* (M3G2S3 and S4), and a hardly noticeable contact to brackish grasslands reflected in the analogous communities of the *Potentillion anserinae* (M3G4S7 and M3G6). The last aforementioned communities occur in upper supralittoral depressions, or largely outside sea water influence in slufter plains (sandy flats behind white dunes), behind dikes or

inland (Table 2-3; Sýkora et al. 1996, NL; Zuidhoff et al. 1996, NL). Similar to vegetation types of the nBS, transitions to fen vegetation have been reported to occur in GB (Adam 1981).

### **Nature Conservation**

### Natura 2000 habitat types

Most Baltic Sea coastal grasslands belong to H1330 (Atlantic salt meadows) and H1630 (Boreal Baltic coastal meadows). H1330 is circumscribed to include more or less saline tidal grasslands in what is defined as the Atlantic and Continental biogeographic zones (EEA 2014). H1630 encompasses brackish littoral grasslands in the Boreal biogeographic zone (pragmatically defined as from the south-eastern edge of Skåne, Sweden, and Lithuania northwards (EEA 2014). The application-oriented biogeographic zones adopted by the EU Habitats Directive correspond in the BS vaguely to zones with negative (-0.2 to -0.1 cm/year) or positive (from 0 to 0.9 cm/year) isostatic movements, respectively (Schiewer 2008; Schwarzer et al. 2008; for distribution maps of H1330 and H1630 see EEA 2014).

The habitat types H1330 and H1630 are ecologically related, and along the BS coast often connected, to other Natura 2000 habitat types, such as annual drift line (H1210; cf. Spergularia marina-Atriplex prostrata type of the Puccinellietum distantis [M1G2S8], Elytrigia repens type of the Artemisietum maritimae [M2G1S1], Artemisia maritima-Atriplex prostrata type of the Atriplicetum litoralis [M3G3S6]; Rusina et al. 2017) and mudflat vegetation (H1310; cf. Sagina maritima-Carex extensa type of the Junco ancipis-Caricetum extensae [M2G3S5], Armeria maritima type of the Armerion maritimae [M3G5S9], BKØ, south-western BP), humid dune slacks (H2190; cf. Carex panicea-Galium palustre type of the Molinion caeruleae [M3G1S2], Caricetum mackenziei [M2G5S12] and Parnassia palustris-Calamagrostis stricta type of the Triglochino-Agrostietum stoloniferae [M2G5S13]), and alluvial Alnus glutinosa forests (H91E0; cf. Filipendula ulmaria type of the Triglochino-*Agrostietum stoloniferae* [M3G1S1]). The diverse meadow vegetation of H6410 (cf. Molinion caeruleae [M2G3S8 and M3G1S2]), hydrophilous tall herb fringe communities (H6430) and alluvial meadows (H6450) grow chiefly in the north (nBS) and scattered elsewhere in a certain distance to the shoreline.

Armerion maritimae and Loto tenuis-Trifolion fragiferi communities are not always unambiguously assigned to H1330 and H1630, due to a certain proportion of species that both habitat types have in common (e.g. Agrostis stolonifera, Argentina anserina, Centaurium littorale, Festuca rubra, Glaux maritima, Juncus gerardi, Plantago maritima, Spergularia marina, Trifolium fragiferum, Triglochin maritima). Only for vegetation types with additional species restricted to the south or north BS, respectively, assignment to H1330 and H1630 is feasible (H1330: e.g. mainly communities of the Festucion maritimae [M1G1S1-S3 and S5]; chiefly the Artemisietum maritimae [M2G1S1 and S2], BKØ; H1630: e.g. Puccinellietum phryganodis

[M1G2S7]; *Caricetum mackenziei* [M2G5S12] and *Parnassia palustris-Calamagrostis stricta* type of the *Triglochino-Agrostietum stoloniferae* [M2G5S13], nBS; Doody 2008; European Commission 2013; Lotman & Lepik 2004, BP; Rŭsina et al. 2017, BP).

Due to much local-scale variation it is unusually difficult to separate "Atlantic" (H1330) and "Boreal" coastal salt meadows (H1630) in the Baltic Sea region. Nevertheless, there are differences in species and community composition as well as in overall geomorphological terms, which should be considered for a refinement of the definitions in the Interpretation Manual of European Union Habitats (European Commission 2013). Geomorphological terms may even lead to a broader geographical concept of H1630, which has been applied for the Red List of Habitats (Janssen et al. 2016).

According to our results, species indicative of H1330 (as against H1630) in the BS region include *Armeria maritima*, *Artemisia maritima*, *Atriplex littoralis*, *Carex extensa*, *Centaurium littorale*, *Centaurium pulchellum*, *Halimione pedunculata*, *Hordeum secalinum*, *Inula britannica*, *Juncus maritimus*, *Limonium vulgare*, *Lotus tenuis*, *Oenanthe lachenalii*, *Parapholis strigosa*, *Plantago coronopus*, *Puccinellia maritima* and *Spergularia media*. Typically associated with H1330 are the habitat types H1210 and H1310. The most saline vegetation in the zonation of salt meadow vegetation types comprised by H1330 is always the one closest to the sea. In contrast, the most saline vegetation in areas with a salt meadow zonation of H1630 may be close to the sea or else in the upper supralittoral or even epilittoral. A species to be added as indicative of H1630 (as against H1330) is *Trigochin palustre* (while *Centaurium littorale* and *C. pulchellum* occur only sporadically and should be excluded). Frequently associated habitat types with H1630 are H2190, H6410, H6430, and further north, H6450 and H91E0.

To do justice to, and to draw attention to, some distinct and rare vegetation types restricted to the nBS (and a few scattered occurrences beyond this area in the BP), we further propose the unique set of boreal and arctic relic species (e.g. *Puccinellia phryganodes, Carex halophila, Carex paleacea, Carex mackenziei, Carex glareosa, Primula nutans, Deschampsia bottnica, Euphrasia bottnica, Hippuris tetraphylla;* European Commission 2013) to be marked out as characteristic for a specific sub-type of H1630. Plant communities corresponding to this sub-type would be the *Puccinellietum phryganodis* [M1G2S7], chiefly the *Caricetum mackenziei* [M2G5S12], the *Parnassia palustris-Calamagrostis stricta* type of the *Triglochino-Agrostietum stoloniferae* [M3G1].

### **Red List species**

Several species of BS coastal grasslands are considered in national Red Lists (Wind & Pihl 2004; Zarzycki & Szeląg 2006; Eesti Teaduste Akadeemia Looduskaitse Komisjon 2008; Gamtos tyrimų centras 2009-2019; Rassi et al. 2010; ArtDatabanken 2015; Latvian Biodiversity CHM 2015). They are threatened for various reasons including the limited occurrences of coastal grasslands in the reference areas; species natural rarity due to distribution limits; and as a result of deterioration of coastal grasslands due to abandonment or land-use intensification (Vartiainen 1980; Dierßen & Dierßen 1996; Wind & Pihl 2004).

Where salt meadows are inherently rare (south-eastern BP), several species are listed in one or more Red Lists of Lithuania, Poland and Latvia (e.g. *Glaux maritima, Juncus gerardi, Parnassia palustris* [M2G5S13, M3G1S1] and *Pedicularis palustris* [M2G5S13] in subtypes of the *Triglochino-Agrostietum stoloniferae, Plantago maritima, Spergularia media* in communities of the *Festucion maritimae* [M1G1] and the *Limonium vulgare-Armeria maritima* type of the *Artemisietum maritimae* [M2G1S2], *Spergularia marina* in the most saline communities of the *Puccinellio maritimae-Salicornietalia* [M1] and the *Atriplicetum littoralis* [M3G3], *Triglochin maritima* in various communities; Zarzycki & Szeląg 2006; Gamtos tyrimų centras 2009-2019; Latvian Biodiversity CHM 2015).

Various coastal grassland species reaching their present-day phytogeographic limits in the BK $\emptyset$ (e.g. Artemisia maritima in the Artemisietum maritimae [M2G1] and the Artemisia maritima-Atriplex prostrata type of the Atriplicetum littoralis [M3G3S6], Bupleurum tenuissimum in the Armeria maritima type of the Armerion maritimae [M3G5S9], Halimione pedunculata and Parapholis strigosa in the Plantagini-Limonietum [M1G1S1], Oenanthe lachenalii in the Oenantho lachenalii-Juncetum maritimi [M2G3S7], the Festuca rubra-Elytrigia repens type of the Potentillo-Festucetum arundinaceae [M3G4S8]) or within the Estonian Archipelago, the Archipelago Sea and/or the Gulf of Finland (Carex distans in different communities of the Puccinellio maritimae-Salicornietalia, the Molinetalia caeruleae and the Potentillo-Polygonetalia avicularis [M2G3 and G4, M3G2S3], Carex extensa in the Sagina maritima-Carex extensa type of the Junco ancipis-Caricetum extensae [M2G3S5], Carex otrubae accompanying several vegetation types chiefly of the Juncetea maritimi and the Molinio-Arrhenatheretea [M2, M3], Centaurium littorale accompanying plant communities of the Junco ancipis-Caricetum extensae [M2G3], the Blysmetum rufi and communities of the Triglochino-Agrostietum stoloniferae [M2G4] and chiefly of the Molinio-Arrhenatheretea [M3], Sagina maritima and Centaurium pulchellum in the Sagina maritima-Carex extensa type of the Junco ancipis-Caricetum extensae [M2G3S5] and the latter also in the Holcus lanatus-Bellis perennis type of the Ranunculo repentis-Alopecuretum geniculate [M3G6S12], Galium verum in the Armeria maritima type of the Armerion maritimae [M3G5S9], Bolboschoenus maritimus type Samolus valerandi in the of the Triglochino-Agrostietum stoloniferae [M2G4S11], Suaeda maritima in the Suaeda maritima type of the Puccinellietum maritimae [M1G1S2], Trifolium fragiferum chiefly in communities of the Juncetea maritimi and the Molinio-Arrhenatheretea [M2G3 and G4, M3G2, M3G3S5, M3G6]).

They are listed in one or more associated national Red Lists (Wind & Pihl 2004; Eesti Teaduste Akadeemia Looduskaitse Komisjon 2008; Rassi et al. 2010; ArtDatabanken 2015; Metzing et al. 2018).

Species of northern distribution (nBS) are frequently assessed as Nearly Threatened or Critically Endangered at their southernmost phytogeographical limits (Estonia, Latvia, Finland; Eesti Teaduste Akadeemia Looduskaitse Komisjon 2008; Latvian Biodiversity CHM 2015; Rassi et al. 2010). *Puccinellia phryganodes* is classified as Critically Endangered also on European level (Bilz et al. 2011).

### Habitat value and future perspectives

While many species of BS coastal grasslands are listed in national Red Lists, the habitat type altogether has been assessed as Endangered on European level (Janssen et al. 2016). It constitutes a valuable habitat for a diverse invertebrate fauna (Andresen et al. 1990; Ford et al. 2013) and provides important breeding, foraging and resting sites for numerous migratory and sedentory birds (van der Graaf et al. 2007; Janssen et al. 2016).

Nature conservation management has to reflect the urgent need of the overall declining BS coastal grasslands (Janssen et al. 2016), aiming to re-establish and preserve its diversity (Helsinki Commission 2013), and to maintain a favourable conservation status of associated Natura 2000 habitat types. To achieve these aims, the preservation or restoration of flooding dynamics, a locally well-adapted and monitored grazing (LUNG 2011) and, if necessary, the reintroduction of non-intensive grazing practices (Dijkema 1990; Janssen et al. 2016) are most important. The reintroduction of traditional land use management on Finnish coastal grasslands, which underwent a major decrease (Helsinki Commission 2013; Janssen et al. 2016), recently resulted in an area increase of such grasslands (Lehtomaa et al. 2018), which is a promising example for nature conservation management in the Baltic Sea region.

# *Elytrigia repens* co-occurs with glycophytes rather than characteristic halophytes in low-growing salt meadows on the southern Baltic Sea coast

### **Technical information**

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The following abbreviations are used: CSMS = characteristic salt meadow species; NMDS = non metric multidimensional scaling

### Supplementary material:

I Appendix S3-1: Species-area relationship.

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### Abstract

Baltic salt meadows of the supralittoral are recognizable by a low vegetation structure of perennial plants, distinct zonation, and the presence of characteristic species of high ecological value. This semi-natural, grazing-dependent vegetation is declining in overall distribution and habitat quality. Abiotic and biotic habitat changes as well as the loss of characteristic species and a simultaneous increase of *Elytrigia repens* are particularly concerning.

We hypothesize that, if *E. repens* increases due to abandonment or other causes, characteristic salt-meadow species will be affected adversely. To investigate the floristic changes and salt meadow species loss over a wide area, we used a dataset of salt meadow plots from along the southern Baltic Sea coast, partitioned by different cover ranges of *E. repens*. Between these groups, we compared the abundance and frequency of characteristic salt meadow species. We additionally tested (Mann-Whitney-U test) relevant structural factors, plot-based indicator values and strategy types.

*E. repens* indicated low incidence of characteristic salt-meadow species. Soil moisture, salinity and light availability were lower where *E. repens* occurred; mean vegetation height was increased. Five species co-occurred with *Elytrigia repens* (*Achillea millefolium, Holcus lanatus, Poa pratensis, Schedonorus arundinaceus, Trifolium repens*), showing simultaneously a low relative abundance in the remaining dataset.

We discuss our findings in terms of frequently observed vegetation changes in the light of salt meadow abandonment. In conclusion, we draw up an easy-to-use method for monitoring salt-meadow medium-term dynamics for applied nature conservation purposes.

### Introduction

On the southern Baltic Sea coast where tidal fluctuation is small, salt meadows are naturally scarce and small-scale. Through utilisation of reed stands and adjacent wet meadows of the supralittoral (supralittoral) zone, salt meadows could be expanded over hundreds of years (Dahlbeck 1945; Schmeisky 1977a, b; Jeschke 1987; Dijkema 1990; Dierßen & Dierßen 1996; Doody 2008). Salt meadows such as the Karrendorf meadows (Karrendorfer Wiesen, Bay of Greifswald, Germany) and the "Beka" nature reserve (Rezerwat przyrody Beka, Puck Bay, Poland) form areas up to (several) hundred hectares. Thus Baltic Sea salt meadows constitute a valuable part of the European historical cultural landscape (Dijkema 1990; Burnside et al. 2007). Each salt meadow forms an intermediate supralittoral vegetation complex between eulittoral (hydrolittoral) communities of reeds and mudflats and epilittoral freshwater meadows and pastures. Along the southern Baltic Sea coast, Juncetea maritimi salt meadows are the main plant communities of the supralittoral (Fukarek 1961, 1969; Schmeisky 1977a, b; Jeschke 1987; Dijkema 1990). In contrast to reed bed and mudflat vegetation, low-growing salt meadows are

mostly grazed (Dahlbeck 1945; Jeschke 1987; Dijkema 1990; Bakker et al. 1993; Scherfose 1993; Dierßen & Dierßen 1996; Timling 2000; Doody 2008; Janssen et al. 2016). In this paper we refer to 'grazing' as low-intensive grazing (< 0.5 cattle/ha, Scherfose 1993), which has been common practice in Baltic Sea salt meadows.

Due to an assumed area loss of 60–90 %, Baltic salt meadows have been assessed Endangered in the EU Baltic Sea littoral states (Janssen et al. 2016). Pollution of marine waters (Janssen et al. 2016), rivers and estuaries (Rozema et al. 2000), urbanization (Janssen et al. 2016) or dike constructions (Jeschke 1987; Wanner et al. 2007) adversely affect salt meadows. On a local level, the abandonment of traditional low-intensive livestock farming has frequently been described as a threat for Baltic salt meadows (Jeschke 1987; Dijkema 1990; Vestergaard 1998; Burnside et al. 2007; Bosiacka et al. 2016; Janssen et al. 2016).

In consequence of salt-meadow abandonment tall competitive species are increasing and shifts in species dominance have repeatedly been described (Bakker 1987; Scherfose 1993; Burnside et al. 2007). While in the lower salt meadows *Phragmites australis* plays a major role (Wanner 2009), in mid- to upper supralittoral vegetation *Elytrigia repens* is commonly involved, a competitive stoloniferous grass increasing in spatial extent and cover especially where grazing is excluded (Schmeisky 1977a; Jeschke 1987; Dijkema 1990; Burnside et al. 2007; Krisch 2007).

Along with the expansion of *E. repens*, a decrease or even loss of certain low-competitive plants was observed in local studies on abandoned salt meadows (Dahlbeck 1945; Dijkema 1990). Differences between grazed and abandoned salt meadows concerning vegetation structure, litter accumulation (Andresen et al. 1990), soil salinity (Dijkema 1990), soil moisture (Burnside et al. 2007), light availability (Andresen et al. 1990; Dijkema 1990) and nutrients (Scherfose 1993) have been described.

In our study we refer to observations made by us and other researchers (Härdtle 1984; Jeschke 1987; Timling 2000) that *Elytrigia repens* occurs mainly in the middle to upper, drier, less saline parts of the supralittoral which are rarely flooded. We hypothesize that, if *E. repens* increases due to abandonment or other causes, characteristic salt-meadow species (henceforth CSMS) will be affected adversely. In the present study we aim to verify these observations and to find evidence for the hypothesis for salt meadows of the southern Baltic Sea coast. We relate *E. repens* to the occurrence of CSMS and describe differences in abiotic characteristics and structural and functional vegetation conditions. In the light of grazing-related vegetation dynamics we further attempt to link our findings to widespread salt-meadow abandonment and propose a time-saving monitoring concept which aims to support decisions on grazing management.

### Methods

### **Study area**

The study area extends along the southern Baltic Sea coast from the Bay of Kiel (Kieler Bucht) in the west (Germany) to the Bay of Gdansk (Zatoka Gdańska) in the east (Poland; Fig. 3-1), comprising salt meadows on alluvial clayey sediments and peat (Scherfose 1993; Janssen et al. 2016). Seasonal fluctuations of brackish sea water occur caused, e.g., by wind or air pressure, but tidal fluctuations are small (Dijkema 1990). Depending on the geographical position sea water salinity ranges from 7.5 ppt in the east to 11.0 ppt in the west (HELCOM Map and Data Service 2008). Subjacent coastal soils are oligo- to (eu-)polyhaline (0–16.5–22 ppt, Scherfose 1993). Climatic conditions are predominantly (sub)oceanic (BIOCLIM data, Karger et al. 2017).



**Fig. 3-1 Map of study area along the southern Baltic Sea coast** (Esri Inc. 2011 version 10.3.1.4959). Relevé numbers per (groups of) study sites (black dots) are indicated. Pie charts display proportions of *Elytrigia repens* cover abundance groups: black = group A (> 5 %); dark grey = group B (< 5 % > 0 %); light grey = group C (0 %).

### **Data collection**

The first author conducted 63 vegetation relevés in 16 m<sup>2</sup> plots in the supralittoral zone, considering homogeneity in terms of vegetation structure and species composition (stored and available via EVA, Chytrý et al. 2016). We recorded total and individual cover abundance of all species and additional structural parameters. We supplemented our data with published and unpublished salt meadow plot data of various sources (Table 3-1). Most of these works do not distinguish between *E. repens* and its variety *E. r.* var. *littoralis* (Bab.) Krisch [*Elymus repens* subsp. *littoreus* (Schumach.) Conert] or *Elytrigia* × *obtusiuscula* (Lange) Hyl. [*Elymus* × *obtusiusculus* (Lange) D.C. McClint.; Krisch 1981]. The latter adjoins *E. r.* var. *repens* yet tolerating moister and

somewhat more saline (alpha-mesohalin to polyhaline, 5.5–16.5 ppt, Scherfose 1987) conditions. Due to frequent morphological transitions, the taxa are poorly delimitable (Krisch 2007). We excluded relevés with eu- to polyhaline vegetation partly explicitly including *E. r.* var. *littoralis* and possibly rare occurrences of *Elytrigia* × *obtusiuscula*. Since our data still do not admit a reliable differentiation between *E. r.* var. *repens* and *E. r.* var. *littoralis*, we refer to *E. repens* s.l. if not otherwise stated.

To ensure comparability and exclude spatial effects, we constrained the compiled external data to relevés of  $\ge 10 \text{ m}^2 \le 20 \text{ m}^2$  plot area (Table 3-1) and checked the resulting dataset for species-area relationship (Appendix S3-1: species-area relationship; R Core Team 2009-2016). Our final dataset comprised 50 relevés from Germany and 59 relevés from Poland (Fig. 3-1). We checked and corrected the dataset for inconsistent taxonomy, following Euro+Med Plantbase (2006-2018). We standardised data to the seven-parted Braun-Blanquet scale, using its mean percentage values (r = 1 %; + = 2 %; 1 = 3 %, 2 = 13 %; 3 = 38 %; 4 = 63 %; 5 = 88 %).

**Table 3-1 Data compilation.** Only low-growing salt-meadow vegetation was considered. Relevés with reeds and dominant stands of single species and eu- to polyhaline vegetation were excluded and variation in plot size reduced.

sources	data received via	country	size of original datasets	reeds and dominant stands of single species excluded	eu to polyhaline vegetation	plot sizes > 20 m <sup>2</sup> and < 10 m <sup>2</sup>
own surveys		DE	31	30	25	25
		PL	47	38	38	38
Machatzki 1994	vegetweb	DE	91	69	37	11
	GIVD: EU-DE-001					
	Jansen et al. 2015					
Wolfram 1996	CoastVeg-Germany	DE	130	112	73	14
	(Maike Isermann) GIVD: EU-DE-035					
Jasnowski 1962; Ćwikliński 1977;	Polish Vegetation Database	ΡL	154	121	72	21
Piotrowska 1974; Bosiacka & Stachowiak	GIVD:EU-PL-001					
2007; Bosiacka & Stępień 2001	Kącki and Śliwiński 2012					
Sum of all relevés	DE; PL		453	370	245	<u>109</u>

### CSMS and their relation to Elytrigia repens

We defined CSMS to comprise character or differential taxa of the class *Juncetea maritimi* Br.-Bl. in Br.-Bl. et al. 1952 occurring in the study area as well as some further characteristic taxa of low-growing moist and (poly-) mesohaline salt-meadow vegetation on the southern Baltic Sea coast (Table 3-2; Dierßen & Dierßen 1996; Berg et al. 2004; Mucina et al. 2016).

