Review

Biogeomorphological aspects of a model barrier island and its surroundings - Interactions between abiotic conditions and biota shaping the tidal and terrestrial landscape: A synthesis

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ABSTRACT

Barrier islands occur in north-western Europe between the North Sea and the Wadden Sea along the coast of Denmark, Germany and the Netherlands. Geomorphological units such as dunes and salt marshes are built by wind, water and sediment. The biota also feed back to the units by trapping sand and silt, transported by water and wind thus (de)stabilizing the local substrate and are able to modify their own abiotic environment. Hence, we refer to them as biogeomorphological units, thus including the role of engineering biota. We consider seven units: tidal basin, island head, intertidal flats, dune arc complex, wash-over complex, island tail with salt marsh, and ~~green~~ beach. We focus on the well-studied West-Frisian island of Schiermonnikoog, the Netherlands, from which we integrated published data. The biogeomorphological units are built with bioengineering species, and in turn provide habitats for plant- and animal species. These communities are subject to succession until climax stages with various timescales. These temporal aspects are derived from long-term measurements in the field, including the study of chronosequences. Biogeomorphological units also affect each other, including feed-backs from animals, plants and micro-organisms. Based on that we present a conceptual model of this particular barrier island. Knowledge gaps that can be identified include 1) interactions among geomorphological units, 2) interactions among these units and bio-engineers to come to biogeomorphological units, and 3) multiple spatial-temporal scales. Human interference such as ~~A~~atmospheric deposition applies to all islands and is difficult to manage. Other human interferences may, however, differ among individual islands and their surroundings. They can be managed such as various intensities of fisheries, sand suppletion, extraction of groundwater, the attitude of local people towards artificial sand-drift dikes and livestock grazing.

1. Introduction

Islands occur in all kinds of sizes and shapes and can differ substantially in the way they are formed. They can suddenly occur after vulcanic eruptions, such as Krakatau (Thornton 1996) or they are the result of long-term geological and ecological processes that interact and gradually form an island. After the last glacial period sea-level rise (SLR) decelerated (7000 to 3000 BP) and the coastal zone developed, forming salt marshes, (inter)tidal flats, and barrier islands. Due to the further decrease of SLR to 0.11 m 100 yr^{-1} over the past 3000 years BP, the Wadden Sea area was formed (Jensen 2019). Barrier islands are coastal islands with a particular type of dune system, which are located parallel to the mainland. Barrier islands occur in north-western Europe between the North Sea and the Wadden Sea. They often occur in chains, consisting of a varying number of islands (Fig. 1). They absorb wave energy at the North Sea side and create areas of protected waters at the Wadden

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Sea side where different types of wetlands such as salt marshes and/or (inter)tidal flats can develop. Salt marshes of the Wadden Sea are meso-tidal with a tidal amplitude of ~2.4 m. They are separated from each other by tidal inlets that feed tidal basins. Each island is surrounded by two tidal basins separated by a tidal watershed. These islands and the tidal basins exhibit a dynamic behaviour (Oost et al., 2012). They include the flow of water and air, suspended sediment transport, sedimentation and erosion of coarse-grained sand and fine-grained silt. Barrier islands have very important functions as they protect the mainland coastline and harbour a high biodiversity.

In recent morpho-ecological studies of the Dutch Wadden Sea barrier islands, the concept of a 'model island' has been developed by experts in geomorphology, hydrology, ecology, and nature management based on internal reports and field experiments. They focused on experiences with coastal protection in the Netherlands and Germany during the past decades. In short the experience was that until recently coastal defense tried to eliminate natural dune-forming processes and promoted fixation of the dune complexes by establishment of sand-drift dikes. This had led to considerable loss of biodiversity as pioneer communities disappeared (Löffler et al., 2011). In the present paper, the focus is on allowing natural dynamics again, in order to develop the full range of pioneer to climax communities, thus creating new pioneer communities at different spatial and temporal scales. This model island represents an idealized image of a Wadden Sea barrier island, including dynamics that can reset climax communities. Large-scale geomorphological units form the island under natural conditions, including the role of plants that trap sand and silt. Each of these units is characterized by a range of abiotic conditions built by wind, water and sediment, and relevant to the diversity of plants and animals (Löffler et al., 2011; Oost et al., 2012). It is based on five visible terrestrial geomorphological units, namely, (1) island head, (2) dune arc complex, (3) wash-over complex, (4) island tail, (5) beach and shoreface (Fig. 2).
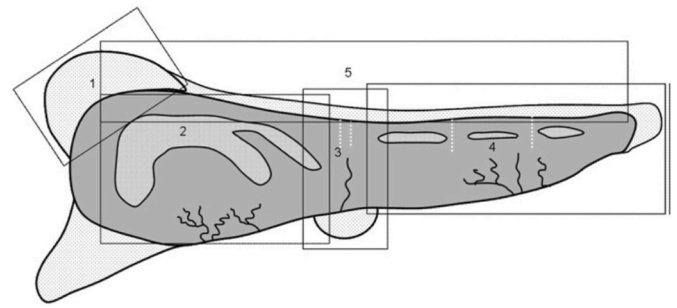