**Table 3-2 Characteristic salt meadow species (CSMS)**, chiefly character or differential taxa of the *Juncetea maritimi* (Dierßen and Dierßen 1996; Berg et al. 2004; Mucina et al. 2016). Strategy types: c = competitor strategist, r = ruderal strategist, s = stress tolerator; life-span: a = annual, p = perennial; life-form: g = geophyte, h = hemicryptophyte; t = therophyte (Klotz et al. 2002).

species	frequency/dataset [ %]	strategy type	life-span	life-form
Atriplex prostrata	25.69	S	а	t
Blysmopsis rufa	0.92	csr	р	g
Bolboschoenus maritimus	32.11	CS	р	g; h
Carex distans	7.34	CS	р	h
Carex extensa	2.75	S	р	h
Cotula coronopifolia	3.67	-	а	t
Eleocharis uniglumis	25.69	csr	р	g; h
Glaux maritima	47.71	S	р	h
Juncus gerardi	61.47	S	р	g
Juncus ranarius	6.42	r	а	t
Juncus maritimus	2.75	CS	р	g
Limonium vulgare	0.92	S	р	h
Lotus tenuis	3.67	CS	р	h
Plantago maritima	38.53	S	р	h
Plantago coronopus	2.75	-	a or p	h
Puccinellia distans	4.59	sr	р	h
Puccinellia maritima	2.75	sr	р	h
Spergularia marina	22.02	S	а	t
Trifolium fragiferum	24.77	csr	р	h
Triglochin maritima	42.20	S	р	g; h
Tripolium pannonicum ssp. tripolium	15.60	CS	a or p	t; h

Data analysis was carried out using statistical computing software R with R Studio (version 2.9.0–3.3.1; R Core Team 2009-2016). For our analyses we used the packages goeveg, *plyr, stats* and *vegan* (Wickham 2011; Oksanen et al. 2016; Goral & Schellenberg 2017).

With few exceptions, most CSMS were present with very low cover abundances. Notwithstanding the above, their occurrence is of high ecological value (Dijkema 1990). We calculated for each relevé CSMS accumulative abundances (= sum of all CSMS cover abundances) as well as frequencies (= number of all occurring CSMS).

We allocated each relevé of the dataset to one of three groups based on cover abundance classes of *E. repens*: group A > 5 %, n = 22; group B < 5 % > 0 %, n = 26; group C = 0 %, n = 61.

For a multiple comparison within *E. repens* abundance classes, we calculated Mann-Whitney-U tests for summed CSMS abundances and frequencies pairwise for the groups A, B and C, respectively. A *post-hoc* Bonferroni adjustment of *p* values corrects *p* values for different group sizes. Explanatory power of *E. repens* cover abundances for the occurrence of CSMS species was calculated using a linear model (stats package). Model selection included testing different

transformations of response (log, square root, arcsine). We checked goodness and model validity by interpretation of diagnostic residual plots and predictions as well as by tests for overdispersion.

### **Characteristics of vegetation**

In order to identify species, abundant where *E. repens* occurs, we calculated the relative abundance (\*according to formula; *racurve* function; *goeveg* package) and frequency of species co-occurring with *E. repens* for each of the above defined groups on square root transformed species data. Calculation was restricted to species with a high relative abundance (> 0.02) in group A.

# \*relative abundance= $\frac{\text{sum of all abundances of species 'a' in group A, B or C}}{\text{sum of all abundances of species 'a' across all groups (A-C)}}$

We calculated Mann-Whitney-U tests (with *post-hoc* Bonferroni adjustment of *p* values) using measured mean (available for 63 relevés) and maximum vegetation height (available for all relevés) as well as plot-wise proportions of plant strategy types (Klotz et al. 2002), soil salinity, soil moisture and light availability as mean Ellenberg Indicator Values (Ellenberg et al. 2001).

To present ecologically most meaningful patterns of the relation between groups A–C, the factor 'Elytrigia' was accentuated for a multivariate analysis. We conducted NMDS with species in the dataset reduced to (1) all CSMS and (2) all species of high relative abundance (> 0.02; according to formula above), calculated separately for each group A–C (goeveg package). *E. repens* was excluded to avoid circular reasoning.

We calculated a 6-dimensionsional scree plot (goeveg package) to specify an adequate number *k* of dimensions (statistic: Bray-Curtis dissimilarity; *vegan* package). To find best fitting options, we performed the NMDS with square root, arcsine, function-implemented auto-transformation and without species data transformation. We plotted the abundance of *E. repens post-hoc* (envfit function; vegan package). We further visualized plant strategy types (weighted means; Klotz et al. 2002) and abiotic values (Ellenberg Indicator Values for soil salinity, soil moisture, light availability; Ellenberg et al. 2001) within groups A–C by fitting them *post-hoc* (*envfit* function; *vegan* package).

### Results

### Relation of *Elytrigia repens* to CSMS

Regional variation was observed in the occurrence of *E. repens*. Group A relevés occurred chiefly in the central part of the study area (Fig. 3-1).

Accumulative abundance and frequency of CSMS showed low values in group A, comprising plots with considerable cover of *E. repens*, in comparison to groups B and C; group C held highest

values of CSMS (Fig. 3-2). While frequency values of groups A, B and C showed significant differences, accumulative abundance did not differ significantly between groups A and B (Table 3-3).

Table 3-3 Mann-Whitney-U test for CSMS accumulative abundance and frequency, abiotic factors and structural and functional traits between each group A–C. Significant values are marked by asterisks. (Mean frequency of stress tolerator species: A = 0.81, B = 1.85, C = 2.99; mean frequency of competitor strategists: A = 3.82, B = 3.04, C = 1.51).



Linear models showed best results for correlation with abundance and frequency of CSMS, when the cover of *E. repens* was applied without transformation. Both models are highly significant ( $p \le 0.001$ ) and showed comparable results and confidence intervals (Fig. 3-3). A sampling bias slightly weakens the generally valid statements of both models, explaining 26 % of the variance in the data.







Fig. 3-3 Linear model of *E. repens* calculated for frequency of characteristic salt meadow species (CSMS). Model calculation for accumulative abundance showed comparable results and is therefore not shown.

### **Characteristics of vegetation**

In group A, with *E. repens* covering > 5 %, nine species occurred with a relative abundance of > 0.02 (Fig. 3-4). Six of the nine were grasses (*Poaceae*); four species showed lower relative abundance and frequency in groups B and C. All five competitive species in group A, *Achillea millefolium, Holcus lanatus, Poa pratensis, Trifolium repens* and *Schedonorus arundinaceus*, showed lower relative abundance in group C, the latter species with slightly less distinct values (Fig. 3-4). *Juncus gerardi* occurred conversely with distinct differences between groups. *Agrostis stolonifera* was represented by slightly lower values in group A than in group C and showed a higher relative abundance in group B than in groups A and C. *Festuca rubra*, in reverse, showed higher relative abundance in group A than in groups B and C. *Argentina anserina* was similarly relatively abundant in all groups. The same patterns were also found for frequency per group (Fig. 3-4).

Soil moisture and soil salinity values differed significantly in groups A and B in comparison to group C (Table 3-3; Fig. 3-5). Light availability was significantly different between groups A and B and between groups B and C; no difference was found between groups A and C (Fig. 3-5). Mean and maximum height of vegetation showed higher values in group A than in groups B and C, the latter yet without significant differences; a wide range of values occurred in each group. Mean height differed significantly between groups A and B as well as between groups A and C (Table 3-3; Fig. 3-5). Mean frequency of stress tolerators showed significant differences between groups A (0.81) and B (1.85) and between groups B and C (2.99). An adverse relation was evident for



competitor strategists with high values in group A and low values in group C (Table 3-3).

Fig. 3-4 Rank abundance curve of species within group A. For species with high relative abundance in group A (> 0.02), relative abundance (rel.ab) and frequency (frq. [%]) are shown for all groups. Arrows indicate if the relative abundance in groups B and C in comparison to group A is higher ( $\uparrow$ ), slightly higher ( $\urcorner$ ), similar ( $\rightarrow$ ), slightly lower ( $\lor$ ) or lower ( $\lor$ ).



**Fig. 3-5 Comparison of abiotic factors of groups A–C.** Levels of significance of the Mann-Whitney-U test for soil moisture, soil salinity and light availability based on Ellenberg Indicator Values and for measured maximum and mean height of vegetation are specified.

# NMDS conducted with non-transformed species data on two dimensions (k = 2) yielded the lowest stress value of 1.73. Group A was characterised by a large proportion of competitor strategists associated with dry soil and low soil salinity (Fig. 3-6). The vegetation of group C was represented by an admixture of stress tolerators, predominantly CSMS (Table 3-2; Fig. 3-6).



Fig. 3-6 NMDS based on the most abundant species of groups A–C (relative abundance > 0.02; except *Elytrigia repens*) and characteristic salt meadow species (CSMS). Relevés are shown as grey dots which sizes refer to frequency of CSMS (frequency\*0.3). Vectors of light availability, soil moisture and soil salinity based on Ellenberg Indicator Values, *Elytrigia repens* cover abundance, weighted proportions of stress tolerators and competitor strategists per relevé are plotted *post-hoc* with default settings. As an exception moisture was drawn with arrow multiplier 9.

### Discussion

### **Data collection**

While group A relevés were most prominent in the central part, most group C relevés occurred at the western edge and eastern parts of the study area. This pattern is neither explained by the west-east sea water salinity gradient (HELCOM Map and Data Service 2008) nor by diluted sea water or groundwater salinity enrichment. Dilution of seawater happens through freshwater inflows such as at the Oder river estuary; enrichment due to ascending saltwater [e.g. Chrząszczewska Island (Wyspa Chrząszczewska), Poland; Bosiacka et al. 2011]. We relate the observed distribution pattern of group A–C relevés to local abiotic conditions and management (see also Hulisz et al. 2016). The focus of the different studies contributing to our dataset may have influenced the local plot selection as well.

### Relation of *Elytrigia repens* to CSMS

Differences in cover of *Elytrigia repens* in salt-meadow vegetation appear to be correlated with shifts in CSMS frequency and abundance (Fig. 3-3), although CSMS comprised species of various *Juncetea maritimi* plant communities. *E. repens* appears thus negatively related to low-growing *Juncetea maritimi* plants in general. Our results are in line with findings of Dijkema (1990), who discusses the increase of *E. repens* in relation to the general loss of halophytic vegetation. It should be emphasized though that our results apply only for the studied areas, although Burnside et al. (2007) made similar observations on the eastern Baltic Sea coast, Dahlbeck (1945) in southern Sweden and Melečková et al. (2014) and Dítětová et al. (2016) for inland saline vegetation of Slovakia.

If we assume increasing proportions of *E. repens* in salt-meadow vegetation owing to abandonment, we can deduce from our findings consequences in grazing-dependent vegetation dynamics. This confirms our hypothesis that CSMS will be negatively affected, if grazing ceases, by increasing *E. repens*. An overall decrease or even loss of low-competitive halophilous plants was also described by Dahlbeck (1945) and Dijkema (1990).

Within the supralittoral zone, an upward shift of salt-meadow vegetation has been described as being grazing-induced (Bakker 1987). CSMS in the middle and upper parts of the supralittoral, such as *Plantago coronopus, Juncus gerardi, Blysmopsis rufa, Eleocharis uniglumis, Glaux maritima, Plantago maritima, Puccinellia distans, P. maritima, Spergularia marina* and *Trifolium fragiferum*, are favoured by grazing (Härdtle 1984; Scherfose 1993). This shift was also described following reintroduction of grazing on formerly abandoned salt meadows (Bakker & Ruyter 1981).

Contradictory results in response to grazing were described for certain CSMS, e.g. *Plantago maritima*, *Triglochin maritima* and *Tripolium pannonicum* subsp. *tripolium* (Bakker et al.

1985; Bakker 1987; Kiehl 1997). Kiehl (1997) interpreted such findings as scale-dependent effects. Due to the commonly patchy spatial distribution of certain CSMS, such species are unevenly represented in plots of different size as within-plot heterogeneity increases with plot size.

Conflicting results may also be attributed to varying effects of grazing in different elevation zones of the supralittoral (Jutila 1999). For instance, Tripolium pannonicum subsp. tripolium is known to be inhibited by grazing in the lower parts of salt meadows (Härdtle 1984; Scherfose 1993) while, according to our results, in the middle to upper supralittoral it is just the opposite (frequency groups A–C [ %]: 0.00, 3.85, 26.23).

While there is general consensus on the effect of grazing to CSMS, the optimal grazing intensity enhancing the growth of CSMS is specified differently (Härdtle 1984; Scherfose 1993). On the one hand this is due to the general difficulties in measuring grazing intensity in non-intensively managed pastures (Esselink et al. 2000), on the other hand and as a general pattern in European salt meadows, variation in salinity and soil moisture co-determine the composition of vegetation (Burnside et al. 2007; Dítě et al. 2015; Hulisz et al. 2016). This may thus locally alter the effect of grazing on certain CSMS. Useful recommendations for conservation management could be generated locally by detailed knowledge about historical management (Doody 2008), the observation of livestock movement (Esselink et al. 2000) or by improved indication methods (see proposal below under "Nature conservation").

### **Characteristics of vegetation**

Group A is characterised by a relatively high cover of *E. repens* and further tall-growing competitive species mostly absent in group C relevés. Although a cover of *E. repens* above 5 % may not mean high abundance of this grass species, it indicates a markedly different vegetation composition and structure (Fig. 3-2, 3-4–3-6).

An increase of tall competitive glycophytes, commonly with *E. repens* among them, in relation to cessation of grazing has frequently been described (Schmeisky 1977a, b; Jeschke 1987; Dijkema 1990; Burnside et al. 2007). This increase may find its expression in seed production, subsurface rhizome density or modification of morphological traits such as shoot length (Härdtle 1984; Amiaud et al. 2008; Wanner 2009; Dierschke 2012). Next to *E. repens, Schedonorus arundinaceus* is mentioned to develop (sub)dominant stands (Fig. 3-4; Kiehl 1997; Jutila 1999; Burnside et al. 2007).

Most notably in terms of relative abundance in group A are *Festuca rubra* and *Agrostis stolonifera* which occur somewhat less (*Festuca*) or more (*Agrostis*) in group C relevés (Fig. 3-4). Assuming group A plots as ungrazed salt-meadow sites, the increase of *Festuca rubra* in abandoned salt meadows of the middle and upper supralittoral as observed in several studies (Christiansen 1937;

Kauppi 1967; Bakker & Ruyter 1981; Kiehl 1997) is in line with our findings. Its increase may especially be linked to a reduced cover of certain CSMS such as *Juncus gerardi* or *Glaux maritima* (Schmeisky 1974; Kiehl 1997).

Grazing enhances the growth of *Agrostis stolonifera* which commonly dominates low-growing salt-meadow vegetation in the supralittoral (Härdtle 1984; Scherfose 1993). This stoloniferous grass rapidly overgrows open patches induced e.g. by trampling (Scherfose 1993).

With similar frequency the grazing tolerant *Argentina anserina* is relatively abundant in all groups A–C (Fig. 3-4). It is also stoloniferous and procumbent, forming layers on dead organic matter accumulating in abandoned meadows (Bakker 1987).

Soil salinity and moisture, important abiotic drivers of salt-meadow vegetation (Dijkema 1990; Burnside et al. 2007; Hulisz et al. 2016), significantly differentiate the relevés of groups A and C (Fig. 3-5, 3-6). Due to increased evaporation, grazed meadows are characterised by more saline soils which diminish the germination success of competitor strategists (Kauppi 1967; Schmeisky 1974; Bakker 1987; Burnside et al. 2007). Bakker (1987) highlights the approximation of salinity in grazed and ungrazed sites in the upper supralittoral, where the evaporation effect is diminished due to the general decrease of salinity with increasing elevation. Contradictory results about soil moisture in relation to the cessation of grazing (cf. Fig. 3-5; Bakker 1987; Burnside et al. 2007) may partly be explained by the fact that eu- to polyhaline vegetation (excluded in our study) is generally moister and less grazing-dependent due to naturally occurring disturbances such as flooding.

A short sward including open patches, characteristic for grazed salt meadows and enhanced by trampling, increases light supply for basal parts of plants and is beneficial for low-growing light-demanding CSMS (cf. Fig. 3-5, group C; Dahlbeck 1945; Kauppi 1967; Härdtle 1984; Andresen et al. 1990; Dierßen & Dierßen 1996; Bakker & de Vries 1992; Kiehl 1997; Leuschner & Ellenberg 2017). Structure, in particular height, of vegetation has been described as rather more important for CSMS than soil salinity differences (Bakker 1987). The opening of swards due to moderate trampling and grazing notably supports CSMS in their early stages of development (Bakker & de Vries 1992). In greenhouse experiments Bakker et al. (1985) and Bakker (1987) found reduced germination success for CSMS along with decreased light influx.

Ungrazed salt-meadow vegetation is characterised by increasing (mean) height and interspecific competition (cf. Fig. 3-6, group A, competitor strategists; Dahlbeck 1945; Dijkema 1990; Scherfose 1993; Amiaud et al. 2008). Where *Elytrigia repens* reaches high cover open patches of bare soil rarely occur (Timling 2000).

### **Nature conservation**

Along with abandonment much of the grazing-dependent, ecologically valuable salt-meadow vegetation decreases, accompanying a general decline of salt-meadows (Dijkema 1990; Dierßen & Dierßen 1996, Janssen et al. 2016). To develop recommendations for conservation management of low-growing salt-meadow vegetation of the middle and upper supralittoral on the southern Baltic Sea coast, local livestock husbandry management and direct or indirect vegetation monitoring are to be focussed. As grazing management depends on local conditions, accessibility and initial vegetation, the use of stocking rates as stand-alone proxy for grazing intensity is not recommended (Kiehl 1997). If applied, stocking rates should rather be connected to local livestock distribution records, which is a time-consuming task (Esselink et al. 2000). This also applies for comprehensive direct monitoring of CSMS.

If *Elytrigia repens* invades the ecologically valuable salt-meadows as a result of cessation of grazing, we suggest an indirect monitoring of this vegetation using *E. repens*, the cover of which is easily recognized and recorded. Specifically we propose to (i) develop a system of permanent plots comprising the different elevation zones, (ii) record cover-abundance of *E. repens* within representative plots, and (iii) repeat this survey approximately at the same time of the year at regular intervals, optimally each year.

Surveying dominance stands of *E. repens* can be combined with categorical records of vegetation structure as suggested by Doody (2008) to aid a decision on grazing management. With a regularly conducted monitoring and survey across administrative borders along the southern Baltic Sea, knowledge about medium-term dynamics can be obtained which is essential to adapt grazing management.

### **Synthesis**

The overarching goal of this dissertation is to explore the saline and brackish grassland vegetation of the Baltic Sea coast in order to provide insights into its ecology, phytosociology and conservation potential. Within the three studies that make up this dissertation, I aimed to (i) convert Fennoscandian species-plot data to make them compatible with other data and thereby significantly contributing to the completeness of the data available for broad-scale vegetation analyses of Baltic Sea coastal grasslands, (ii) classify and characterise saline and brackish grasslands from the entire Baltic Sea coast to generate for the first time an overview on their diverse plant communities and ecology from a transnational perspective, (iii) regard the classified plant communities from a North-west European perspective to evaluate their similarities and contrasts with tidal salt grasslands outside the studies' scope, (iv) discuss their nature conservation aspects on European scale to investigate their conservation potential, (v) investigate the relation between *Elytrigia repens* and characteristic species of Baltic Sea coastal grasslands to get insights into shifts in species composition and other structural and soil abiotic changes and (vi) elaborate a plot-based monitoring concept for Baltic Sea coastal grasslands to provide a long-term monitoring system and thus, contribute to the conservation of this vulnerable grasslands.

Full summaries and conclusion are given at the end of each study. In the following, I draw together the individual strands of research to synthesise the key findings of this dissertation and implications for conservation practice and future research.

### Key findings and implications of study 1

# The successful utilisation of Fennoscandian vegetation-plot data for transnational vegetation studies

My co-authors and I initially conducted a literature and database review of saline and brackish vegetation records from the Baltic Sea area and other data from the entire Fennoscandia. This resulted in the clear determination of three species-quantity scales that were applied in numerous studies of the 20th century: the Norrlin scale, the Hult-Sernander scale and the Drude scale. We found that these scales were all progressive in character, i.e. they varied from fine-scale differences in grades at the lower end to coarse-scale at the upper end. This is an important data-quality feature in relation to our understanding of vegetation units and thus, to subsequent analyses of vegetation-plot data.

According to our findings the ten-grade Norrlin scale is based on density measures in the lower (1–7) and on the admixture of other species in the upper grades (8–10) of the scale, whereas the grades of the Hult-Sernander scale were first outlined in abundance values and later developed

to cover scales. The Drude scale was reported to base on cover-abundance and additional information on the admixture of species. For the Hult-Sernander scale and the Drude scale we found six and three regularly used variants, respectively, which differed in the number of grades (n = 5-12). Additionally, for the Drude scale we found differences in the interpretation of scale grades in terms of their applied transformation to percentage values. Although some uncertainties remained for the Drude scale for which it is not clear whether it was mainly used in the sense of an abundance or a cover scale, we found evidence that measurements (in the case of the Norrlin scale) or estimations of scale grades of all examined species-quantity scales ensure the indirect or direct record of species cover. Thus, their transformation to percentage cover values is justifiable.

We proposed a transformation of scale grades to percentage values for each of the above named scales and its variants that was derived by information given in the reviewed literature or by our calculations of hypothetical percentage-cover values. To reach a purposeful decision for the possible varying interpretations (conversions) of the Drude scale grades for each individual dataset, we suggested to calculate the sum of all individual species covers per plot on the basis of each of the proposed transformation types. Hence, one can display potential but unintentional over- or underestimation.

### Study 1: Implications and contributions to science

To have suitable data available and to understand the methods underlying these data is the overall basis of any reliable scientific analysis. Here, we enhanced the understanding on three species-quantity scales frequently applied in Fennoscandian data and elaborated a proposal on their transformation that will be incorporated in TURBOVEG 2 (and the prototype of TURBOVEG 3) to support a future standardised data entry. Thus, our results allowed us to considerably increase the amount of quantitative Fennoscandian data for the second study of this thesis and correspondingly increase the quality of its underlying dataset.

Results of this study enable a clearly defined, standardised use of numerous data derived from Fennoscandian vegetation studies. Transformed data (will) fill important gaps in the data volume of European vegetation databases and thus accordingly in the European Vegetation Archive (EVA).

### Key findings and implications of study 2

# A transnational view on Baltic Sea coastal grasslands – diverse plant communities in a complex littoral gradient

Our phytosociological classification of plot-based saline and brackish vegetation data from the entire Baltic Sea coast resulted in three main clusters (M1–3), whose further subdivision account for 33 subgroups. At a transnational scale, the subgroups reflect the entire variation of plant communities of Baltic Sea coastal grasslands. Local variations that were reflected in single relevés or studies of limited geographical scope were not distinguished in the classification, which is also known from other large-scale classifications of coastal grasslands (Rodwell et al. 2000).

We found plant communities of the main clusters (M1–3) to be partitioned by species composition along soil salinity, which generally decreases with increasing height above sea level (Ward et al. 2016). However, locally pronounced discontinuity or a reverse in the salinity gradient led to greater variability in the littoral placement of plant communities determined in the literature. Differences in soil moisture mostly varied among plant communities within each main group, resulting in less saline and driest communities in the main cluster 3 (M3). Soil base content, nutrient availability and climatic conditions were less strongly related to the ecological variance in plant communities.

The plant communities we identified, which in the narrow sense make up the characteristic saline to brackish coastal grasslands of the Baltic Sea belong to the herb-rich grassland vegetation of the phytosociological class *Juncetea maritimi* and the subsaline grasslands of the *Molinio-Arrhenatheretea*. Further plant communities, which in an overarching sense are part of the brackish and saline grasslands, regularly reflect a close linkage with diverse adjacent vegetation types and their integrative embedment in the coastal landscape. In the low and middle supralittoral they largely comprise transitions to the halophilous and nitrophilous strandline vegetation of the *Cakiletea maritimae*, to brackish and freshwater influenced reeds of the *Phragmito-Magnocaricetea* as well as disturbed sandy sites of the *Saginetea maritimae*. Further upwards in the littoral zonation, transitions to dry grasslands of the *Koelerio-Corynephoretea canescentis*, strongly freshwater-influenced types of the *Molinio-Arrhenatheretea and* calcareous mineral-rich fen vegetation of the *Scheuchzerio palustris-Caricetea fuscae* occur.

Within the *Juncetea maritimi* we found seven plant communities of the alliances *Festucion maritimae* and *Puccinellio maritimae-Spergularion salinae* which are known to grow directly above the mean low water line. Our analyses showed that they contain high proportions of stress tolerators and scattered occurrences of certain annuals indicating the close proximity of the low tidal marsh. Individual communities are known to grow further upwards in shallow

depressions of the middle supralittoral, implied by low proportions of species of the subsaline alliance *Loto tenuis-Trifolion fragiferi* (Härdtle 1984; Westhoff et al. 1998; Rodwell et al. 2000).

One plant community belonging to the *Puccinellion phryganodis* was found in the northernmost parts of the study area and was described to grow in parts of the upper supralittoral and epilittoral (Siira 1970, 1985).

Mainly belonging to the second main cluster (M2), we found twelve plant communities of the diverse alliance *Armerion maritimae* reported to grow in the middle, and to a lesser extent, in the upper supralittoral (Rebassoo 1975; Jeschke 1987; Dierßen & Dierßen 1996). Owed to the here prevalent heterogenic soil properties (Vestergaard 2002) which vary on micro topographic scale (Ward et al. 2016), these plant communities form narrowly interconnected patterns with the found and likewise diverse plant communities of the subsaline *Loto tenuis-Trifolion fragiferi* (*Molinio Arrhenatheretea*).

With an emphasis in M3, we discovered a broad variety of comparatively species-rich, freshwater-influenced, wet, peaty or dry plant communities containing rather high proportions of CSR-strategists or strongly competitive species (Dierßen & Dierßen 1996; Sýkora et al. 1996; Zuidhoff et al. 1996; Dierschke 1997, 2012; Jutila 2017; Rŭsina 2017; Lehtomaa et al. 2018).

The identified plant communities are known to depend on no to low (n=19), moderate (n=11) or strong (n=3) grazing impact (Dahlbeck 1945; Rebassoo 1975; Härdtle 1984; Siira 1985; Willers 1988; Jutila 2001; Berg et al. 2004; Rautiainen et al. 2007).

# Lessons learned from a transnational perspective – distribution patterns and relation to communities from beyond the studies' scope

The overall picture of all data included in our study revealed an even distribution of saline and brackish grasslands along the southern Baltic Sea coast and an increasingly sporadic occurrence towards east and north, with striking exceptions where individual large sedimentation basins occur or along the skerry coasts, which hold small-sized but diverse coastal grasslands (Dijkema 1990).

We observed that transnational geographical patterns of the identified Baltic Sea plant communities overall relate to the gradient in sea-water salinity, tidal range and to a lower extent to differences in climatic conditions. This underlines a zonal characteristic in these otherwise azonal grasslands. Furthermore, distribution limits of many individual plant communities relate to species-range boundaries.

Accordingly, rather saline Baltic Sea coastal plant communities affected by continuous contact with sea-water (within M1) are most common in the area close to the transition to the North Sea and provide pronounced similarities in species composition with North-west European coastal grassland plant communities. However, we determined that most of the polyhaline to oligohaline

Baltic Sea plant communities (mainly within M2) are common in the entire study area or are broadly distributed in large parts. The latter frequently reflects the pronounced vegetation turnover between the temperate climate and the southern boreal climate so that they occur either in the south or the north of the Baltic Sea area. Plant communities that we found in the entire study area or limited to the southern part are largely comparable to those of the generally somewhat more saline communities of the North-west European coast.

The plant communities which we found in the north of the study area commonly contain boreal-arctic relic species (Siira & Haapala 1969; Jutila b Erkkilä 1998; Rautiainen et al. 2007). They thus relate to Arctic coastal plant communities, which is a peculiarity in the Baltic Sea coastal vegetation (Thannheiser 1975, 1995). We additionally noted more northerly distributed plant communities, which are unique for the Baltic Sea coast. This and the fact that they have never been described according to formal syntaxomic standards our study points out the need for an in-depth syntaxonomical description and allocation.

# Conclusions drawn from a transnational perspective – conservation aspects on habitat and species level

We found that most of the 33 plant communities we described can be attributed to the Natura 2000 (Annex I) habitat types 'Atlantic salt meadows' (H1330) and 'Boreal Baltic coastal meadows' (H1630) whose common border per definition approximately coincides with biogeographical zones (Doody 2008; Evans 2012). Due to the coastline characterised by strong gradients, the more or less pronounced variations of saline and brackish Baltic Sea grasslands on local level and their embedment into the coastal landscape, there is a close ecological and floristical link between these two habitat types as well as with other habitat types.

In consequence of the close floristic linkage of H1330 and H1630, we were unable to clearly assign all the plant communities we found. Nonetheless, we could assign plant communities with species restricted to the south-western part of the study area, characteristic for H1330 and communities including species that occur only in the north of the Baltic Sea and which are unique for the description of H1630.

Considering our results on patterns in plant community distribution and their floristic characteristics, we recommended to (i) improve the list of indicative plants of both types, (ii) to designate a sub-type with boreal and arctic relic species in order to better reflect some rare plant communities and (iii) to underline the separation of habitat types with enhanced descriptions of differing characteristics in the littoral gradient and with reasonable chosen geomorphological terms. The latter may lead to a broader geographical concept of H1630, similar to that applied for the Red List of Habitats (Janssen et al. 2016).

Our data revealed that saline and brackish grasslands from the Baltic Sea coast support several characteristic plant species with varying degree of extinction risk assigned on national level (Wind & Pihl 2004; Zarzycki & Szeląg 2006; Eesti Teaduste Akadeemia Looduskaitse Komisjon 2008; Gamtos tyrimų centras 2009-2019; Rassi et al. 2010; Latvian Biodiversity CHM 2015; Westling & Gärdenfors 2015). We found that these species are frequently listed either where they reach their distribution limit or where coastal grasslands have a generally limited occurrence. It was commonly reported that Red List species are especially threatened by land-use intensification and abandonment of coastal grasslands. This relates to the results of the third study of this thesis, where we examined the relation of many of these threatened and characteristic coastal grassland species to *Elytrigia repens*, a species which is known to increase in cover after abandonment (Jeschke 1987; Dijkema 1990).

*Puccinellia phryganodes* occurs only in the most northern part of the study area and is listed as Critically Endangered on European level (Bilz et al. 2011).

### Study 2: Implications and contributions to science

We classified and presented the entire and highly diverse variation of plant communities of Baltic Sea coastal grasslands for the first time on a transnational scale. Identified distribution patterns and variation in plant communities relate to sea-water salinity, tidal range and climatic conditions and reflect regional phytogeographical patterns. Most of the described plant communities each depend on a specific grazing regime.

Characterised euhaline to  $\alpha$ -mesohaline plant communities are most similar to North-west European coastal grasslands. Some relate to Arctic communities. Others are found only in the Baltic Sea area and call for adequate syntaxonomic descriptions.

With transitions to adjacent habitat types, found plant communities either belong to the Natura 2000 habitat types H1330 or H1630. We identified the need to revise these habitat types, and provided suggestions to enhance their characterisation. Improving the Natura 2000 habitat type descriptions will contribute to the better setting of conservation goals and monitoring activities in order to preserve Baltic Sea coastal grasslands, which inhabit many species included in national Red Lists, predominantly threatened by land-use intensification and abandonment.

### Key findings and implications of study 3

### Threatened by abandonment – the loss of coastal grassland species

My co-authors and I studied middle and upper supralittoral coastal grassland vegetation of the southern Baltic Sea coast on vegetation-plot level, which showed that the occurrence of *Elytrigia repens* appears to be negatively related to the occurrence of characteristic species of low-growing saline and brackish grasslands. Characteristic species belong to diverse vegetation types of the class *Juncetea maritimi* with most of them withstanding high stress (e.g. salinity, high soil water saturation) and being hemicryptophytes and, to a lesser extent, geophytes and therophytes.

We found that whenever *E. repens* was lacking in the vegetation-plots (group C), the accumulative abundance and frequency of characteristic species achieved median values of 44 % plot<sup>-1</sup> and 5 species plot<sup>-1</sup>, respectively. However, if *E. repens* occurred with a cover above five percent (group A), with 2 % plot<sup>-1</sup> and 1 species plot<sup>-1</sup>, corresponding values were significantly lower.

If we consider relevés of group A as abandoned, our analyses acknowledge the loss of characteristic coastal grassland species and thus, the loss of vegetation quality subsequent to cessation of grazing. Our results are in accordance with findings from the eastern Baltic Sea coast (Burnside et al. 2007) and with statements of Dijkema (1990), who surveyed coastal grasslands from the Baltic Sea and the North Sea coast.

We further demonstrated that overall proportions of stress tolerators were significantly lower in group A in comparison to groups B (*E. repens* cover-abundance < 5%) and C; proportions of competitive species showed a reversed picture. The latter included Achillea millefolium, *Holcus lanatus, Poa pratensis, Schedonorus arundinaceus* and *Trifolium repens* which belong to the nine most relative abundant species (relative abundance > 0.02) of group A but occurred with low relative abundance and frequency in groups B and C. Considering group A relevés as abandoned, the increase of tall competitive glycophytes with graminoids frequently among them, is in line with results of local studies of saline and brackish Baltic Sea coastal grasslands (Schmeisky 1977a, b; Jeschke 1987; Burnside et al. 2007) as well as with changes generally described for grassland habitats in relation to abandonment (Carboni et al. 2015).

*Agrostis stolonifera* and *Festuca rubra*, both graminoid species of group A which are in general most relative abundant in the middle and/or upper supralittoral, show high relative abundance in group A and only slightly more and less relative abundance in groups B and C, respectively. Assuming relevés of group A as abandoned, our results are in accordance with the generally reported increase of *Festuca rubra* subsequent to cessation of grazing (Kauppi 1967; Bakker & Ruyter 1981; Kiehl 1997).

Our study revealed further differences in soil salinity and soil moisture, for which values differed significantly in groups A and B in comparison to group C, where both factors achieved highest values. Vegetation height tended to be highest in group A in comparison to groups B and C, which was significant for the measured mean height of vegetation, while light availability was somewhat lower in group A than in groups B and C.

# Quality assessments on Baltic Sea coastal grasslands – a good chance to preserve their diversity!

The examination of vegetation changes, which are caused by abiotic or anthropogenic factors, is generally needed and should be conducted through a well-considered monitoring of grasslands habitats (Carboni et al. 2015). We elaborated a monitoring method suitable to assess the quality of coastal grasslands and to develop recommendations for the conservation management of middle and upper supralittoral coastal grassland vegetation. We suggested to conduct monitoring of *Elytrigia repens* on permanent plots in different littoral zones. We further recommended to repeat the monitoring approximately at the same time of the year, to allow for an optimal comparability of resulting data over the years. Additionally, we proposed to additionally map the proportion and distribution of *E. repens* on site level.

### Study 3: Implications and contributions to science

Results of the study show that *Elytrigia repens* indicates low occurrences of characteristic species of middle and upper supralittoral low-growing saline and brackish grasslands of the southern Baltic Sea coast. The occurrence of *E. repens* is in accordance with further competitive species, comparatively low soil salinity, soil moisture and light availability and an increased mean vegetation height.

If *E. repens* increases due to abandonment, a decrease in the quality and quantity (if we regard the proven increase of glycophytes as the beginning of a total area loss) of saline and brackish grasslands is evident from our results. In the light of the overall decrease in both factors (Janssen et al. 2016) and as cessation of grazing is known as a driver for the loss of saline and brackish coastal vegetation (Andresen et al. 1990; Dijkema 1990; Burnside et al. 2007), both in turn underlines the urgent need of a well-adjusted grazing management.

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We developed a userfriendly monitoring method which is easy to implement in conservation practise. If regularly conducted, this monitoring method allows to draw conclusions on the quality and medium-term changes in species composition. If conducted on different sites and in different regions in the same standardised manner, one can derive general trends in grassland quality on supra-regional level. Results of the proposed monitoring may contribute to a research-driven development of conservation strategies and thus, to the conservation of high quality coastal grasslands of the southern Baltic Sea coast.

#### Future perspectives and challenges

#### The future benefits of proposed data transformation

The results of study 1 of this thesis facilitate the standardised transformation of Fennoscandian data of the 20th century. In the light of the decrease in surface area and quality of saline and brackish grasslands from the Baltic Sea over the last 100–150 years (Janssen et al. 2016), this reduction of the lack of historic data presents an opportunity to draw conclusions on the overall surface area loss of Baltic Sea coastal grasslands (Normander et al. 2009). It further allows a high-quality resurvey of vegetation-plots (Kapfer et al. 2016) to investigate vegetation changes and assess the loss of biodiversity. The increase of data availability may also support the development of sufficiently detailed syntaxonomic concepts of further Fennoscandian vegetation types.

Especially the Drude scale was commonly also applied in many East European vegetation studies as well as in parts of Russia which were not considered in study 1 (Tikhodeyeva & Lebedeva 2015; personal communication between Milan Chytrý and Yakov P. Didukh 2018). Thus, it is conceivable that the results of study 1 may also facilitate the increase of vegetation-plot data outside Fennoscandia.

# What else can we ask, what else can we answer? – Studying coastal grasslands on the basis of phytosociological research in a changing world

Climate change is assumed to adversely affect the overall distribution of the dynamic habitats of Baltic Sea coastal grasslands and their plant species diversity in the near future (Boormann 2003; Strandmark et al. 2015). Due to the close interaction of coastal topography, hydrology and the vegetation of coastal grasslands, climate change may easily cause tremendous negative effects (Burnside et al. 2008). Amongst others, it is predicted to alter seasonal flooding and to cause significantly higher waves in the future (Groll et al. 2017). Thus, accretion and erosion rates will increase, directly affecting the dynamic of coastal habitats (Boormann 2003). Assumed disturbance in soil hydrology (Kont et al. 1997), which may be related to changes in soil salinity, may considerably alter plant communities. In summary, one can assume that the ecological functioning of coastal grasslands will be adversely affected.

Current phytosociological approaches of studying vegetation are of high relevance to increase the understanding on plant communities and to develop useful tools for nature conservation issues in a changing world (Biurrun et al. 2019). But how can we deepen the insights gained from study 2? How could we increase the understanding on the preservation of saline and brackish grasslands of the Baltic Sea coast with a view on climate change-induced potential modifications? The answer could be the combined application of methods used in coastal grassland vegetation research that might offer further insights and thus, may enhance the understanding of climate change-related vegetation and habitat changes. The resulting plant communities (phytosociological associations or subordinate ranks) of the transnational, phytosociological approach conducted in study 2, could be used as 'basic examination units' for such combined studies, which guarantee a complete and detailed contemplation of plant community variants of the entire Baltic Sea coast and which justify a comparison of data from different study sites. Based on this basic examination units, micro-topographical studies can give insights of plant and plant community presence as well as on differences in edaphic factors in a resolution of few centimeters (Burnside et al. 2008; Ward et al. 2016). So far, they have been examined in local studies on some main vegetation types such as 'Lower Shore grasslands' or 'Tall grasslands'. The examination units could also serve as basis for functional approaches, with which, if conducted with a broad view on terrestrial and aquatic influencing factors, salt grassland functioning, ecosystem processes and responses can be studied (Strandmark et al. 2015).

As identified plant community and species diversity, level differences on micro-scale and grassland functioning matter in relation to climate change-induced potential modifications, this combined approach has the potential to increase the understanding and thus, to develop research-driven recommendations for the future handling and protection of Baltic Sea coastal grasslands.

#### The transfer of the elaborated monitoring method

The monitoring method which we developed in the third study of this thesis may has the potential to be transferred to other coastal areas, outside the studies' scope.

*Elytrigia repens* occurs along the entire Baltic Sea coast (GBIF 2017) and, accompanied by further glycophytes, is associated with the cessation of grazing in coastal grasslands beyond the area surveyed by us (Burnside et al. 2007). A similar observation was made also beyond the Baltic Sea coast extent at the coast of the brackish White Sea (Ilya Kucherov, personal communication

2019). To rerun study three on grazing-dependent coastal saline and brackish grasslands in other parts or at the entire extent of the Baltic Sea, the White Sea or further coastal areas where *E. repens* was reported to occur in relation to abandonment, may enhance the understanding of changes in species composition and abiotic factors in relation to the occurrence of *E. repens* in other regions and/or on a geographically broader scale. This could give reason to suggest to apply the monitoring method elaborated here, also elsewhere.

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# Academic Curriculum Vitae

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since 07/2015	Member of the IAVS Young Scientists								
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11/2015 Coastal Ecology Workshop, Westerhever, Germany

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- 10/2013 **O**pen Landscapes, Hildesheim (Germany), member of the organizing team; talk

# List of publications

accepted	<b>Pätsch R</b> , Jašková A, Milan C, Kucherov IB, Schaminée JHJ, Bergmeier E, Janssen JAM. Making them visible and usable – vegetation-plot observations from Fennoscandia based on historical species quantity scales. <i>Applied Vegetation Science</i> .
accepted	<b>Pätsch R</b> , Schaminée JHJ, Janssen JAM, Hennekens SM, Bruchmann I, Jutila H, Meisert A, Bergmeier E. Between land and sea –a classification of saline and brackish grasslands of the Baltic Sea coast. <i>Phytocoenologia</i> .
2019	<b>Pätsch R</b> , Bruchmann I, Schellenberg J, Meisert A, Bergmeier E. <i>Elytrigia repens</i> co-occurs with glycophytes rather than characteristic halophytes in low-growing salt meadows on the southern Baltic Sea coast. <i>Biologia</i> 74: 385–394. https://doi.org/10.2478/s11756-019-00195-1
2018	<b>D</b> engler J, Wagner V, Dembicz I (, <b>Pätsch R,</b> ) et al. GrassPlot - a database of multi-scale plant diversity in Palaearctic grasslands. <i>Phytocoenologia</i> 48: 331–347. https://doi.org/10.1127/phyto/2018/0267
2018	Dengler J, Becker T, Heinken T, Kurzböck CM, <b>Pätsch R</b> . News from GrassVeg.DE, the German grassland vegetation database. <i>Palaearctic Grasslands</i> (former EDGG Bulletin) 37: 26–29. https://doi.org/10.21570/EDGG.PG.37.26-29 (editorial review)
2010	<b>Pätsch R</b> , Hentschel J, Linares-Palomino R, Zhu RL & Heinrichs J Diversification and taxonomy of the liverwort <i>Jubula</i> Dumort. ( <i>Jungermanniopsida: Porellales</i> ) inferred from nuclear and chloroplast DNA sequences. <i>Systematic Botany</i> . 35: 6–12. https://doi.org/10.2307/40540520

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## Appendix

## **Electronic version of the framework**

See attached CD-Rom.

## Supplementary material of study 1

### **S1-1 Literature sources**

Table S1-1-1 Inventoried studies which applied the scales of Norrlin, Hult-Sernander and Drude; the compilation does not claim completeness. We consulted the listed literature sources as references for our proposed scale transformations to mid-percentage values. Numbers of references relate to Fig. 1-1.

Species scales:	Used in the following studies:				
Norrlin scale	Finland: Häyrén (1914-1915); Brandt (1933); Lemberg (1946);				
	Brunberg-Schwanck & Barlund (1948); Skult (1956)				
	<u>Russia</u> : Lumiala (1937); Perttula (1949); CHARM (2002-2005);				
	Hannus & von Numers (2010)				
	<u>Sweden</u> : Palmgren (1912, 1961)				
Hult-Sernander scale	<u>Finland</u> : Ruuhijärvi (1960); Eurola (1962); Vartiainen (1980);				
	Singsaas (1989); Vuorinen et al. (2017)				
	Norway: Klokk (1981, 1982); Iversen (1984); Vevle (1985);				
	Galten (1987); Rosén (1988); Moen (1990); Losvik (1991, 1993);				
	Aarrestad (2000); Nilsen & Moen (2009)				
	<u>Sweden</u> : Du Rietz (1925); Almquist (1929); Krogerus (1932);				
	Dahlbeck (1945); Sjors (1948); Gjærevoll (1949); Gillner (1960);				
	Fransson (1963, 1972); Larsson (1967); Tyler (1968, 1971);				
	Nylander (1972); Maimer et al. (1978); Persson (1984); Cramer				
	& Hylleboll (1967), Transpational (within Econoscandia): Oksanon & Virtanon				
	(1995): Virtanen et al. (1999): Virtanen et al. (2006)				
Drude scale	<u>Finland:</u> Galanina & Heikkilä (2007)				
	<u>Russia</u> : Regel (1923, 1927, 1928); Konovalov (1928); Sokolov				
	(1928); Uskov (1930); Solonevich, K. (1933, 1936); Zinserling				
	(1933); Korovkin (1934); Bobrova & Kachurin (1935); Nekrasova				
	(1935, 1938); Avrorin et al. (1936); Blagoveshchenskii (1936);				
	Galkina (1936); Nikolsky & Izotov (1936); Salazkin (1936);				
	Sokolova (1936); Solonevich & Solonevich (1936); Lyubimova $(1027)$ Duckling $(1020)$ Management $(1070)$ Solo				
	(19537); Pusnkina (1938); Voropanov (1950); Solonevich (1963);				
	Neshatayev & Neshatayeva (1993)				

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## S1-2 Transformation of the Norrlin scale

Table S1-2-1 Hypothetical species covers for grades +, r, rr and 1–7 of the Norrlin scale. We assume that plant individuals are circular with a diameter of 3 cm, 20 cm, 50 cm and 100 cm, respectively. Distance measurements were taken from the edge of each hypothetical plant individual. The calculation is based on a 100 m<sup>2</sup> plot. Grade 1 and 2 of the Norrlin scale are merged into a single grade (used mean cover values are marked in bold).  $\bar{x}$  = arithmetic mean of minimum (min.) mean and maximum (max.) percentage species relative covers for each grade; calculations based on species with 3 cm diameter are excluded.

tween plant cm]		hy i	pothetic individua	al circular pl als: Ø = 20 cr	ant n	hypothetical circular planthypothetical circular plantindividuals: $\emptyset = 50$ cmindividuals: $\emptyset = 100$ cm								x		
Distance be individuals [	Grade	max. frequ.	min. cover [ %]	mean cover [ %]	max. cover [ %]	max. frequ.	min. cover [ %]	mean cover [ %]	max. cover [ %]	max. frequ.	min. cover [ %]	mean cover [ %]	max. cover [ %]	min. cover [ %]	mean cover [ %]	max. cover [ %]
	+, r.,															
-	rr.	1	0.00	0.02	0.03	1	0.00	0.10	0.20	1	0.00	0.39	0.79	0.0	0.2	0.3
914.4	1	4	0.03	0.08	0.13	2	0.20	0.29	0.39	2	0.79	1.18	1.57	0.3	0.5	0.7
475.2	2	4	0.13	0.13	0.13	2	0.39	0.39	0.39	2	1.57	1.57	1.57	0.7	0.7	0.7
182.88	3	25	0.13	0.46	0.79	25	0.39	2.65	4.91	16	1.57	7.07	12.57	0.7	3	6
91.44	4	81	0.79	1.67	2.54	49	4.91	7.26	9.62	25	12.57	16.10	19.63	6	8	11
45.72	5	225	2.54	4.81	7.07	100	9.62	14.63	19.64	49	19.63	29.06	38.48	11	16	22
15.24	6	784	7.07	15.85	24.63	225	19.64	31.91	44.18	64	38.48	44.37	50.27	22	31	40
2.54	7	1936	24.63	42.73	60.82	361	44.18	57.53	70.88	81	50.27	56.94	63.62	40	52	65

#### S1-3 Original description of the Drude scale.

Description of "Die Grade der Häufigkeit" ["The grades of commonness"] from Drude (1890), page 223–224:

"Den höchsten Grad der Häufigkeit erreichen die geselligen Pflanzen (plantae sociales, abgekürzt in Formationsskizzen soc.), von denen eine einzige Pflanzenart für sich allein eine ganze Formation zu bilden im stande ist. Kommt dies auch höchst selten vor - denn selbst im dürren Kiefernwald ist wenigstens der Boden noch mit anderen Pflanzen bedeckt und die Pilze fehlen nie, sind oft für einen Wald physiologisch notwendige Begleiter - so ragen doch oft einzelne Arten so über die anderen hervor, dass sie unbedingt in erste Linie zu stellen sind. Oder aber mehrere, unter sich ziemlich gleichmäßig gemischte Arten bilden zusammen einen geschlossenen Bestand, wie die Eiche mit Kiefer und Birke zusammen, und es werden als dann diese mehreren Arten als "unter sich sozial" zusammengefasst. - In dem Bestande gewisser Hauptarten besetzen häufig andere, diesem fremde Arten kleine Partien des Bodens selbständig allein, aber niemals in zusammenhängenden Strecken; die von mir angewendete, ursprünglich Grisebach entlehnte Bezeichnungsweise nennt diese Arten herden- oder truppweise angeschlossen (plantae gregariae, abgekürzt gr.), wie z. B. grosse Staudengruppen hie und da in einer sonst von fast reiner Grasnarbe gebildeten Bergwiese. - Nun folgen die nicht zusammenhängend eigene Strecken bedeckenden, sondern überall und zahlreich in vereinzelten Exemplaren zwischen die geselligen oder truppweise angeordneten Arten beigemischten Formationsglieder (plantae copiose intermixtae, abgekürzt cop.), wobei es sich empfielt, die abnehmenden Grade des häufigen Vorkommens In Beimischung mlt cop. 3, cop. 2 und cop. 1 zu unterscheiden. - Nur vereinzelt und sehr dünn gesäete, in grossen Zwischenräumen hie und da eingestreute (nicht mehr "beigemischte") Arten (plantae sparsae oder p. sporadice intermixtae, abgekürzt sp.) führen zu den ganz seltenen Formationsgliedern über, welche als "vereinzelt" (plantae solitariae, abgekürzt sol.) bezeichnet werden."

["The highest degree of abundance is reached by gregarious plants (*plantae sociales*, abbreviated in the formation sketches *soc*.), of which a single species is capable of forming an entire formation. Although this rarely happens - even in a dry pine forest at least the soil is covered with other plants and the fungi are never absent, they are often a physiological necessity in a forest individual species often rise above other species that way that they necessarily are to rank foremost. Or several, rather uniformly distributed species compose a closed stand, like oak with pine and birch admixed, which comprises these species as "sociable amongst themselves". Besides the main species of the stand there are other species, which occupy their own small parts of the ground, but never in a continuous cluster; the applied terminology, originally borrowed from Grisebach, addresses such species as associated in herds or troops (*plantae gregariae*, abbreviated *gr*.), such as for example patches of perennial herbs which are scattered here and there within a mountain meadow, which is otherwise almost entirely a grass-covered sward. –

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Next are the non-gregariously growing species which occur admixed everywhere and numerously as single plant individuals between the gregarious or patchy other plants of the formation (*plantae copiose intermixtae*, abbreviated *cop*.), whereby it is recommended to distinguish between decreasing degrees of abundance as *cop*. *3*, *cop*. *2* and *cop*. *1*. – Species which occur only sporadically and occasionally, scattered and distantly (not regularly "admixed"; *plantae sparsae* or *p. sporadice intermixtae*, abbreviated *sp*.) lead over to the very rare species of the formation, which are referred to as "isolated" (*plantae solitariae*, abbreviated *sol*.)."]

Reference: Drude, O. (1890). Handbuch der Pflanzengeographie. Stuttgart, DE: J. Engelhorn.

## Supplementary material of study 2

#### S2-1 Data sources.

Table S2-1-1 Data sources used for the final analysis. Most relevés are stored in and available via EVA.

TV3 database name	GIVD code	GIVD database name	Custodian	Deputy custodian	Relevés [n]	Citation
European Mire VDB	EU-00-022	European Mire Vegetation Database	Tomáš Peterka	Martin Jiroušek	1	1
Germany Coastal VDB	EU-DE-035	Coastal Vegetation Germany	Maike Isermann		124	
Germany_vegetweb2	EU-DE-013	VegetWeb Germany	Friedemann Goral	Florian Jansen	92	2
Germany_vegmv	EU-DE-001	VegMV	Florian Jansen	Christian Berg	1544	3
GrassVeg.DE	EU-DE-020	German Grassland Vegetation Database (GrassVeg.DE)	Jürgen Dengler	Ricarda Pätsch	33	4
Latvian Grassland VDB	EU-LV-001	Semi-natural Grassland Vegetation Database of Latvia	Solvita Rūsiņa		34	5
Lithuania	EU-LT-001	Lithuanian vegetation Database	Valerius Rašomavičius	Domas Uogintas	6	
Nordic_Baltic EDGG	EU-00-002	Nordic-Baltic Grassland Vegetation Database (NBGVD)	Jürgen Dengler	Łukasz Kozub	24	6
European Coastal Vegetation						
Database-A	EU-00-017	European Coastal Vegetation Database	John Janssen		1337	
Poland	EU-PL-001	Polish Vegetation Database	Zygmunt Kącki	Grzegorz Swacha	119	7
Russia_volga	EU-RU-002	Lower Volga Valley Phytosociological Database	Valentin Golub	Viktoria Bondareva	61	8

## Data not yet implemented in a

#### database

Data description	Data derived from	
Coastal Nordic grasslands	Dietbert Thannheiser	38
Coastal grasslands of Finland	Heli Jutila (partly non-published)	141
Coastal grasslands of Estonia	Niall Burnside	178
		sum: 3732

<sup>1</sup>Peterka T, Jiroušek M, Hájek M & Jiménez-Alfaro B 2015. European Mire Vegetation Database: a gap-oriented database for European fens and bogs. *Phytocoenologia* 45: 291–298.

<sup>2</sup>Jansen F, Ewald J & Jandt U 2015. vegetweb 2.0 – Neuauflage eines Vegetationsdatenportals für Deutschland. *Tuexenia* 35: 309–319.

<sup>3</sup>Jansen F, Dengler J & Berg C 2012. VegMV, The vegetation database of Mecklenburg-Vorpommern. *Biodiversity & Ecology* 4: 149–160.

<sup>4</sup>Dengler J, Becker T, Heinken T, Kurzböck C & Pätsch R 2018. News from GrassVeg.DE, the German grassland vegetation database. *Palaearctic Grasslands* 37: 26–29. <sup>5</sup>Rūsiņa S 2012. Semi-natural Grassland Vegetation Database of Latvia. In: Dengler J, Oldeland J, Jansen F, Chytrý M, Ewald J, Finckh M, Glöckler F, Lopez-Gonzalez G, Peet RK, Schaminée JHJ [eds.]: Vegetation databases for the 21st century. – *Biodiversity & Ecology* 4: 409–409. continued on next page

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<sup>6</sup> Dengler J & Rūsiņa S 2012. Database Dry Grasslands in the Nordic and Baltic Region. In: Dengler J, Oldeland J, Jansen F, Chytrý M, Ewald J, Finckh M. Glöckler F, Lopez-Gonzalez G, Peet RK, Schaminée JHJ [eds.]: *Vegetation databases for the 21st century.* – [Biodiversity & Ecology Vol. 4], pp. 319–320.
<sup>7</sup>Kącki Z & Śliwiński M 2012. The Polish Vegetation Database: structure, resources and development. *Acta Societatis Botanicorum Poloniae* 81(2): 75–79.
<sup>8</sup>Golub V, Sorokin A, Starichkova K, Nikolaychuk L, Bondareva V & Ivakhnova T 2012. Lower Volga Valley Phytosociological Database. In: Dengler J, Oldeland J, Jansen F, Chytrý M, Ewald J, Finckh M, Glöckler F, Lopez-Gonzalez G, Peet RK, Schaminée JHJ [eds.]: *Vegetation databases for the 21st century.* – [Biodiversity & Ecology Vol. 4], p. 419.

### S2-2 Data selection and reduction

Table S2-2-1 Detailed list of species for relevé selection (a) and exclusion (b). The type of vegetation, species lifeform or life-span aimed to be included or excluded is shown for all listed species.

(a): Relevés are included with a minimum of two species (min 2) to be present in one relevé or with a minimum of four species (min 4) to be present in one relevé.

Abbreviations of vegetation:

ag = adjacent grasslands Jm = Juncetea maritimi (class)

(b): Relevés are excluded if one or more than one of below named species achieves a (summed) cover > 3 %, > 25 % or > 75 %.

Abbreviations of vegetation:

ann = vegetation dominated by annual species
dom = dominant stands of single species
lig = lignified chamaephytes and phanerophytes
stra = strandline vegetation
wat = vegetation of water bodies

be-du = beach and dune vegetation
frin = wet meadow fringe vegetation
re-he = reed communities and helophytes
Ther = Thero-Salicornietea
wet = herb dominated wetland vegetation

2	۱
a	1

			Vegetation type aimed
Species	min 2	min 4	to be included
Agrostis stolonifera		$\checkmark$	ag
Argentina anserina		$\checkmark$	ag
Argentina anserina subsp. groenlandica		$\checkmark$	ag
Armeria alpina subsp. halleri	$\checkmark$	✓	Jm
Armeria maritima	$\checkmark$	$\checkmark$	Jm
Armeria maritima subsp. elongata	$\checkmark$	$\checkmark$	Jm
Artemisia maritima	$\checkmark$	✓	Jm
Blysmopsis rufa		✓	ag
Blysmus compressus		$\checkmark$	ag
Bolboschoenus maritimus		~	ag
Bupleurum tenuissimum	$\checkmark$	✓	Jm
Carex extensa	$\checkmark$	$\checkmark$	Jm
Cochlearia anglica	$\checkmark$	$\checkmark$	Jm
Cochlearia officinalis	$\checkmark$	$\checkmark$	Jm
Cochlearia officinalis agg.		$\checkmark$	ag
Eleocharis parvula		$\checkmark$	ag
Elytrigia repens		~	ag
(incl. Elytrigia repens subsp. littoreus)			
Elytrigia repens subsp. littoreus		$\checkmark$	ag
Festuca arenaria		~	ag
Festuca rubra		✓	ag
Festuca rubra agg.		~	ag
Festuca rubra subsp. litoralis		✓	ag
Glaux maritima	~	✓	Jm

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Salt grasslands along the	e Baltic Sea	coast – Appendix
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Juncus compressus		$\checkmark$	ag
Juncus compressus agg.		$\checkmark$	ag
Juncus gerardi	~	$\checkmark$	Jm
Leontodon saxatilis		$\checkmark$	ag
Limonium vulgare	✓	$\checkmark$	Jm
Lotus tenuis		$\checkmark$	ag
Parapholis strigosa	✓	$\checkmark$	Jm
Plantago major subsp. intermedia		$\checkmark$	ag
Plantago major subsp. winteri		$\checkmark$	ag
Plantago maritima	✓	$\checkmark$	Jm
Puccinellia capillaris	$\checkmark$	$\checkmark$	Jm
Puccinellia distans	✓	$\checkmark$	Jm
Puccinellia maritima	✓	$\checkmark$	Jm
Puccinellia nutkaensis	$\checkmark$	$\checkmark$	Jm
Rumex crispus		$\checkmark$	ag
Schedonorus arundinaceus		$\checkmark$	ag
Scorzoneroides autumnalis		$\checkmark$	ag
Spergularia marina	✓	$\checkmark$	Jm
Spergularia media	✓	$\checkmark$	Jm
Suaeda maritima	$\checkmark$	$\checkmark$	Jm
Trifolium fragiferum		$\checkmark$	ag
Trifolium repens		$\checkmark$	ag
Triglochin maritima	$\checkmark$	$\checkmark$	Jm
Tripolium pannonicum subsp. tripolium	$\checkmark$	$\checkmark$	Jm

## b)

,				Vegetation type, plant life-form or –span
Species	>3 %	>25 %	>75 %	aimed to be included
Acer platanoides	$\checkmark$			lig
Acer pseudoplatanus	$\checkmark$			lig
Acer species	$\checkmark$			Re
Achillea millefolium			$\checkmark$	dom
Agrostis capillaris			$\checkmark$	dom
Agrostis gigantea			$\checkmark$	dom
Agrostis vinealis			$\checkmark$	dom
Alnus glutinosa	$\checkmark$			lig
Alnus incana	$\checkmark$			lig
Atriplex littoralis		$\checkmark$		stra / ann
Atriplex prostrata		$\checkmark$		stra / ann
Betula pendula	$\checkmark$			lig
Betula pubescens	✓			lig
Betula species	$\checkmark$			lig
Bidens tripartitus		$\checkmark$		ann / wet

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Bolboschoenus maritimus		$\checkmark$		re-he
Cakile maritima	✓			be-du
Calamagrostis stricta		✓		re-he
Calluna vulgaris	✓			lig
Caltha palustris		$\checkmark$		wat
Calystegia sepium		$\checkmark$		re-he
Cornus suecida	✓			lig
Crataegus monogyna subsp. monogyna	✓			lig
Empetrum nigrum	✓			lig
Epilobium hirsutum			✓	dom
Erica tetralix	$\checkmark$			lig
Festuca ovina			✓	dom
Filipendula ulmaria		✓		frin
Frangula alnus	✓			lig
Frangula species	✓			lig
Fraxinus excelsior	✓			lig
Fraxinus species	✓			lig
Galeopsis bifida			✓	dom
Galium palustre		✓		frin
Galium verum			✓	dom
Hippophae rhamnoides	✓			lig
Honckenya peploides	✓			be-du
Hydrocotyle vulgaris		✓		re-he / wat
Juniperus communis	√			lig
Lathyrus palustris		✓		frin
Lepidium latifolium			✓	dom
Leymus arenarius	✓			be-du
Lysimachia vulgaris		$\checkmark$		frin
Lythrum salicaria		$\checkmark$		frin
Mentha aquatica		$\checkmark$		re-he
Myrica gale	✓			lig
Ononis spinosa			✓	dom
Oxybasis glauca		✓		ann / wet / stra / ann
Oxybasis rubra		$\checkmark$		ann / wet / stra / ann
Persicaria amphibia		$\checkmark$		wat
Phalaroides arundinaceus		$\checkmark$		re-he
Phragmites australis		$\checkmark$		re-he
Picea abies	$\checkmark$			lig
Picea abies subsp. abies	$\checkmark$			lig
Pinus sylvestris	✓			lig
Populus tremula	$\checkmark$			lig
Quercus robur	$\checkmark$			lig
Ranunculus peltatus subsp. baudotii	$\checkmark$			wat
Ranunculus sceleratus		✓		ann / wet

Rosa rugosa	$\checkmark$		lig
Rubus caesius	✓		lig
Rumex maritimus		$\checkmark$	ann / wet
Salicornia europaea		$\checkmark$	Ther / ann
Salicornia procumbens		$\checkmark$	Ther / ann
Salix aurita	✓		lig
Salix caprea	✓		lig
Salix cinerea	✓		lig
Salix herbacea	✓		lig
Salix lapponum	✓		lig
Salix myrsinifolia	✓		lig
Salix pentandra	✓		lig
Salix phylicifolia	✓		lig
Salix repens	✓		lig
Salix rosmarinifolia	✓		lig
Salix species	✓		lig
Salix starkeana	✓		lig
Salix viminalis	✓		lig
Sambucus nigra	✓		lig
Schoenoplectus lacustris		✓	re-he
Schoenoplectus tabernaemontani		$\checkmark$	re-he
Scirpus sylvaticus		$\checkmark$	re-he
Suaeda maritima		$\checkmark$	Ther / ann
Tanacetum vulgare		✓	frin
Typha latifolia		✓	re-he
Urtica dioica		$\checkmark$	frin
Valeriana officinalis		$\checkmark$	frin

**Table S2-2-2 Criteria for relevé selection and exclusion.** The initial dataset is based on an EVA questionnaire (S1\_Tab.1) and further requested data (after implementation partly delivered to EVA) from the Baltic Sea coast.

Criteria for relevé selection and exclusion	Number of relevés remained in the dataset
Distribution of data restricted to the Baltic Sea coast (extension refers to	
HELCOM Map and Data Service 2018)	9562
Selection of relevés belonging to the Juncetea maritimi and associated	
freshwater-influenced grassland communities	6511
Exclusion of lignified chamaephytes, shrubs and trees, dominant stands,	
strandline vegetation, annual dominated vegetation, annual wetland herb	
dominated vegetation, reed communities and helophytes, beach and dune	
vegetation, tall herb wet meadow fringe vegetation, vegetation of water	
bodies (regards single species abundances in relevés)	5610
Exclusion of beach and dune vegetation, reeds, annual dominated	
vegetation, lignified chamaephytes, shrubs and trees (regards summed	
abundances of species present in one relevé)	5546
Exclusion of relevés < 1 m <sup>2</sup> and > 80 m <sup>2</sup>	3844
Exclusion of relevés without ensured spatial connection to saline	
vegetation	3735
Relevés excluded because of species identification errors	<u>3732</u>

### **S2-3 Nomenclature particularities**

Table S2-3-1 List of taxa with names deviating from the ones used in the Euro+Med Plantbase (2006-2019).

Nomenclature [Euro+Med]	Used deviations in nomenclature
Calamagrostis neglecta	Calamagrostis stricta
Carex cuprina	Carex otrubae
Deschampsia cespitosa subsp. bottnica	Deschampsia bottnica
Festuca stricta subsp. trachyphylla	Festuca brevipila
Poa pratensis subsp. irrigata	Poa humilis
Rhinanthus angustifolius	Phinanthus constinue
Rhinanthus angustifolius subsp. angustifolius	Rhinanthus serotinus
Schoenoplectus lacustris subsp. glaucus	Schoenoplectus tabernaemontani
Sonchus maritimus	Sonchus arvensis

Table S2-3-2 List of taxon names found in databases, which have been transferred and incorporated in used species (group) concepts.

Species (group)	Included taxa
Armeria maritima	Armeria maritima subsp. elongata
	Armeria vulgaris subsp. intermedia
	Armeria maritima subsp. maritima
Atriplex prostrata	Atriplex calotheca
	Atriplex hastata subsp. salina
	Atriplex prostrata aggr.
Carex canescens aggr.	Carex brunnescens
Cerastium holosteoides	Cerastium fontanum
	Cerastium fontanum subsp. vulgare
Festuca rubra	Festuca rubra aggr.
	Festuca rubra subsp. litoralis
	Festuca rubra subsp. rubra
Galium mollugo aggr.	Galium album
	Galium mollugo
Heracleum sphondylium	Heracleum sphondylium subsp. sibiricum
	Heracleum sphondylium subsp. sphondylium
Leucanthemum vulgare aggr.	Leucanthemum ircutianum
	Leucanthemum vulgare
Odontites litoralis	Odontites verna
	Odontites verna subsp. litoralis
Ononis spinosa	Ononis spinosa subsp. hircina
	Ononis spinosa subsp. procurrens
Parapholis strigosa	Parapholis filiformis
	Parapholis incurva
Plantago major	Plantago major subsp. intermedia
	Plantago major subsp. major
	Plantago major subsp. winteri
Polygonum aviculare aggr.	Polygonum aviculare subsp. neglectum
	Polygonum depressum
	Polygonum rurivagum
Salicornia europaea aggr.	Salicornia appressa
	Salicornia europaea
	Salicornia procumbens
	Salicornia species
Taraxacum sect. Taraxacum	Taraxacum aequilobum
	Taraxacum copidophyllum
Taraxacum sect. Palustria	Taraxacum balticum
	Taraxacum palustre

## S2-4 Shifts in synoptic tables

Table S2-4-1 Manual changes in the synoptic tables after the TWINSPAN classification. Re-allocations were made only if (i) the differentiation of the cluster by differential species constancy values was improved and (ii) the silhouette value of clusters remained consistent ( $\rightarrow$ ) or was enhanced ( $\uparrow$ ).

sub	-gro	ups	Number of relevés with re-allocation	Silhouette value before re-allocation	Silhouette value after re-allocation	Trend of Silhouette value
4	$\rightarrow$	5	4			
5	$\rightarrow$	4	10			
				4: 0.22	4: 0.22	$\rightarrow$
				5: 0.0002	5: 0.06	$\uparrow$
5	$\rightarrow$	3	1		·	·
				5: 0.06	5: 0.06	$\rightarrow$
				8: -0.05	8: -0.05	$\rightarrow$
8	$\rightarrow$	3	1		·	·
				1: 0.001	1:0.003	$\uparrow$
				8: -0.05	8: -0.05	$\rightarrow$

			Number of relevés	Silhouette value before	Silhouette value after	Trend of
sut	o-gro	ups	with re-allocation	re-allocation	re-allocation	Silhouette value
1	$\rightarrow$	7	4			
				1: -0.002	1:0.01	$\uparrow$
				3: 0.04	3: 0.04	$\rightarrow$
8	$\rightarrow$	10	1			
				2:0.08	2:0.09	$\uparrow$
				12:0.04	12: 0.04	$\rightarrow$
8	$\rightarrow$	6	1			
				2: 0.09	2:0.1	$\uparrow$
				5: -0.02	5: -0.02	$\rightarrow$
7	$\rightarrow$	6	1			
				3: 0.04	3: 0.04	$\rightarrow$
				5: -0.02	5: -0.02	$\rightarrow$
2	$\rightarrow$	4	3			
				7: 0.04	7: 0.05	$\uparrow$
				8: -0.08	8: -0.08	$\rightarrow$
4	$\rightarrow$	1	1			
				8: -0.08	8: -0.08	$\rightarrow$
				1:0.01	1:0.01	$\rightarrow$
4	$\rightarrow$	7	2			
				8: -0.08	8: -0.07	$\uparrow$
				3: 0.04	3: 0.05	$\uparrow$
4	$\rightarrow$	5	7			
				8: -0.07	8: -0.07	$\rightarrow$
				4: 0.13	4:0.13	$\rightarrow$

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4	$\rightarrow$	3	21			
				8: -0.07	8: -0.07	$\rightarrow$
				6: 0.19	6: 0.2	$\uparrow$
13	$\rightarrow$	12	2			
				10: 0.05	10: 0.05	$\rightarrow$
				9: -0.03	9: -0.03	$\rightarrow$
12	$\rightarrow$	4	1			
				9: -0.03	9: -0.03	$\rightarrow$
				8: -0.07	8: -0.07	$\rightarrow$
5	$\rightarrow$	10	1			
				4: 0.13	4:0.14	$\uparrow$
				12:0.04	12:0.04	$\rightarrow$
			Number of relevés	Silhouette value before	Silhouette value after	Trend of
sut	o-gro	ups	with re-allocation	re-allocation	re-allocation	Silhouette value
5	$\rightarrow$	9	2			-
				8: -0.06	8: -0.04	$\uparrow$
				3: -0.04	3: -0.04	$\rightarrow$
4	$\rightarrow$	5	1			
				9: 0.05	9: 0.05	$\rightarrow$
				8: -0.04	8: -0.04	$\rightarrow$
1	$\rightarrow$	2	1			
				11:0.07	11: 0.07	$\rightarrow$
				10: -0.007	10: -0.007	$\rightarrow$
3	$\rightarrow$	4	18			
				12: -0.004	12:0.002	$\uparrow$
				9: 0.05	9: 0.08	$\uparrow$
4	$\rightarrow$	8	2		-	<u>.</u>
				9: 0.08	9: 0.09	$\uparrow$
				6: 0.05	6: 0.05	$\rightarrow$

Table S2-4-2 Removal of thirty-two relevés from five different sub-groups which turned out to be geographicaloutliers lacking differential species of the respective clusters.

Sub-group	Number of
	removed relevés
M1G1S3	7
M1G2S7	6
M2G5S12	4
M2G5S13	1
M3G3S6	14

### S2-5 Synoptic tables

Table S2-5-1 Combined synoptic table of classified saline and brackish plots (relevés) of the first main cluster (M1). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009). Frequency values of species with frequency values < 20 % are listed below the table.

Group - Sub-group	G1S1	G1S2	G1S3	G1S4	G1S5	G2S6	G2S7	G2S8
Number of relevés	24	64	125	40	109	48	15	120
Average species number	8.8	6.7	9.6	4.6	6.8	7.1	8.7	8.0
Limonium vulgare	<b>75</b> <sup>73</sup>	5	17 <sup>5.5</sup>	0	0	0	0	0
Armeria maritima	<b>67</b> <sup>63</sup>	0	22 11	0	2	0	7	0
Parapholis strigosa	<b>54</b> <sup>65</sup>	0	2	0	0	0	7	0
Halimione pedunculata	33 <sup>45</sup>	11 8.4	1	0	1	0	0	0
Suaeda maritima	8	<b>39</b> <sup>34</sup>	12 1.4	10	0	0	0	18 <sup>8.1</sup>
Glaux maritima	<b>50</b> <sup>1.4</sup>	31	<b>88</b> <sup>30</sup>	35	<b>50</b> <sup>1.8</sup>	42	47	42
Festuca rubra	17 <sup>8.8</sup>	3	<b>35</b> <sup>32</sup>	3	$11^{1.6}$	2	7	1
Juncus ranarius	0	0	6 <sup>1</sup>	0	1	29 <sup>38</sup>	0	10 6.8
Puccinellia phryganodes	0	0	0	0	0	0	<b>80</b> 88	0
Triglochin palustris	0	0	2	0	15 <sup>0.3</sup>	21 <sup>6.9</sup>	<b>67</b> <sup>56</sup>	11
Juncus bufonius	4	3	0	0	0	10 8.3	13 <sup>13</sup>	13 <sup>12</sup>
Atriplex prostrata	4	31 <sup>2.6</sup>	<b>39</b> <sup>9.3</sup>	18	32 <sup>3.3</sup>	21	20	<b>60</b> <sup>27</sup>
Phragmites australis	4	2	6	10	21 <sup>10</sup>	10	13 <sup>1.1</sup>	33 <sup>23</sup>
Argentina anserina subsp. anserina	0	0	2	0	5	0	13 <sup>14</sup>	20 <sup>26</sup>
Triglochin maritima	46	<b>56</b> <sup>5.7</sup>	<b>70</b> <sup>16</sup>	<b>85</b> <sup>28</sup>	42	35	33	22
Bolboschoenus maritimus	4	9	27 <sup>0.8</sup>	<b>50</b> <sup>20</sup>	<b>65</b> <sup>33</sup>	10	0	<b>44</b> <sup>15</sup>
Puccinellia distans	13	27	20	13	1	<b>98</b> <sup>45</sup>	<b>87</b> <sup>36</sup>	<b>64</b> <sup>19</sup>
Plantago major	0	2	2	0	1	25 <sup>29</sup>	0	22 <sup>23</sup>
Spergularia media	<b>71</b> <sup>42</sup>	66 <sup>38</sup>	<b>40</b> <sup>15</sup>	0	8	0	0	3
Puccinellia maritima	<b>88</b> <sup>31</sup>	<b>84</b> <sup>29</sup>	<b>86</b> <sup>29</sup>	8	<b>85</b> <sup>29</sup>	8	0	16
Salicornia europaea	<b>67</b> <sup>23</sup>	<b>67</b> <sup>23</sup>	<b>55</b> <sup>14</sup>	0	15	6	<b>67</b> <sup>23</sup>	22
Plantago maritima	<b>71</b> <sup>22</sup>	<b>50</b> <sup>6.4</sup>	<b>87</b> <sup>35</sup>	10	16	38	<b>53</b> <sup>8.9</sup>	9

Juncus gerardi	<b>88</b> <sup>29</sup>	20	<b>84</b> <sup>26</sup>	15	41	<b>58</b> <sup>6.5</sup>	<b>73</b> <sup>18</sup>	18
Spergularia marina	13	53	<b>59</b> <sup>4.1</sup>	10	39	<b>83</b> <sup>22</sup>	<b>80</b> <sup>20</sup>	<b>94</b> <sup>31</sup>
Agrostis stolonifera	17	14	<b>62</b> <sup>7.7</sup>	35	<b>83</b> <sup>23</sup>	<b>67</b> <sup>11</sup>	<b>73</b> <sup>16</sup>	<b>67</b> <sup>11</sup>
Tripolium pannonicum subsp. tripolium	<b>67</b> <sup>2.9</sup>	<b>83</b> <sup>16</sup>	<b>80</b> <sup>13</sup>	<b>95</b> <sup>25</sup>	<b>83</b> <sup>15</sup>	31	0	<b>66</b> <sup>2.2</sup>

Achillea millefolium G2S7: 7, G2S8: 1; Agrostis gigantea G1S5: 2, Agrostis vinealis G1S3: 4, Alopecurus geniculatus G1S3: 1, G1S5: 5, G2S6: 19, G2S8: 8; Artemisia maritima G1S2: 3, G1S3: 9, G1S5: 2, G2S8: 1; Artemisia vulgaris G2S8: 1; Atriplex littoralis G1S2: 5, G1S3: 11, G1S4: 5, G1S5: 8, G2S6: 2, G2S8: 13; Atriplex longipes G1S2: 2, G1S4: 3, G1S5: 3. Atriplex patula G1S2: 2. G2S6: 2. G2S8: 3: Bassia hirsuta G1S2: 3. Blvsmopsis rufa G1S3: 1. G1S5: 1. Blvsmus compressus G2S6: 2. Bupleurum tenuissimum G1S1: 4. G2S7: 7, Calamagrostis epigejos G2S8: 1; Calamagrostis stricta G2S7: 7, Carex extensa G1S3: 8, G1S4: 5, G1S5: 4, Carex alareosa G2S7: 27, Carex leporina G1S5: 1, Centaurium littorale G1S3: 2, Centaurium pulchellum G1S3: 6, Chenopodium album G1S3: 1, G2S8: 1; Cirsium arvense G1S4: 3, G1S5: 1, G2S8: 2; Cirsium vulgare G2S6: 2, Cochlearia analica G1S3: 3. G1S4: 15. G1S5: 6. G2S8: 1: Cochlearia danica G1S3: 1. G1S4: 3. Cochlearia officinalis G1S5: 1. Cotula coronopifolia G1S3: 1. G1S5: 6. G2S8: 1: Deschampsia bottnica G1S4: 5, G2S6: 2, Eleocharis acicularis G2S6: 8, Eleocharis palustris G1S4: 3, G2S8: 3; Eleocharis parvula G1S3: 2, G2S8: 3; Eleocharis uniqlumis G1S4: 8, G1S5: 5, G2S6: 8, G2S7: 7, G2S8: 5; Elytriaia repens G1S3: 4, G1S4: 8, G1S5: 2, G2S6: 4, G2S7: 7, G2S8: 17; Elytriaia x laxa G1S3: 2, G1S5: 2, Eriaeron canadensis G2S8: 1; Eupatorium cannabinum G1S4: 3, Galium palustre G2S8: 1; Holcus lanatus G2S6: 2, Juncus articulatus G2S6: 6, G2S7: 7, G2S8: 1; Juncus balticus G2S7: 7, Juncus compressus G2S8: 1; Juncus maritimus G1S3: 3, G1S5: 3, Lepidium latifolium G1S4: 3, Leymus arenarius G2S8: 1; Lolium perenne G2S6: 6, G2S7: 7, Lotus tenuis G1S3: 2, G2S8: 1; Lysimachia vulgaris G2S8: 1; Matricaria chamomilla G2S8: 1; Matricaria discoidea G1S5: 1, G2S8: 2; Melilotus albus G2S6: 2, Myosurus minimus G2S8: 1; Ochlopoa annua G1S2: 2, G2S6: 10, G2S8: 2; Odontites litoralis G1S1: 4, G1S3: 1, G1S4: 3, G1S5: 2, G2S6: 2, Oenanthe lachenalii G1S5: 2, G2S8: 1; Oxybasis alauca G1S3: 5, G2S6: 2, G2S8: 17; Oxybasis rubra G2S8: 7: Persicaria amphibia G2S8: 1: Phalaroides arundinacea G1S4: 3. Plantago arenaria G2S8: 1: Plantago coronopus G1S1: 4. G1S3: 2. G2S7: 7. G2S8: 1: Poa humilis G1S5: 1, G2S8: 1; Poa palustris G2S8: 1; Poa pratensis G2S6: 2, Poa trivialis G2S6: 2, Polygonum aviculare aggr. G1S3: 3, G2S6: 13, G2S8: 9; Polygonum oxyspermum G2S8: 1; Potentilla reptans G2S8: 1; Puccinellia nutkaensis G2S6: 2, G2S7: 13, Ranunculus flammula G1S5: 1, Ranunculus peltatus subsp. baudotii G1S4: 3, Ranunculus sceleratus G2S8: 10; Rumex crispus G1S5: 2, G2S8: 5; Saging maritima G1S1: 4, G1S3: 5, Saging procumbens G1S5: 1, G2S8: 1; Samolus valerandi G1S5: 1, Schedonorus arundinaceus G1S3: 1, G2S8: 7; Schoenoplectus tabernaemontani G1S5: 3, G2S6: 4, G2S8: 5; Scorzoneroides autumnalis G1S3: 1, G2S6: 2, G2S7: 7, G2S8: 2; Sedum sexangulare G2S7: 7, Senecio vulgaris G2S8: 1; Sisymbrium altissimum G2S8: 1; Sonchus arvensis G2S8: 1; Trifolium fragiferum G2S6: 4, G2S8: 2; Trifolium hybridum G2S8: 1; Trifolium pratense G2S6: 2, Trifolium repens G1S3: 2, G2S6: 6, G2S8: 1; Tripleurospermum maritimum G2S8: 2; Tussilago farfara G2S8: 1; Vicia sativa subsp. nigra G2S8: 1

Table S2-5-2 Combined synoptic table of classified saline and brackish plots (relevés) of the second main cluster (M2). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009). Frequency values of species with frequency values < 20 % are listed below the table.

Group - Sub-group	G1S1	G1S2	G2S3	G2S4	G3S5	G3S6	G3S7	G3S8	G4S9	G4S10	G4S11	G5S12	G5S13			
Number of relevés	87	54	163	548	24	250	50	42	272	73	107	38	91			
Average species number	8.0	9.6	7.6	8.0	11.6	11.9	12.3	12.1	10.0	15.0	10.1	10.9	11.8			
Elytrigia repens	<b>87</b> <sup>59.2</sup>	6	1	11	0	<i>28</i> <sup>11.1</sup>	26 <sup>9.2</sup>	14	11	0	6	0	1			
Cochlearia anglica	22 34.6	11 <sup>15.3</sup>	1	1	0	0	0	0	0	0	0	0	0			
Limonium vulgare	5	<b>81</b> <sup>83</sup>	5	1	0	2	0	0	0	0	0	0	0			
Puccinellia maritima	0	31 <sup>37.6</sup>	18 <sup>19.4</sup>	4	0	2	0	0	1	0	1	0	0			
Spergularia media	6 <sup>3.9</sup>	22 30.4	12 14.4	3	0	1	0	0	0	0	0	0				
Sagina maritima	1	2	1	2	<b>83</b> <sup>84.7</sup>	3	0	2	0	0	0	0	0			
Carex extensa	1	7	7	12 <sup>1.2</sup>	<b>83</b> <sup>68.7</sup>	5	4	0	2	14 <sup>3.1</sup>	1	0	0			
Centaurium pulchellum	0	0	9	4	<b>79</b> <sup>69.6</sup>	5	6	0	1	7	3	0	5			
Plantago coronopus	0	0	1	2	<b>71</b> <sup>75.9</sup>	5	4	0	1	0	0	0	0			
Juncus maritimus	2	6	1	5	8	2	<b>70</b> <sup>64.2</sup>	0	4	8	2	0	0			
Oenanthe lachenalii	6	0	0	5	0	6	<b>68</b> <sup>62.7</sup>	0	3	10 1.4	9 <sup>1.2</sup>	0	0			
Schedonorus arundinaceus	9 <sup>4.7</sup>	0	1	3	4	15 <sup>12.3</sup>	22 <sup>21</sup>	2	7 <sup>1.9</sup>	1	1	0	4			
Inula britannica	1	0	1	0	0	2	22 <sup>32.6</sup>	0	1	11 <sup>13.7</sup>	0	0	0			
Molinia caerulea	0	0	0	1	0	1	0	<b>48</b> <sup>65.5</sup>	1	0	1	0	0			
Carex panicea	0	0	0	1	0	2	0	<b>43</b> <sup>51.5</sup>	1	16 <sup>15.8</sup>	0	0	0			
Taraxacum sect. Taraxacum	0	0	0	0	4 1	4 0.1	0	<b>36</b> <sup>50.3</sup>	1	1	0	0	0			
Trifolium pratense	0	0	1	1	0	5 <sup>0.5</sup>	10 <sup>7</sup>	<b>36</b> <sup>41.7</sup>	4	7 2.8	0	0	0			
Carex flacca	0	0	0	0	0	2 0.3	0	21 <sup>41.8</sup>	1	0	0	0	0			
Peucedanum palustre	0	0	1	0	0	0	4 <sup>2</sup>	21 <sup>32.1</sup>	0	0	0	8 <sup>8.7</sup>	3 <sup>0.7</sup>			
Blysmopsis rufa	0	0	1	2	13 <sup>3.3</sup>	3	0	5	6	<b>81</b> <sup>71.7</sup>	2	5	2			
Poa humilis	0	0	2	1	0	15 <sup>12.7</sup>	4	0	12 <sup>8.3</sup>	27 <sup>28.4</sup>	1	0	7 <sup>1.7</sup>			
Schoenoplectus tabernaemontani	1	0	0	3	0	2	6 <sup>0</sup>	0	5	11 <sup>6.1</sup>	<b>36</b> <sup>37.1</sup>	13 <sup>8.8</sup>	0			
Samolus valerandi	0	0	0	2	0	1	0	0	2	1	28 44.5	0	1			
Carex mackenziei	0	0	0	1	0	2	0	0	0	4	6	<b>74</b> <sup>76.3</sup>	3			

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Carex halophila	0	0	1	1	0	0	0	0	1	5 <sup>2.8</sup>	1	<b>37</b> <sup>50.9</sup>	3
Carex glareosa	0	0	4	2	0	3	0	0	1	8 4.1	0	26 <sup>28</sup>	22 22.2
Carex paleacea	0	0	1	2	0	1	0	0	1	0	0	29 44.1	7 6.1
Lysimachia thyrsiflora	0	0	1	0	0	0	0	0	0	0	0	24 44.2	2 0.3
Eriophorum angustifolium	0	0	1	1	0	0	0	0	1	0	0	24 <sup>43.5</sup>	2 0.2
Argentina anserina subsp. groenlandica	0	0	2	7 5.1	0	0	0	0	1	0	2	24 32.4	9 <sup>8.6</sup>
Parnassia palustris	0	0	0	2	0	4	0	0	1	4	0	$13 \ ^{10.2}$	<b>45</b> <sup>51.5</sup>
Pedicularis palustris	0	0	0	1	0	1	0	0	0	0	0	16 18.2	32 42.6
Artemisia maritima	<b>43</b> <sup>33.9</sup>	<b>61</b> <sup>52.6</sup>	2	2	4	3	2	0	0	0	0	0	0
Atriplex prostrata	<b>59</b> <sup>35.8</sup>	24 <sup>7.7</sup>	2	15 <sup>0.5</sup>	8	8	24 <sup>7.6</sup>	0	9	5	30 12.4	3	3
Bolboschoenus maritimus	30 16.9	0	10	16 4.5	8	10	8	2	9	8	<b>46</b> <sup>31.4</sup>	0	0
Lotus tenuis	0	0	6	3	0	25 <sup>22.5</sup>	30 <sup>28.8</sup>	0	7 <sup>1.5</sup>	8 <sup>2.5</sup>	1	0	0
Odontites litoralis	0	2	6	7	0	18 <sup>6</sup>	6	<b>48</b> <sup>32.2</sup>	7	14 <sup>1.8</sup>	0	8	<b>37</b> <sup>23</sup>
Juncus articulatus	0	0	0	3	4	4	0	5	10 <sup>3.5</sup>	<b>40</b> <sup>36.5</sup>	22 <sup>17.1</sup>	0	4
Carex nigra	0	0	1	1	0	4	0	19 <sup>9.1</sup>	8	<b>36</b> <sup>25.2</sup>	3	<b>37</b> <sup>26.4</sup>	18 <sup>7.7</sup>
Calamagrostis stricta	0	0	5	7	0	2	0	0	2	3	1	<b>84</b> <sup>56</sup>	<b>91</b> 61.6
Armeria maritima	9	<b>63</b> <sup>44.5</sup>	33 <sup>18.3</sup>	6	25 11.1	14 <sup>1.8</sup>	8	0	0	1	0	0	0
Centaurium littorale	0	0	2	3	<b>42</b> <sup>26.2</sup>	10	12	<b>38</b> <sup>23</sup>	3	<b>44</b> <sup>28.1</sup>	0	0	3
Trifolium repens	0	0	1	4	17 <sup>3.4</sup>	<b>43</b> <sup>26.4</sup>	18 4.6	2	27 <sup>12.6</sup>	<b>44</b> <sup>27</sup>	4	3	2
Trifolium fragiferum	0	0	4	6	8	28 <sup>16.3</sup>	8	0	30 <sup>17.9</sup>	<b>48</b> <sup>34.4</sup>	8	0	0
Plantago major	5	0	2	6	17 <sup>7.4</sup>	16 <sup>6.7</sup>	8	0	21 <sup>11.3</sup>	23 <sup>14</sup>	21 12.2	0	1
Carex distans	0	0	1	3	<b>38</b> <sup>19.5</sup>	17 <sup>2.7</sup>	34 <sup>16.6</sup>	<b>38</b> <sup>20</sup>	2	<b>47</b> <sup>27.1</sup>	3	0	0
Scorzoneroides autumnalis	5	2	12	10	8	<b>74</b> <sup>31.6</sup>	<b>38</b> <sup>7.7</sup>	<b>69</b> <sup>28.1</sup>	31 <sup>3</sup>	<b>48</b> <sup>14.2</sup>	4	3	<b>37</b> <sup>7.3</sup>
Galium palustre	1	0	2	3	0	8	24 <sup>7.5</sup>	26 <sup>9.3</sup>	6	21 4.7	27 <sup>10</sup>	32 <sup>13.6</sup>	<b>43</b> <sup>22.8</sup>
Eleocharis uniglumis	0	0	6	7	0	10	0	0	<b>39</b> <sup>10.9</sup>	<b>52</b> <sup>19.8</sup>	<b>72</b> <sup>33.5</sup>	<b>66</b> <sup>29.3</sup>	<b>49</b> <sup>18.1</sup>
Triglochin palustris	0	0	1	5	4	8	0	0	28 <sup>9.7</sup>	<b>44</b> <sup>22.7</sup>	32 <sup>13.1</sup>	<b>50</b> <sup>27.6</sup>	30 11.4
Tripolium pannonicum subsp. tripolium	<b>53</b> <sup>18.9</sup>	<b>72</b> <sup>31.9</sup>	<b>49</b> <sup>16.4</sup>	<b>41</b> <sup>11</sup>	8	11	34 <sup>6.3</sup>	0	7	0	<b>45</b> <sup>13.6</sup>	0	0
Plantago maritima	28	<b>93</b> <sup>20.5</sup>	<b>99</b> <sup>24.4</sup>	<b>61</b> <sup>2.1</sup>	42	<b>82</b> <sup>14.3</sup>	<b>72</b> <sup>8.4</sup>	<b>95</b> <sup>22</sup>	31	<b>66</b> <sup>4.8</sup>	3	13	<b>64</b> <sup>3.6</sup>
Phragmites australis	23	2	5	<b>35</b> <sup>0.7</sup>	29	<b>38</b> <sup>2.4</sup>	<b>58</b> <sup>14.6</sup>	10	<b>41</b> <sup>4.1</sup>	<b>38</b> <sup>2.6</sup>	<b>59</b> <sup>15.1</sup>	<b>45</b> <sup>6.5</sup>	<b>60</b> <sup>16.1</sup>
Triglochin maritima	17	<b>78</b> <sup>9.8</sup>	<b>67</b> <sup>3.7</sup>	57	17	<b>70</b> 5.5	46	<b>90</b> <sup>17.4</sup>	<b>78</b> <sup>10.2</sup>	<b>89</b> <sup>16.5</sup>	<b>71</b> <sup>5.8</sup>	<b>76</b> <sup>9</sup>	37

Argentina anserina subsp. anserina	33	0	2	12	33	<b>67</b> <sup>16.5</sup>	<b>66</b> <sup>16</sup>	<b>52</b> <sup>7.9</sup>	<b>63</b> <sup>14.1</sup>	<b>78</b> <sup>23.1</sup>	<b>53</b> <sup>8.5</sup>	3	<b>44</b> <sup>2.9</sup>
Festuca rubra	<b>85</b> <sup>10.3</sup>	<b>96</b> <sup>17.3</sup>	<b>71</b> <sup>1.3</sup>	61	<b>96</b> <sup>17</sup>	<b>96</b> <sup>16.9</sup>	<b>90</b> <sup>13.4</sup>	<b>90</b> <sup>13.7</sup>	53	58	12	21	60
Glaux maritima	56	<b>74</b> <sup>2.4</sup>	<b>83</b> <sup>8.3</sup>	<b>83</b> <sup>8.2</sup>	<b>79</b> <sup>5.6</sup>	<b>83</b> <sup>8.2</sup>	<b>84</b> <sup>8.7</sup>	<b>71</b> <sup>0.7</sup>	<b>71</b> <sup>0.4</sup>	<b>88</b> <sup>11</sup>	56	11	<b>74</b> <sup>2.1</sup>
Agrostis stolonifera	62	<b>81</b> <sup>0.5</sup>	64	<b>89</b> <sup>6</sup>	<b>88</b> <sup>4.9</sup>	<b>89</b> <sup>5.8</sup>	<b>90</b> <sup>6.7</sup>	67	<b>95</b> <sup>10.5</sup>	<b>93</b> <sup>9</sup>	<b>87</b> <sup>4.5</sup>	61	<b>86</b> <sup>3.6</sup>
Juncus gerardi	57	<b>91</b> <sup>5.5</sup>	<b>96</b> <sup>9.8</sup>	<b>92</b> <sup>6.4</sup>	<b>88</b> <sup>2.9</sup>	<b>94</b> <sup>8.3</sup>	64	67	<b>96</b> <sup>9.3</sup>	<b>95</b> <sup>8.4</sup>	53	<b>97</b> <sup>10.7</sup>	<b>99</b> <sup>11.9</sup>

Achillea millefolium G1S1: 3, G2S3: 1, G2S4: 1, G3S5: 4, G3S6: 5, G3S7: 18, G4S9: 1, G4S10: 1; Achillea ptarmica G4S9: 1; Acorus calamus G4S9: 1; Agrostis canina G3S6: 1, G5S12: 16, G5S13: 2; Agrostis capillaris G3S6: 1, G3S7: 4, G4S10: 1, G5S13: 2; Agrostis gigantea G2S4: 2, G3S6: 2, G3S7: 6, G4S9: 2, G4S11: 5, G5S13: 10; Agrostis vinealis G1S1: 6, G2S3: 2, G2S4: 1; Allium schoenoprasum G2S3: 1, G2S4: 1, G3S6: 1, G3S8: 2, G4S9: 1; Alnus alutinosa G2S3: 1, G5S13: 4; Alnus incana G2S4: 1, G5S13: 2; Alopecurus arundinaceus G2S4: 1. G3S6: 1. G4S9: 1. G4S11: 3: Alopecurus aeniculatus G1S1: 1. G2S3: 1. G2S4: 2. G3S6: 1. G4S9: 11. G4S11: 11: Ammophila arenaria G3S5: 4: Angelica archangelica subsp. litoralis G2S3: 1, G2S4: 1, G3S6: 1, G4S9: 1; Angelica palustris G3S6: 1; Angelica sylvestris G3S6: 1, G3S8: 2, G4S9: 1, G5S13: 4; Anthoxanthum odoratum G3S6: 1; Apium araveolens G1S1: 1, G3S5: 4, G4S10: 1, G4S11: 5; Arenaria serpyllifolia G2S4: 1; Arrhenatherum elatius G4S9: 1; Artemisia vulgaris G3S6: 1; Atriplex littoralis G1S1: 11, G1S2: 2, G2S4: 3, G3S6: 1, G4S9: 1; Atriplex longipes G1S1: 2, G2S4: 1, G3S5: 13, G4S9: 1; Atriplex patula G1S1: 1, G2S4: 1, G4S11: 2; Atriplex praecox G2S4: 1; Bellis perennis G2S4: 1, G3S6: 3, G4S9: 1, G4S10: 1, G4S11: 2; Betula pubescens G3S6: 1, G5S13: 2; Bidens frondosus G4S9: 1; Bidens tripartitus G4S9: 1; Blysmus compressus G3S6: 2, G4S9: 2; Briza media G3S6: 1, G3S8: 5; Bromus hordeaceus G3S6: 2; Bromus racemosus G4S9: 1; Bupleurum tenuissimum G1S2: 4, G2S3: 2, G2S4: 1, G3S6: 4, G3S7: 2; Cakile maritima G3S7: 2; Calamagrostis canescens G3S7: 2; Calamagrostis epigejos G3S6: 1, G4S9: 1, G5S13: 1; Calammophila baltica G2S4: 1, G3S5: 8, G3S7: 2; Calla palustris G4S11: 2; Callitriche hermaphroditica G5S12: 3; Caltha palustris G2S4: 1, G4S9: 2, G4S11: 3, G5S12: 11, G5S13: 3; Calystegia sepium G3S6: 1, G3S7: 2, G4S9: 1; Cardamine pratensis G4S11: 12, G5S13: 1; Carex acuta G4S9: 1; Carex acutiformis G4S11: 1; Carex aquatilis G5S12: 21; Carex canescens aggr. G5S12: 3, G5S13: 5; Carex demissa G3S6: 1, G3S7: 2, G4S10: 10, G4S11: 1; Carex disticha G1S1: 1, G2S4: 1, G3S6: 1, G4S9: 1, G4S10: 1; Carex hirta G2S4: 1; Carex leporina G3S6: 1; Carex otrubae G1S1: 5, G2S4: 1, G3S6: 1, G3S7: 2, G4S9: 3, G4S11: 3; Carex pilulifera G2S4: 1, G3S6: 1, G3S8: 5, G4S9: 1, G4S10: 14; Carex recta G2S3: 1, G3S6: 1, G4S9: 1; Carex viridula G2S4: 1, G3S6: 1, G3S8: 7, G4S9: 1, G4S10: 19, G5S13: 4; Carex vulpina G3S6: 1, G4S9: 3, G4S11: 1; Carum carvi G4S9: 1; Centaurea jacea G2S4: 1, G3S6: 1, G3S7: 14, G3S8: 5, G4S9: 5, G4S11: 1; Centaurium erythraea G2S3: 1, G2S4: 5, G3S7: 4, G3S8: 10, G4S9: 1; Cerastium holosteoides G2S4: 1, G3S5: 17, G3S6: 2, G4S9: 1. G4S10: 1: Cerastium semidecandrum G3S5: 8: Chenopodium album G3S6: 1: Cicuta virosa G5S12: 11: Cirsium arvense G2S4: 3. G3S5: 4. G3S6: 1. G3S7: 4. G4S9: 1: Cirsium palustre G4S9: 1; Cochlearia danica G1S1: 6, G1S2: 4, G2S3: 1, G3S6: 1; Cochlearia officinalis G1S1: 1, G2S4: 1, G3S6: 1; Comarum palustre G5S12: 11, G5S13: 4; Cotula coronopifolia G4S9: 1: Dactvlis alomerata G4S9: 1: Danthonia decumbens G3S6: 1. G3S8: 2. G4S10: 10: Deschampsia bottnica G2S4: 1. G4S9: 1. G4S11: 3. G5S13: 3: Deschampsia cespitosa G1S1: 1, G2S4: 1, G3S6: 1, G4S9: 3, G4S10: 10, G5S13: 3; Elatine triandra G4S9: 1; Eleocharis acicularis G2S4: 1, G4S11: 2, G5S13: 2; Eleocharis palustris G2S3: 2, G2S4: 3, G3S6: 4, G3S8: 19, G4S9: 12, G4S11: 4, G5S12: 16, G5S13: 1; Eleocharis parvula G4S11: 1; Eleocharis quinqueflora G2S4: 1, G3S5: 4, G3S6: 2, G3S8: 2, G4S9: 1, G4S10: 15, G5S13: 1; Elytrigia atherica G3S6: 2; Elytrigia juncea G3S7: 2; Elytrigia x laxa G1S1: 1, G2S4: 1, G3S6: 1, G3S7: 2; Empetrum nigrum G2S3: 1, G2S4: 1; Epilobium palustre G4S9: 1, G5S12: 11, G5S13: 3; Equisetum arvense G3S5: 4, G4S9: 1, G5S13: 2; Equisetum fluviatile G3S6: 1; Equisetum palustre G2S4: 1, G3S5: 4, G3S6: 1, G4S9: 1; Eriophorum latifolium G4S9: 1; Eupatorium cannabinum G4S10: 4; Euphrasia bottnica G5S12: 5; Euphrasia stricta G2S3: 1, G3S6: 1; Festuca arenaria G2S4: 1, G3S8: 2, G4S9: 1; Festuca oving G2S4: 1, G3S6: 1; Festuca polesica G2S4: 1; Filipendula ulmaria G2S3: 1, G2S4: 1, G3S6: 2, G4S9: 1, G5S12: 3, G5S13: 15; Fraxinus excelsior G3S6: 1; Galium trifidum G2S4: 1, G3S8: 2, G4S9: 1; Galium uliginosum G3S6: 1, G4S10: 4; Galium verum G2S4: 1, G3S6: 1, G3S7: 2, G3S8: 2; Gentianella uliginosa G2S4: 1; Glechoma hederacea G2S4: 1; Glyceria maxima G4S9: 1; Hieracium umbellatum G2S3: 1, G4S9: 1; Hierochloe odorata G1S1: 1, G3S6: 1, G3S8: 2, G5S13: 1; Hippophae rhamnoides G2S3: 1. G2S4: 1. G5S13: 1: Hippuris tetraphylla G5S12: 3: Hippuris vulaaris G4S11: 1. G5S12: 8: Holcus lanatus G3S6: 2. G4S9: 1. G4S11: 1: Holcus mollis G4S9: 1; Honckenya peploides G1S1: 2, G3S5: 8, G3S7: 2; Hordeum secalinum G4S9: 1; Hydrocotyle vulgaris G2S4: 1, G3S6: 1, G3S7: 2, G4S9: 1, G4S10: 19, G4S11: 2; continued on next page

Juncus alpinoarticulatus G4S9: 1, G4S10: 1, G5S13: 4; Juncus bufonius G2S3: 1, G2S4: 1, G3S6: 2, G4S9: 2, G4S10: 3, G4S11: 1, G5S13: 1; Juncus compressus G1S2: 2, G2S4: 1, G3S6: 2, G4S9: 4, G4S11: 1; Juncus effusus G4S9: 1, G4S11: 1; Juncus filiformis G4S11: 1, G5S12: 3, G5S13: 1; Juncus ranarius G2S4: 1, G3S6: 1, G3S7: 2, G4S9: 4, G4S11: 5; Juniperus communis G3S8: 10, G4S11: 1; Lathyrus palustris G2S4: 1, G5S12: 16, G5S13: 15; Lathyrus pratensis G3S7: 4, G4S9: 1; Lemna minor G4S11: 1, G5S12: 3; Lemna trisulca G5S12: 5; Leontodon saxatilis G2S4: 1, G4S10: 4; Lepidium latifolium G1S1: 6, G2S4: 1; Leymus arenarius G2S4: 1, G3S6: 1, G5S13: 1; Linum catharticum G3S8: 10, G4S10: 7; Lolium perenne G1S1: 1, G2S4: 1, G3S6: 4, G4S9: 1, G4S11: 1; Lotus corniculatus G2S4: 1, G3S6: 3, G3S7: 2, G3S8: 2, G4S9: 2, G4S10: 1; Lotus maritimus G3S6: 1, G3S7: 6, G3S8: 7, G4S9: 1; Lotus pedunculatus G3S6: 3, G3S8: 5; Lycopus europaeus G4S9: 1; Lysimachia nummularia G4S9: 1; Lysimachia vulgaris G3S7: 2, G3S8: 2, G4S9: 2, G4S10: 4, G4S11: 2; Lythrum salicaria G2S3: 1, G2S4: 1, G3S6: 1, G4S9: 3, G4S11: 2, G5S13: 1; Matricaria discoidea G1S1: 1, G2S4: 1; Medicago lupulina G3S6: 1; Melilotus albus G2S4: 1, G4S9: 1; Melilotus dentatus G2S3: 1, G3S6: 1; Mentha aquatica G1S1: 1, G2S4: 1, G3S6: 1, G3S7: 12, G4S9: 1, G4S10: 1, G4S11: 15; Montia fontana G4S9: 1, G5S12: 3; Myosotis scorpioides G2S4: 1, G3S8: 2, G4S9: 3, G4S11: 11; Myrica gale G5S13: 1; Myriophyllum spicatum G5S12: 3; Ochlopoa annua G3S6: 1, G4S9: 1, G5S12: 3; Odontites vulgaris G1S1: 1, G2S4: 1, G3S6: 1, G3S7: 2, G4S9: 1, G4S10: 3, G4S11: 1; Ononis spinosa G3S6: 1; Ophioglossum vulgatum G2S3: 1, G2S4: 1, G3S6: 4, G3S7: 10, G3S8: 10. G4S9: 1. G4S10: 7. G4S11: 2. G5S13: 1: Oxybasis alauca G4S9: 1: Oxybasis urbica G4S9: 1: Parapholis striaosa G1S2: 13. G2S3: 9. G2S4: 1. G3S6: 2: Persicaria amphibia G3S6: 1, G4S9: 2; Persicaria maculosa G4S9: 1; Petasites spurius G3S7: 2; Phalaroides arundinacea G2S3: 2, G2S4: 1, G3S6: 1, G3S8: 2, G4S9: 2, G4S11: 1; Phleum pratense G3S6: 1; Pinus sylvestris G3S8: 5, G5S13: 1; Plantago lanceolata G2S4: 1, G3S6: 1, G3S7: 2, G4S9: 1, G4S10: 1; Poa palustris G4S9: 1; Poa pratensis G1S1: 3, G2S3: 1, G2S4: 2, G3S6: 17, G3S7: 2, G4S9: 13, G4S10: 8, G4S11: 1, G5S12: 8, G5S13: 1; Poa trivialis G1S1: 1, G2S4: 1, G3S6: 2, G4S9: 1, G4S11: 4; Polygala amarella G2S4: 1, G3S8: 5; Polyaonum aviculare aggr. G1S1: 3, G2S4: 1, G3S6: 1, G4S9: 1, G4S9: 1, G4S11: 1; Potentilla erecta G3S8: 2; Potentilla reptans G2S4: 1, G3S6: 1, G4S9: 1; Primula nutans G2S4: 1, G4S9: 1, G4S10: 1, G5S12: 16, G5S13: 8; Prunella vulgaris G3S8: 2; Puccinellia distans G1S1: 3, G1S2: 15, G2S3: 2, G2S4: 5, G3S6: 2, G4S9: 5, G4S10: 1, G4S11: 5, G5S12: 5, G5S13: 1; Puccinellia nutkaensis G2S3: 1, G2S4: 1, G3S6: 1, G4S9: 1, G4S10: 1, G4S11: 1, G5S13: 2; Puccinellia phryganodes G2S3: 1, G2S4: 3, G4S9: 1, G4S11: 2, G5S13: 3; Ranunculus acris G2S4: 1, G3S6: 1, G5S13: 1; Ranunculus flammula G2S4: 1, G4S11: 1; Ranunculus peltatus subsp. baudotii G4S11: 1; Ranunculus repens G2S4: 1, G4S9: 1; Ranunculus reptans G4S11: 1; Ranunculus sardous G3S6: 1, G4S10: 1; Ranunculus sceleratus G2S4: 1, G3S6: 1, G4S9: 1, G4S9: 1, G4S11: 7; Rhinanthus minor G3S8: 2, G5S13: 1; Rhinanthus serotinus G2S4: 1, G3S6: 1, G3S8: 7, G5S13: 7: Rosa rugosa G3S5: 4: Rubus saxatilis G5S13: 1: Rumex crispus G1S1: 8, G2S4: 1, G3S5: 13, G3S6: 3, G3S7: 2, G4S9: 3, G4S11: 9, G5S13: 1; Rumex hydrolapathum G4S9: 1, G4S11: 18; Rumex maritimus G4S9: 1; Sagina nodosa G2S3: 1, G2S4: 1, G3S5: 13, G3S6: 3, G3S8: 5, G4S9: 1, G4S10: 7, G5S13: 3: Saging procumbens G2S4: 1. G3S5: 17. G3S6: 2. G3S8: 2. G4S9: 1. G4S10: 14: Salicornia europaeg G1S2: 4. G2S3: 2. G2S4: 3. G3S6: 1: Salix phylicifolia G2S4: 1. G4S9: 1, G5S12: 13, G5S13: 3; Salix repens G5S12: 11; Schedonorus pratensis G3S6: 1, G4S9: 4; Schoenoplectus lacustris G2S4: 1, G3S8: 2, G4S9: 2, G4S11: 4; Schoenus niaricans G3S6: 1: Sedum acre G2S4: 1: Sedum sexanaulare G3S6: 1: Serratula tinctoria G3S7: 4: Silene flos-cuculi G4S9: 1. G4S10: 7: Sium latifolium G4S9: 1. G4S11: 15: Sonchus arvensis G1S1: 8, G1S2: 4, G2S3: 1, G2S4: 3, G3S5: 8, G3S6: 4, G3S7: 10, G3S8: 19, G4S9: 1, G4S11: 3, G5S12: 5, G5S13: 10; Sonchus asper G1S1: 1; Sonchus oleraceus G1S1: 1, G3S6: 1, G3S7: 10, G4S10: 1; Sonchus palustris G2S4: 1; Spergula arvensis G2S4: 1; Spergularia marina G1S1: 3, G1S2: 4, G2S3: 7, G2S4: 8, G3S6: 5, G4S9: 11, G4S10: 3, G4S11: 14, G5S12: 13, G5S13: 3; Stachys palustris G3S6: 1; Suaeda maritima G1S1: 1, G1S2: 2, G2S3: 2, G2S4: 1, G4S11: 1; Subularia aquatica G5S12: 3; Succisa pratensis G3S6: 1, G4S9: 1; Tanacetum vulgare G2S4: 1, G3S6: 1, G4S9: 1; Taraxacum sect. Palustria G2S4: 1, G3S5: 4, G3S6: 2, G3S8: 10, G4S9: 1; Trifolium dubium G4S10: 4; Tripleurospermum inodorum G3S5: 4, G4S11: 1; Tripleurospermum maritimum G1S1: 3, G2S4: 1, G3S6: 2; Typha angustifolia G4S11: 6; Valeriana excelsa G2S4: 1, G3S6: 1, G5S13: 8; Valeriana officinalis G3S6: 1, G4S9: 1, G4S9: 1, G4S11: 1; Veronica beccabunga G4S9: 1; Veronica lonaifolia G3S6: 1; Vicia cracca G1S1: 5, G2S3: 1, G2S4: 1, G3S5: 4, G3S6: 5, G3S7: 18. G3S8: 7. G4S9: 3. G5S13: 3: Vulpia unilateralis G2S4: 1: Zannichellia palustris G5S12: 3

Table S2-5-3 Combined synoptic table of classified saline and brackish plots (relevés) of the third main cluster (M3). Standardised fidelity ( $\phi$ -coefficient) is superscripted next to related frequencies per sub-group (constancy in percent). Species with frequency values  $\geq 20$  % are included; frequencies  $\geq 35$  % are written in bold letters. Grey shaded cells specify positive and italic numbers specify positive-negative differential taxa (Tsiripidis et al. 2009). Frequency values of species with frequency values < 20 % are listed below the table.

Group - Sub-group	G1S1	G1S2	G2S3	G2S4	G3S5	G3S6	G4S7	G4S8	G5S9	G5S10	G6S11	G6S12
Number of relevés	68	66	277	56	55	121	44	58	76	135	170	230
Average species number	18.4	17.1	15	16.3	13	11.4	14.3	15.3	14.4	20.4	20.3	18.4
Filipendula ulmaria	<b>79</b> <sup>69.1</sup>	18 <sup>8</sup>	1	0	4	0	0	9	0	7	0	4
Parnassia palustris	<b>60</b> 66.9	15 <sup>10.9</sup>	1	0	0	0	0	0	0	0	0	0
Lathyrus palustris	<b>54</b> <sup>71.5</sup>	0	1	0	0	0	0	0	0	1	0	0
Poa humilis	<b>53</b> <sup>34.7</sup>	18 4.1	22 <sup>7.5</sup>	20 5.4	4	1	14 <sup>0.1</sup>	9	7	13	1	3
Calamagrostis stricta	<b>46</b> <sup>57</sup>	6 1.7	1	0	4	0	0	2	0	0	0	0
Angelica sylvestris	<b>43</b> <sup>59.7</sup>	2	1	0	0	0	0	2	0	1	0	0
Rhinanthus serotinus	<b>38</b> <sup>52</sup>	8 5.3	1	2	0	0	0	0	0	1	0	0
Eriophorum angustifolium	29 <sup>45.4</sup>	8 7.7	1	0	0	0	0	0	0	0	0	0
Valeriana excelsa	24 44.5	2	1	0	0	0	0	0	0	0	0	0
Comarum palustre	21 40.4	3 <sup>2.3</sup>	0	0	0	0	0	0	0	0	0	0
Odontites litoralis	21 <sup>20.5</sup>	8 <sup>3</sup>	16 14.7	0	2	1	5	0	9 <sup>5.2</sup>	3	0	0
Carex panicea	3	30 34.6	10 6.4	0	0	0	0	2	0	15 <sup>13.3</sup>	1	1
Galium uliginosum	4 <sup>2</sup>	20 <sup>27.9</sup>	2	0	0	0	76	0	0	5 <sup>3.3</sup>	0	1
Lotus pedunculatus	0	20 22.6	9 <sup>6.3</sup>	0	0	1	0	9 <sup>6.3</sup>	0	9 <sup>6.7</sup>	1	5 <sup>1.2</sup>
Molinia caerulea	0	21 <sup>32.3</sup>	3	0	0	0	0	7 <sup>6.9</sup>	0	5 <sup>3.9</sup>	0	0
Carex distans	0	3	24 <sup>22.9</sup>	16 <sup>13</sup>	2	1	0	12 <sup>7.9</sup>	8 2.5	4	0	2
Hordeum secalinum	0	0	0	<b>66</b> <sup>77.8</sup>	0	0	0	0	0	3	0	1
Inula britannica	0	0	7	<b>41</b> <sup>33.7</sup>	9 <sup>0.1</sup>	5	14 <sup>4.9</sup>	14 <sup>5</sup>	1	16 <sup>6.9</sup>	1	1
Bolboschoenus maritimus	0	2	6	5	27 <sup>18.2</sup>	15 <sup>5.5</sup>	20 11.2	3	1	2	16 <sup>6.5</sup>	16 <sup>6.7</sup>
Spergularia marina	0	0	2	4	24 <sup>30.8</sup>	8 6.8	0	0	1	1	0	7 4.1
Artemisia maritima	0	0	2	2	2	24 <sup>35.2</sup>	0	2	8 7.9	0	0	0
Atriplex littoralis	1	0	0	0	4 <sup>3</sup>	20 36.4	0	0	1	0	0	0
Persicaria amphibia	1	6 <sup>1.9</sup>	1	4	4	1	23 <sup>25.5</sup>	3	0	3	0	12 <sup>9.9</sup>
Angelica archangelica subsp. litoralis	0	2	1	0	0	2	20 <sup>35</sup>	2	0	2	0	1
Carex vulpina	0	0	5 <sup>0.6</sup>	11 <sup>8.8</sup>	4	3	20 22.8	0	0	0 cont	0 inued on r	12 <sup>10.9</sup> Text page

Festuca rubra	<b>97</b> <sup>11.5</sup>	<b>91</b> <sup>6.6</sup>	<b>89</b> <sup>4.9</sup>	<b>91</b> <sup>6.7</sup>	60	<b>87</b> <sup>3.3</sup>	77	<b>98</b> <sup>12.5</sup>	<b>92</b> <sup>7.5</sup>	<b>89</b> <sup>5</sup>	81	39
Oenanthe lachenalii	0	3	8 0.5	7	5	7	16 <sup>10.2</sup>	34 <sup>31.9</sup>	0	5	0	1
Valeriana officinalis	0	8 6.8	3	0	0	0	0	29 <sup>42.6</sup>	0	1	0	0
Agrostis gigantea	9 <sup>3.4</sup>	6	5	2	0	5	7 <sup>0.9</sup>	26 <sup>24.9</sup>	1	10 4.5	1	3
Galium verum	0	5	4	0	4	3	7 <sup>1.3</sup>	22 <sup>21.5</sup>	13 <sup>9.5</sup>	11 6.9	0	0
Armeria maritima	0	0	15 <sup>8.7</sup>	7	4	3	0	0	<b>57</b> <sup>57.1</sup>	2	0	0
Cerastium semidecandrum	0	0	1	0	4	2	0	0	<b>39</b> 55	1	0	0
Bupleurum tenuissimum	0	0	5 <sup>3.4</sup>	0	2	2	0	0	25 <sup>40.3</sup>	0	0	0
Rumex acetosella	1	0	1	0	0	0	0	0	25 <sup>37.6</sup>	8 8.6	2	1
Cochlearia danica	0	0	1	0	0	2	5 <sup>3.8</sup>	0	22 <sup>38</sup>	0	0	0
Bromus hordeaceus	0	0	1	4	2	1	2	0	20 25.4	7 5.8	0	9 <sup>7.8</sup>
Plantago lanceolata	0	9 <sup>0.4</sup>	4	2	4	2	2	2	20 11.7	<b>44</b> <sup>38.1</sup>	4	13 <sup>5</sup>
Rumex acetosa	12 4.7	11 <sup>3.4</sup>	1	9 <sup>1.5</sup>	2	0	0	3	5	33 <sup>29.2</sup>	1	14 <sup>7.6</sup>
Anthoxanthum odoratum	6	12 6.1	6	9 <sup>2.3</sup>	0	0	0	2	9 <sup>2.6</sup>	32 <sup>29.5</sup>	0	8 <sup>1</sup>
Dactylis glomerata	0	2	0	0	2	1	2	3	4	25 <sup>30.3</sup>	0	14 14.5
Galium mollugo aggr.	0	2	1	0	0	0	0	5 <sup>4</sup>	4 1.8	23 <sup>35.7</sup>	0	1
Potentilla reptans	0	0	4	4	4	7 1.7	14 <sup>9.4</sup>	14 <sup>9.6</sup>	0	22 20.2	0	5
Stellaria graminea	3	5 <sup>1.7</sup>	1	2	2	1	0	0	8 7.1	20 <sup>26.9</sup>	0	2
Lathyrus pratensis	0	9 <sup>6.7</sup>	2	0	0	1	11 <sup>10</sup>	7 <sup>3.5</sup>	0	20 22.6	0	4
Schedonorus pratensis	0	15	6	13	0	1	11	7	0	33 <sup>13.9</sup>	<b>90</b> <sup>60.1</sup>	20 <sup>3</sup>
Juncus articulatus	0	14	10	7	2	0	0	2	0	1	<b>98</b> <sup>72.9</sup>	<b>35</b> <sup>18.1</sup>
Phleum pratense	1	3	1	2	4	0	0	2	0	12 0.7	<b>88</b> <sup>73.9</sup>	21 <sup>9.7</sup>
Juncus bufonius	4	0	1	4	7	2	0	2	0	0	<b>81</b> <sup>74.4</sup>	11 1.6
Juncus effusus	0	8	2	5	2	1	0	3	0	7	<b>76</b> <sup>63.5</sup>	27 <sup>15.2</sup>
Juncus conglomeratus	0	8 1.6	1	2	0	0	0	3	0	6	<b>52</b> 56.7	3
Lolium multiflorum	0	0	0	0	0	0	0	0	1	1	<b>51</b> 66.5	2
Eleocharis uniglumis	12 <sup>3.6</sup>	12 4	16 <sup>8.5</sup>	0	4	1	2	0	0	0	<b>36</b> <sup>29.8</sup>	18 10.7
Juncus compressus	0	0	5 <sup>1.9</sup>	0	2	0	2	0	0	1	29 <sup>40.3</sup>	7 4.3
Glyceria declinata	0	0	0	0	0	0	0	0	0	0	29 50.4	2
Persicaria maculosa	0	0	0	0	2	0	0	0	0	0	24 40.9	4 <sup>3.6</sup>
Trifolium hybridum	0	0	0	0	2	0	0	0	0	1	24 43.2	1

Sagina procumbens	7 2.6	5	8 <sup>2.9</sup>	0	2	2	0	0	9 <sup>5</sup>	1	21 <sup>20.2</sup>	11 7.2
Bellis perennis	0	2	8 2.4	16 <sup>13.3</sup>	7 <sup>2</sup>	2	2	0	7 1.1	4	0	22 <sup>20.7</sup>
Galium palustre	<b>66</b> <sup>37.9</sup>	<b>70</b> <sup>40.7</sup>	6	4	7	2	20 <sup>2</sup>	24 4.9	0	5	2	9
Peucedanum palustre	<b>35</b> <sup>33.3</sup>	18 <sup>13.2</sup>	2	0	0	0	0	28 24.2	0	1	0	0
Ophioglossum vulgatum	10 4	20 15.1	4	0	0	2	7	22 <sup>18.4</sup>	4	14 <sup>8.5</sup>	0	0
Deschampsia cespitosa	21 <sup>9.7</sup>	24 <sup>13.3</sup>	3	20 8.8	7	1	2	5	4	30 18.5	1	10
Atriplex prostrata	1	0	4	7	<b>35</b> <sup>19.6</sup>	<b>61</b> <sup>43.6</sup>	14 <sup>0.7</sup>	10	8	6	0	8
Tripolium pannonicum subsp. tripolium	0	0	5	4	20 16.7	30 <sup>28.6</sup>	14 <sup>8.8</sup>	2	1	0	0	3
Sonchus arvensis	10 0.5	5	8	0	9	18 8.4	25 <sup>15.3</sup>	<b>36</b> <sup>26.7</sup>	1	6	0	0
Centaurea jacea	0	6	7	20 7.4	0	0	11	<b>59</b> 43.9	4	33 <sup>20.2</sup>	0	1
Trifolium pratense	7	29 <sup>7.3</sup>	25 4.4	21 <sup>1.7</sup>	13	1	9	26 5.1	7	<b>46</b> <sup>20.4</sup>	34 11.4	13
Poa trivialis	0	6	4	25 <sup>4.7</sup>	5	2	20 1.2	2	5	12	<b>88</b> <sup>52.9</sup>	<b>57</b> <sup>29</sup>
Alopecurus geniculatus	3	3	6	13	18 <sup>1.7</sup>	1	0	0	1	2	<b>86</b> <sup>57.2</sup>	<b>61</b> <sup>36.7</sup>
Ranunculus repens	6	11	4	5	5	2	20 4.6	0	1	13	<b>60</b> <sup>37.9</sup>	<b>53</b> <sup>31.7</sup>
Polygonum aviculare aggr.	1	0	1	2	11 <sup>5</sup>	7	5	0	8 1.3	4	23 <sup>19.4</sup>	20 15.4
Carex nigra	<b>93</b> <sup>52.2</sup>	<b>73</b> <sup>37.6</sup>	18	2	0	0	5	7	0	19	33 <sup>8.4</sup>	10
Agrostis stolonifera	<b>91</b> <sup>13.8</sup>	<b>79</b> <sup>5.7</sup>	82 <sup>8</sup>	<b>93</b> <sup>14.9</sup>	<b>95</b> <sup>16</sup>	54	57	50	34	69	60	<b>79</b> <sup>5.9</sup>
Agrostis capillaris	<b>43</b> <sup>24.7</sup>	6	5	5	2	3	2	2	<b>50</b> <sup>31.1</sup>	<b>36</b> <sup>18.6</sup>	1	15 <sup>1</sup>
Triglochin maritima	10	30 13.7	<b>35</b> <sup>17.5</sup>	<b>41</b> <sup>23</sup>	11	3	18 <sup>3.3</sup>	16 <sup>1</sup>	1	1	1	5
Glaux maritima	9	27 <sup>10.7</sup>	<b>38</b> <sup>20</sup>	21 <sup>5.7</sup>	27 <sup>10.7</sup>	20 4.3	16 <sup>1</sup>	10	3	0	1	4
Plantago maritima	24 <sup>1.6</sup>	27 <sup>4.3</sup>	<b>61</b> <sup>29.1</sup>	<b>46</b> <sup>18.4</sup>	11	21 <sup>0.1</sup>	2	16	33 <sup>8.4</sup>	13	0	2
Lotus tenuis	0	3	30 <sup>16.1</sup>	18 5.1	24 <sup>10.3</sup>	4	0	7	7	16 <sup>3.6</sup>	34 <sup>20</sup>	6
Holcus lanatus	0	17	16	<b>50</b> <sup>19.3</sup>	2	7	14	17	16	<b>74</b> <sup>36.5</sup>	12	<b>53</b> <sup>21.2</sup>
Plantago major	7	11	29 <sup>1</sup>	<b>39</b> <sup>8.3</sup>	29 <sup>1.4</sup>	24	16	9	3	15	<b>92</b> 43.9	<b>53</b> <sup>17.3</sup>
Schedonorus arundinaceus	<b>37</b> <sup>0.9</sup>	8	18	<b>39</b> <sup>2.5</sup>	35	<b>47</b> <sup>7.4</sup>	<b>95</b> <sup>37.9</sup>	<b>78</b> <sup>26.7</sup>	13	40 <sup>3</sup>	0	14
Cirsium arvense	3	0	6	21 <sup>3</sup>	15	<b>49</b> <sup>24.6</sup>	<b>36</b> <sup>14.8</sup>	24 <sup>5.2</sup>	8	28 <sup>8.3</sup>	2	19 <sup>1.2</sup>
Vicia cracca	15	20	12	7	5	8	<b>41</b> <sup>14.7</sup>	<b>67</b> <sup>34.1</sup>	16	<b>53</b> <sup>23.3</sup>	4	6
Lolium perenne	0	0	9	20 0.9	11	3	0	0	34 <sup>12.2</sup>	17	<b>75</b> <sup>44.1</sup>	<b>53</b> <sup>26.5</sup>
Cerastium holosteoides	13	11	15	29 <sup>3.9</sup>	4	17	11	9	<b>67</b> <sup>31.5</sup>	<b>41</b> <sup>13.2</sup>	16	<b>44</b> <sup>15.2</sup>
Ranunculus acris	<b>53</b> <sup>19.4</sup>	<b>41</b> <sup>11</sup>	14	<b>45</b> <sup>13.6</sup>	5	3	20	22	4	<b>59</b> <sup>23.8</sup>	3	30 <sup>3.7</sup>
Phraamites australis	<b>35</b> <sup>3.3</sup>	23	32 <sup>0.9</sup>	29	<b>44</b> <sup>8.7</sup>	29	<b>57</b> <sup>17.4</sup>	<b>69</b> <sup>25.3</sup>	5	27	1	14

Trifolium fragiferum	0	2	<b>47</b> <sup>19.8</sup>	18	31 <sup>8</sup>	2	2	3	12	7	<b>92</b> <sup>53.7</sup>	27 5.4
Juncus gerardi	<b>60</b> <sup>18.2</sup>	<b>50</b> <sup>11.6</sup>	<b>74</b> <sup>27.3</sup>	<b>66</b> <sup>22</sup>	<b>49</b> <sup>11</sup>	13	11	17	12	13	1	18
Scorzoneroides autumnalis	<b>60</b> <sup>14.3</sup>	<b>55</b> <sup>10.7</sup>	<b>66</b> <sup>18.1</sup>	<b>64</b> <sup>16.8</sup>	36	6	32	17	<b>43</b> <sup>3.8</sup>	23	10	35
Poa pratensis	10	17	39	<b>66</b> <sup>14.6</sup>	<b>45</b> <sup>2</sup>	28	32	12	<b>68</b> <sup>16</sup>	<b>51</b> <sup>5.4</sup>	<b>75</b> <sup>20.2</sup>	<b>63</b> <sup>12.5</sup>
Achillea millefolium	3	11	16	<b>46</b> <sup>7.8</sup>	13	<b>39</b> <sup>3</sup>	<b>45</b> <sup>7.2</sup>	<b>72</b> <sup>24.3</sup>	<b>62</b> <sup>17.6</sup>	<b>76</b> <sup>26.8</sup>	4	23
Rumex crispus	3	0	3	18	<b>36</b> <sup>7.1</sup>	<b>41</b> <sup>10.5</sup>	<b>64</b> <sup>25.8</sup>	7	16	33 <sup>4.5</sup>	<b>51</b> <sup>17.3</sup>	<b>40</b> <sup>9.9</sup>
Trifolium repens	35	<b>56</b> <sup>2.8</sup>	<b>71</b> <sup>11.9</sup>	<b>68</b> <sup>9.9</sup>	47	12	5	10	<b>72</b> <sup>12.6</sup>	<b>56</b> <sup>2.5</sup>	<b>99</b> <sup>28.6</sup>	<b>86</b> <sup>20.6</sup>
Argentina anserina subsp. anserina	<b>79</b> <sup>2.6</sup>	<b>82</b> <sup>4.2</sup>	<b>81</b> <sup>3.8</sup>	<b>96</b> <sup>14.5</sup>	<b>82</b> <sup>4.2</sup>	<b>77</b> <sup>0.8</sup>	<b>93</b> <sup>12.2</sup>	<b>90</b> <sup>9.8</sup>	28	76	59	67
Elytrigia repens	18	15	43	<b>95</b> <sup>17.3</sup>	<b>87</b> <sup>12.5</sup>	<b>93</b> <sup>16.5</sup>	66	<b>97</b> <sup>18.5</sup>	<b>80</b> <sup>8</sup>	<b>77</b> <sup>5.9</sup>	<b>80</b> <sup>7.8</sup>	64

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G2S3: 2, G2S4: 2, G3S6: 1, G4S7: 2, G4S8: 2, G5S10: 4, G6S12: 1: Ononis spinosa G2S3: 6, G2S4: 2, G3S6: 10, G4S8: 3, G5S9: 3, G5S10: 6, G6S12: 1: Onopordum acanthium G5S9: 1; Ornithopus perpusillus G5S9: 1; Oxybasis glauca G3S5: 4, G3S6: 1, G6S12: 1; Parapholis strigosa G3S5: 2; Pedicularis palustris G1S1: 15, G2S3: 1; Persicaria lapathifolia G2S4: 2, G3S5: 4, G4S7: 2, G4S8: 2, G6S11: 1, G6S12: 3; Persicaria minor G6S11: 2; Petasites friaidus G1S1: 1; Phalaroides arundinacea G1S1: 3, G2S3: 2, G2S4: 5, G3S5: 4, G5S10: 1, G6S12: 10; Picea abies G1S1: 1; Picris hieracioides G5S10: 1; Pilosella lactucella G1S2: 2; Pilosella officinarum G3S6: 1, G5S9: 5, G5S10: 2; Pimpinella saxifraga G2S3: 1, G4S8: 3, G5S9: 1, G5S10: 8; Pinquicula vulgaris G1S2: 2, G2S3: 1; Pinus sylvestris G1S1: 9, G1S2: 2, G5S10: 1; Plantago coronopus G2S3: 15, G3S5: 2, G3S6: 6, G5S9: 17; Plantago media G6S11: 14, G6S12: 1; Poa anaustifolia G5S10: 7; Poa nemoralis G1S1: 1; Poa palustris G5S10: 1, G6S12: 1; Polyaala amarella G1S2: 2; Polyaala vulaaris G2S4: 2: Polyaonum oxyspermum G2S3: 1. G3S6: 2: Potentilla analica G5S10: 1: Potentilla araentea G1S1: 1. G5S9: 1. G5S10: 1: Potentilla erecta G1S2: 11. G2S3: 1. G4S8: 9. G5S10: 8; Primula farinosa G1S2: 5; Primula nutans G1S1: 1; Prunella vulgaris G1S2: 9, G2S3: 4, G5S10: 3, G6S12: 3; Prunus serotina G6S11: 1; Prunus spinosa G2S3: 1, G6S11: 1; Puccinellia distans G2S3: 2, G3S5: 7, G3S6: 2, G4S8: 2, G5S9: 1, G6S12: 3; Puccinellia maritima G2S3: 1, G3S6: 1, G6S12: 1; Pulicaria dysenterica G4S8: 2; Pyrus communis subsp. pyraster G5S10: 1; Quercus robur G2S3: 1, G3S6: 1, G4S8: 2; Ranunculus bulbosus G4S7: 2, G5S9: 9, G5S10: 1; Ranunculus flammula G1S2: 5, G6S11: 14, G6S12: 3; Ranunculus polyanthemos G5S10: 1; Ranunculus sardous G2S3: 1, G3S5: 2, G6S12: 1; Ranunculus sceleratus G3S5: 9, G6S11: 1, G6S12: 10; Rhinanthus minor G1S1: 6, G1S2: 3, G2S3: 1, G5S10: 1; Rorippa islandica G6S12: 1; Rorippa palustris G6S11: 4; Rosa canina G5S10: 1; Rosa tomentosa G5S10: 1; Rubus arcticus G1S1: 6; Rubus caesius G3S6: 1, G4S7: 2, G5S10: 1, G6S12: 1; Rubus idaeus G5S10: 1; Rubus saxatilis G1S1: 1, G4S8: 2; Rumex conglomeratus G6S12: 1; Rumex hydrolapathum G1S1: 3, G1S2: 5, G6S12: 1; Rumex lonaifolius G4S7: 2; Rumex maritimus G3S5: 5, G4S7: 2, G6S12: 1; Rumex obtusifolius G3S5: 2, G5S10: 1, G6S11: 1, G6S12: 1; Rumex palustris G3S6: 2; Rumex sanguineus G6S12: 2; Rumex thyrsiflorus G5S9: 1; Sagina apetala G6S12: 1; Sagina maritima G1S2: 2, G2S3: 5, G2S4: 2, G3S5: 5, G3S6: 6, G5S9: 7, G5S10: 1, G6S12: 1; Sagina nodosa G1S1: 3, G1S2: 9, G2S3: 10, G3S6: 2, G5S9: 7, G5S10: 3, G6S12: 3; Salicornia europaea G5S9: 1; Salix cinerea G1S2: 2, G6S12: 1; Salix phylicifolia G1S1: 13; Salix repens G1S1: 6, G2S3: 1; Saxifraga granulata G5S9: 1; Scabiosa columbaria G5S10: 1; Schoenoplectus lacustris G1S1: 3, G1S2: 3, G2S3: 1, G6S12: 1; Schoenoplectus tabernaemontani G1S2: 3, G2S3: 3, G3S5: 2, G6S12: 9; Scirpus sylvaticus G6S12: 1; Scorzonera humilis G2S3: 1, G5S10: 2; Scrophularia umbrosa G4S7: 2; Scutellaria galericulata G1S2: 2, G2S3: 1, G5S10: 1, G6S12: 2; Sedum acre G2S3: 2, G3S6: 1, G5S9: 9, G5S10: 1; Sedum sexangulare G2S3: 1, G5S9: 1; Selinum carvifolia G1S1: 3, G2S3: 1, G4S8: 5, G5S10: 3; Senecio viscosus G2S3: 1; Senecio vulgaris G3S6: 2; Serratula tinctoria G2S3: 1, G4S8: 9, G5S10: 3; Seseli libanotis G5S10: 1; Sesleria caerulea G1S2: 5, G2S3: 1, G5S10: 1; Silene dioica G1S1: 1, G5S10: 1; Silene flos-cuculi G1S1: 1, G1S2: 11, G2S3: 4, G2S4: 14, G3S5: 4, G4S7: 5, G4S8: 10, G5S10: 8, G6S12: 5; Silene latifolia G3S6: 2, G4S7: 2, G5S9: 3; Silene nutans G5S9: 1: Silene vulgaris G4S8: 2. G5S10: 1: Sisymbrium officinale G5S9: 1. G6S12: 1: Sium latifolium G6S12: 1: Solanum dulcamara G3S6: 2. G6S12: 1: Solanum niarum G3S6: 1; continued on next page

*Solidago virgaurea* G5S10: 1; *Sonchus asper* G3S6: 3, G4S7: 5, G6S12: 1; *Sonchus oleraceus* G3S5: 2, G5S10: 1; *Sonchus palustris* G3S6: 4, G4S7: 9, G4S8: 3, G6S12: 1; *Sorbus aucuparia* G1S1: 1; *Sparganium microcarpum* G6S12: 1; *Spergularia media* G2S3: 1, G3S5: 2, G3S6: 3; *Stachys palustris* G3S5: 5, G3S6: 1, G4S7: 5; *Stellaria crassifolia* G1S1: 1; *Stellaria media* G1S1: 1, G2S4: 2, G3S5: 2, G3S6: 1, G4S7: 2, G5S9: 4, G5S10: 1; G6S11: 1, G6S12: 9; *Stellaria palustris* G1S2: 2, G2S3: 1, G6S12: 1; *Succisa pratensis* G1S2: 8, G2S3: 2, G4S8: 5, G5S9: 1, G5S10: 5; *Symphytum officinale* G4S7: 2, G5S10: 1; *Tanacetum vulgare* G1S1: 4, G2S3: 4, G3S5: 2, G4S8: 2, G5S9: 1, G5S10: 7, G6S12: 1; *Taraxacum sect. Erythrosperma* G5S9: 4; *Taraxacum sect. Obliqua* G2S3: 1; *Taraxacum sect. Palustria* G1S2: 5, G2S3: 3, G2S4: 4, G3S6: 1; *Taraxacum sect. Taraxacum* G1S2: 14, G2S3: 10, G3S5: 4, G3S6: 3, G4S7: 2, G4S8: 10, G5S9: 9, G5S10: 9, G6S12: 18; *Teesdalia nudicaulis* G5S9: 1; *Thalictrum flavum* G1S1: 1, G1S2: 2, G2S3: 1, G4S7: 2, G4S8: 2, G5S9: 1, G5S10: 1; *Trifolium arvense* G5S9: 7, G5S10: 1; *Trifolium campestre* G3S5: 2, G4S7: 2, G5S9: 5, G5S10: 1; *Trifolium dubium* G1S2: 1, G5S10: 3; *Teintalis europaea* G1S1: 4; *Trifolium medium* G5S10: 1; *Trifolium campestre* G3S5: 2, G4S7: 2, G3S6: 1, G5S10: 1; *Trifolium dubium* G1S2: 2, G2S3: 1, G5S10: 3, G6S11: 15, G6S12: 4; *Trifolium arvense* G5S9: 7, G5S10: 1; *Trifolium campestre* G3S5: 2, G4S7: 2, G3S6: 10, G5S10: 1; *Trifolium dubium* G1S2: 2, G2S3: 1, G5S510: 3, G6S11: 15, G6S12: 4; *Trifolium medium* G5S10: 2; *Trifolium campestre* G3S5: 2, G4S6: 3, G4S7: 2, G3S6: 1, G5S10: 1; *Trifolium dubium* G1S2: 2, G2S3: 1, GSS51: 4, G3S5: 4, G3S5: 3, G5S10: 2, G5S10: 2; *Trifolium arvense* G3S5: 2, G4S6: 3, G4S7: 2, G5S6: 1, G6S11: 1, G6S12: 19; *Tripleurospermum micodrum* G2S3: 1, G3S5: 4, G3S5: 3, G5S10: 2, G4S8: 2, G5S10: 2; *Verbacum matimum* G1S1: 3, G2S3: 1, G3S5: 2, G4S7: 7, G5S10: 1, G6S112: 1; *Veronica acentata* G6S12: 1; *Veronica acentagallis-aquatic* 

### S2-6 Evaluation of structural, abiotic and climatic factors

Table S2-6-1 Position and significance of fitted variables within the DCA-axes one and two (length of axis 1: 5.98, 2: 4.76); sorting follows decreasing  $r^2$ -values. Variables with  $r^2$ -values < 0.1 are not considered for the DCA. Only bold variables are shown in the DCA diagramm (Fig. 2-3, manuscript). Correlating climatic variables have been aggregated: climate-a: annual mean temperature (minimum temperature of the coldest month, mean temperature of the driest, wettest, warmest and coldest quarter; correlation < 0.8: precipitation of driest and coldest quarter annual temperature range, temperature annual range; correlation < 0.8: precipitation seasonality). climate-c: annual precipitation (correlation > 0.8): precipitation of warmest quarter, maximum temperature of warmest month, isothermality.

Variables	DCA1	DCA2	r2	Pr(> r)
EIV - salinitv	0.981320	-0.192380	0.814800	0.001***
EIV - moisture	0.542180	0.840260	0.576500	0.001***
EIV - reaction	0.863830	-0.503790	0.504000	0.001***
strong competitors	-0.679820	-0.733380	0.495200	0.001***
species [n]	-0.956190	0.292750	0.452800	0.001***
stress tolerators	0.999710	0.024030	0.442400	0.001***
annual mean temperature <sup>climate-a</sup>	-0.211650	-0.977350	0.225700	0.001***
mean temperature of coldest quarter <sup>climate-a</sup>	-0.209890	-0.977720	0.216200	0.001***
minimum temperature of coldest month <sup>climate-a</sup>	-0.222600	-0.974910	0.212600	0.001***
temperature seasonality <sup>climate-b</sup>	0.211940	0.977280	0.197500	0.001***
mean temperature of warmest guarter <sup>climate-a</sup>	-0.233410	-0.972380	0.194600	0.001***
CSR-strategists	-0.636670	0.771140	0.192100	0.001***
temperature annual range <sup>climate-b</sup>	0.225230	0.974300	0.191700	0.001***
mean temperature of driest quarter <sup>climate-a</sup>	-0.191550	-0.981480	0.172000	0.001***
hemikrvptophytes	-0.641090	-0.767470	0.152400	0.001***
mean diurnal temperature range <sup>climate-b</sup>	0.272270	0.962220	0.149700	0.001***
EIV - nutrients	-0.073390	-0.997300	0.146200	0.001***
precipitation seasonality <sup>climate-b</sup>	0.208160	0.978100	0.134300	0.001***
precipitation of driest month <sup>climate-a</sup>	-0.134410	-0.990930	0.126200	0.001***
precipitation of driest quarter <sup>climate-a</sup>	-0.134580	-0.990900	0.109800	0.001***
CR-strategists	-0.535180	-0.844740	0.097400	0.001***
chamaephytes	0.001340	-1.000000	0.086800	0.001***
precipitation of coldest quarter <sup>climate-a</sup>	-0.074930	-0.997190	0.082100	0.001***
plurien-pollakanth	-0.549050	-0.835790	0.070600	0.001***
plurienn-hapax	-0.635040	0.772480	0.062500	0.001***
annual precipitation <sup>climate-c</sup>	-0.015950	-0.999870	0.042100	0.001***
isothermality	0.037980	-0.999280	0.036200	0.001***
CS-strategists	0.423500	-0.905900	0.030300	0.001***
mean temperature of wettest quarter <sup>climate-a</sup>	-0.272910	-0.962040	0.029700	0.001***
bienn	0.576510	-0.817090	0.029000	0.001***
ruderals	-0.999120	0.041930	0.022900	0.001***
SR-strategists	0.244990	-0.969530	0.014800	0.001***
maximum temperature of warmest month <sup>climate-c</sup>	-0.174470	-0.984660	0.010600	0.001***
precipitation of warmest quarter <sup>climate-c</sup>	0.112360	-0.993670	0.008600	0.001***
annuals	0.688110	-0.725610	0.008500	0.001***
geophytes	0.997080	-0.076320	0.007400	0.001***
precipitation of wettest month	0.729950	0.683500	0.006900	0.001***
nanophanerophytes	-0.729410	-0.684080	0.004500	0.001***
precipitation of wettest quarter	0.639130	-0.769100	0.003400	0.005**
hydrophytes	0.435240	0.900320	0.003400	0.007**
therophytes	-0.386640	-0.922230	0.000400	0.493

Table S2-6-2 Multiple comparison (Mann-Whitney-U test; *p*-values) of main clusters M1-3 for Ellenberg indicator values, life-forms, life-span, plant strategy types and mean numbers of species, showing striking patterns (Ellenberg indicator values: differences  $\geq$  one category; Cover abundance: differences  $\geq$  20 %). We used a posthoc Bonferroni adjustment to correct *p* values for different sizes of sub-groups.

	abiotic factors	stru	uctural factors		
	soil	soil	hemicrypto-		
	salinity	moisture	phytes	perennials	geophytes
M1/M2	2.00E-16 ***	2.00E-16 ***	1	2.00E-16 ***	2.00E-16 ***
M2/M3	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	0.00038 ***	2.00E-16 ***
M1/M3	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***
	competitor	stress	CSR-	number of	
	strategists	tolerators	strategists	species	
M1/M2	2.00E-16 ***	9.10E-15 ***	2.00E-16 ***	2.00E-16 ***	
M2/M3	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	
M1/M3	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	2.00E-16 ***	

Fig. S2-6-1 Whisker-plots for all sub-groups (M1G1S1 – M3G6S12) of Ellenberg indicator values, life-forms, life-span, mean species numbers and climatic factors (Bioclim data, according to Karger et al. 2017). Width of whisker-plots refers to the number of relevés within each main cluster (M1-3); grey shades go along with "spider"-graphs of Fig. 2-3: M1 = medium grey; M2 = light grey; M3 = dark grey.











34 36 isothermality 34 36 38 40 42 44 1 1 1 1 1		• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	+	• • • • • • • • • • • • • • • • • • •	M1G2S7	H M1G2S8	+		• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	• - M2G3S5	••••••••••••••••••••••••••••••••••••••		• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •		•	H M3G1S2	•• +	•••	• • • • M3G3S5	+	• • • • • • • • • • • • • • • • • • •	 	• • • • • • • • • • • • • • • • • • •	■ – M3G6S11	H
temperature seasomality [sd] 600 650 700 750 800 850 900 1 1 1 1 1 1	• •	+ O • M1G1S2	+ • M1G1S3			• • • • • • • • • • • • • • • • • • •	•		-M2G1S1	-M2G1S2	►	H	- M2G3S5	+- <b>■●</b> M2G3S6	-M2G3S7	• •	+- <b>1</b> →+ ● • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •	• • • • • • • • • • • • • • • • • • •		H	• • • • • • • • • • • • • • • • • • •		++ • • • •+	-M3G2S4	• • • • • • • • • • •			 M3G5S9		••	+□ • HM3G6S12
maximal temperature of warmest month [°C] 21 22 23 24 25 26 27 1 1 1 1 22	MIGISI		+M1G1S3	• • • • • • • • • • • • • • • • • • •	H			+ M1G2S8	+		• • • • • • • • • • • • • • • • • • •	• +	• • <b>–</b> M2G3S5	● +● M2G3S6	+	• • • • • • • • • • • • • • • • • • •	HHHM2G4S9	••••••••••••••••••••••••••••••••••••••	• • • • • • • • • • • • • • • • • • •	M2G5S12	••••••••••••••••••••••••••••••••••••••	+	• • • • • • • • • • • • • • • • • • •	H	••••••••••••••••••••••••••••••••••••••	• • • • • • • • • • • • • • • • • • •	+-[] M3G3S6	+ M3G4S7	 HM3G5S9	H M3G5S10	<ul> <li>M3G6S11</li> </ul>	H



![](_page_172_Figure_0.jpeg)

![](_page_173_Figure_0.jpeg)

![](_page_174_Figure_0.jpeg)

![](_page_175_Figure_0.jpeg)

## **S2-7** Analogues in literature

**Table S2-7-1 Analogues descriptions of all found sub-groups.** The origin of literature is indicated: BKØ [Belt Sea-Kattegat-Øresund area including the south-western Swedish coast and the German Sea coast]; BP [Baltic Proper]; GeB [German Bight]; GB [Great Britain]; NL [The Netherlands].

Sub-groups	Analogues in literature
M1G1S1	Limonium vulgare-Armeria maritima sub-community of the Puccinellia maritima salt-
	marsh (Rodwell et al. 2000, GB); Limonium-Armeria nodum of the Puccinellietum
	maritimae (Adam 1981, GB); Plantagini-Limonietum (Preising et al. 1990, GeB). The
	latter includes <i>Suaeda maritima</i> and <i>Parapholis strigosa</i> , which are missing in M1G1S1.
M1G1S2	Puccinellietum maritimae (Dahlbeck 1945, BKØ; Krisch 1974, BKØ; Rebassoo 1975, BP;
	Härdtle 1984, BKØ, restricted to relevés with Suaeda maritima).
M1G1S3	Puccinellietum maritimae (Härdtle 1984, BKØ, restricted to relevés with Festuca rubra);
	Glaux maritima sub-community of the Puccinellia maritima salt-marsh (Rodwell et al.
	2000, GB). Atriplex prostrata is missing in the latter description.
M1G1S4	Agrostis stolonifera-Puccinellia maritima-Isozion (Dahlbeck 1945, BKØ); Tripolio-
	Triglochinetum maritimi (Rebassoo 1975, BP).
M1G1S5	Puccinellietum maritimae agrostietosum (Westhoff et al. 1998, NL). In comparison to
	this corresponding vegetation type, Cochlearia officinalis is rare in our data and Elytrigia
	atherica is absent.
M1G2S6	Puccinellietum distantis typicum (Preising et al. 1990, GeB); characteristic form of the
	Puccinellietum distantis (Berg et al. 2004, BKØ). M1G2S6 deviates slightly by
	accompanying glycophytes.
M1G2S7	Puccinellietum phryganodis (Siira and Haapala 1969, nBS; Siira and Merilä 1985, nBS;
	Dierßen & Dierßen 1996).
M1G2S8	Puccinellietum distantis polygonetosum (Berg et al. 2004, BKØ).
M2G1S1	Potentilla anserina form of the Artemisietum maritimae (Berg et al. 2004, $BK\emptyset$ );
	<i>Artemisietum maritimae</i> var. <i>Potentilla anserina</i> (Gillner 1960, BKØ). Unlike our data, the
	latter description lacks <i>Bolboschoenus maritimus</i> and abundant <i>Elytrigia repens</i> .
M2G1S2	Artemisia maritima-Isozion and Statice limonium-Isozion (Dahlbeck 1945, BKØ);
	Artemisietum maritimae (Gillner 1960, BKØ; Westhoff et al. 1998, NL); characteristic
	form of the Artemisietum maritimae (Berg et al. 2004, BKØ). Suaeda maritima and
	Atriplex littoralis, mentioned as frequent associates in the latter two works, are rare or
	absent in our data.
M2G2S3	Plantago maritima-Isozion (Dahlbeck 1945, BKØ); Plantaginetum maritimae (Rebassoo
	1975, BP); characteristic form of the Armerion maritimae (Hardtle 1984, $BK\emptyset$ ); Plantago
	maritima community (Willers 1988, NBS).
M2G2S4	Glauco maritimae-Juncetum gerardi juncetosum gerardi (Rebassoo 1975, BP); Juncetum
	gerardi var. Phragmites australis (Willers 1988, nBS). The latter description includes
	(almost) absent in our data
Macass	annost abscrit in our data.
IVI2G322	ephemeral salt-marsh vegetation with <i>sagina maritima</i> (Rodwell et al. 2000, GB,

M2G3S6	Juncetum gerardi Leontodon autumnalis type (Gillner 1960, BKØ); Juncetum gerardi var. Trifolium fragiferum (Dierßen & Dierßen 1996); Juncetum gerardi Lotus tenuis type (Berg et al. 2004, BKØ); Juncetum gerardi leontodontetosum (Westhoff et al. 1998, NL; Preising et al. 1990, GeB); Festucetum rubrae var. Leontodon autumnalis (Rebassoo 1975, BP).
M2G3S7	Juncus maritimus community (Härdtle 1984, BKØ); Oenantho lachenalii-Juncetum maritimi (Westhoff et al. 1998, NL; Berg et al. 2004, BKØ); Festuca arundinacea sub- community of the Juncus maritimus salt-marsh (Rodwell et al. 2000, GB, Juncetum maritimi). The descriptions partly lack Inula britannica and/or include Apium graveolens and Samolus valerandi, which are (almost) absent in our data.
M2G3S8	Halophilic meadows (Almquist 1929, BP and nBS); sea-shore meadows (Tyler 1969b, BP, Table 1-C); <i>Carex flacca</i> nodum of the <i>Juncetum gerardi</i> (Adam 1981, GB). Each of the analogous communities reflects only parts of the species composition. M2G3S8 includes species of the <i>Molinetalion caerulae</i> .
M2G4S9	Agrostis stolonifera-Isozion (Dahlbeck 1945, BKØ); Glauco maritimae-Juncetum gerardi agrostidetosum stoloniferae (Rebassoo 1975, BP); Eleocharis uniglumis salt-marsh (Rodwell et al. 2000, GB); Agrostis stolonifera-Eleocharis uniglumis (Jutila 2001a, nBS).
M2G4S10	Blysmetum rufi (Gillner 1960, BKØ; Adam 1981, GB; Härdtle 1984, BKØ; Dierßen & Dierßen 1996; Westhoff et al. 1998, NL; Berg et al. 2004, BKØ).
M2G4S11	Halo-Bolboschoenetum maritimi phragmitetosum australis var. Samolus valerandi (Rebassoo 1975, BP); (Phragmiteto-)Scirpetum maritimae (Gillner 1960, BKØ; Tyler 1969a); (Oenanthe lachenalii-) Samolus valerandi community of the Armerion maritimae (Krisch 1974, 1990, BKØ). Some descriptions lack Samolus valerandi or, contrary to our findings, associate the type with Oenanthe lachenalii.
M2G5S12	Eleocharetum uniglumis caricetosum mackenziei (Tyler 1969b, BP); Caricetum paleaceae caricetosum mackenziei, Caricetum mackenziei (Willers 1988, nBS); Eleocharis uniglumis-Carex mackenziei community (Jutila 2001a, nBS).
M2G5S13	Juncetum gerardi calamagrostietosum neglectae, Calamagrostis neglecta community var. Eleocharis uniglumis (Willers 1988, nBS). Each of the above descriptions comprises only parts of the differential species composition.
M3G1S1	<i>Filipendulo-Iridetum pseudacori</i> (Adam 1981, GB). Frequent <i>Iris pseudacorus</i> is absent in our data. The sub-group includes species related to the <i>Caricion fuscae</i> and the <i>Filipendula ulmaria-Angelica sylvestris</i> mire of the <i>Filipendulion ulmariae</i> (Rodwell et al. 1991, GB).
M3G1S2	Festucetum rubrae var. Carex panicea and var. Molinia caerulea (Rebassoo 1975, BP); Potentilla anserina-Carex nigra dune-slack community (Rodwell et al. 2000, GB, Agropyro-Rumicion); Carex fusca community of the Caricion fuscae (Fukarek 1961, BKØ); Juncetum gerardi caricetosum nigrae (Tyler 1969a, BKØ ['Festuco-Caricetosum nigrae']).
M3G2S3	Juncetum gerardi leontodontetosum (Westhoff et al. 1998, NL); Leontodon autumnalis type of the Festuca rubra salt-marsh (Rodwell et al. 2000, GB); Trifolio fragiferi- Agrostietum stoloniferae (Sýkora et al. 1996, NL); Blysmus compressus community of the Loto tenuis-Trifolion fragiferi (Krisch 1990, BKØ). Differential taxa of the Loto tenuis- Trifolion fragiferi rarely occur in our data.

M3G2S4	Hordeetum secalini (Berg et al. 2004, BKØ; Krisch 1974, 1990, BKØ ["Hordeetum nodosi Krisch 1972"]). Varying species of the <i>Molinio-Arrhenatheretalia</i> and some floristics of
	the Cynosurion cristati occur (cf. Zuidhoff et al. 1996, NL).
M3G3S5	Potentillo-Festucetum arundinaceae (Krisch 1990, BKØ, column 45); Atriplicetum
	littoralis asteretosum (Berg et al. 2004, BKØ).
M3G3S6	Potentillo-Festucetum arundinaceae (Krisch 1990, BKØ, column 46); Elytrigia repens drift
	litter community of the Agropyro-Rumicion (Tyler 1969b, BP); Atriplicetum littoralis
	chenopodietosum (Berg et al. 2004, BKØ).
M3G4S7	Variant of the basal community of the Potentillion anserinae (Sýkora et al. 1996, NL;
	Wolfram 1996, BKØ); coastal form of the Potentillo anserinae-Festucetum arundinaceae
	juncetosum gerardi (Dierschke 2012).
M3G4S8	Agrostis stolonifera-Festuca arundinacea nodum of the Molinietalia caeruleae (Adam
	1981, GB); Potentillo-Festucetum arundinaceae (Krisch 1974, BKØ); Elytrigia repens and
	Festuca arundinacea drift litter communities of the Agropyro-Rumicion (Tyler 1969b,
	BP); Festucetum arundinaceae (Rebassoo 1975, BP, only single relevés).
M3G5S9	Bromus hordeaceus-Isozion (Dahlbeck 1945, BKØ).
M3G5S10	Arrhenatheretalia (Zuidhoff et al. 1996, NL; Dierschke 1997).
M3G6S11	Ranunculo (repentis)-Alopecuretum geniculati (Dierßen & Dierßen 1996; Wolfram 1996,
M3G6S12	BKØ; Berg et al. 2004, BKØ); <i>Ranunculo repentis-Alopecuretum geniculati</i> var.
	eleocharietosum uniglumis (Dierschke 2012). The descriptions each reflect only part of
	the species composition of M3G6S11 and M3G6S12.

# Supplementary material of study 3

### S3-1: Species-area relationship

**Fig. S3-1-1 Non-significant model (***p* **= 0.077) of species-area relationship.** The plot size (relevé area) does not explain the variance in species numbers

![](_page_178_Figure_5.jpeg)