Fig. 2. Model of a barrier island with its characteristic large-scale morpho-ecological units: (1) island head; (2) dune arc with dune slacks; (3) wash-over complex; (4) island tail with salt marsh; (5) beach and shoreface with sand-banks (after Löffler et al., 2011; Oost et al., 2012).

In a recent review there is increasing learning that in addition to the important long-term (centurial to millennial) roles of sediment supply and sea-level rise, shorter-term (annual to centurial) ecomorphodynamic interactions (i.e., interactions between morphology, fluid dynamics, and/or sediment transport with biological processes play a critical role in determining how barrier-marsh systems will evolve in the future. These processes are influenced by changes in the intensity and/or frequency of storms and changes in the geographic distribution of dune-building vegetation, as well as couplings by wash overs between barrier and back-barrier marsh environments (Moore et al., 2018). More or less all coastal geomorphologies have been modelled, suggesting general rules for barrier islands (Murray and Moore (2018). Barrier islands do, however, differ in size and dynamics as demonstrated along the Atlantic coast of Virginia, USA (Deaton et al., 2017) and the Wadden Sea coast (Fitzgerald et al., 2018). The latter explain that barrier islands without a

Fig. 1. Location of the study site Schiermonnikoog (online version in colour).

back-barrier marsh are much more vulnerable for SLR than barrier island with a back-barrier salt marsh. High marsh settings seem, on average, to be pacing global sea level rise (3 mm yr^{-1}), and that low marshes currently accrete at rates more than double that of sea-level rise (6.9 mm yr^{-1}), suggesting that marshes are less vulnerable than previously predicted (Kirwan et al., 2016). It should be noted, however, that back-barrier salt marshes along the Virginian coast with vertical accretion less than 0.7 mm yr^{-1} are more vulnerable and very dynamic with redistribution of coastal sand reservoirs (Fitzgerald et al., 2018) than those along the coast of the Wadden Sea with vertical accretion rates around 3 mm yr^{-1} (Esselink et al., 2017). The review by Moore et al. (2018) focuses on future survival of barrier systems under climate change. Feedbacks between dunes and dune-building vegetation are included, however, the role of other biota and human interference is not mentioned. The fate of other biota once the abiotic components together with bioengineering species have built the units is lacking.

Here, we explore how an in-depth understanding of the geomorphology of a model barrier island in the Wadden Sea requires the understanding of climate, geomorphology, soil and sediment and its biota: plants, animals and micro-organisms. So far, the concept is focused on geomorphology and creation of a variation of habitats for plants and animals in five terrestrial units (Löffler et al., 2011; Oost et al., 2012). A barrier island does, however, not stand alone. It is affected by its (inter)tidal surroundings. These are well characterized as ecotopes for the international Wadden Sea. Ecotopes are discrete classes of the geo-physical environment and the adapted living communities (Fig. 3) (Baptist et al., 2019). We try to indicate to what extent the concept of biogeomorphological units of a barrier island in the present synthesis for Schiermonnikoog, may be generalized for the international Wadden Sea. Barrier islands are also found along the east coast of North America from the coast of Long Island to the Atlantic coast of Florida (Bertness 1999). All Wadden Sea islands ~~islands~~ have their own characteristics, which makes generalization difficult (Löffler et al., 2011; Baptist et al., 2019). Differences can be specified for the important issue of tidal basins. The 39 tidal basins in the entire Wadden Sea can be reckoned among four clusters according to their ecotopes (Baptist et al., 2019).

The first cluster (eight basins covering 35% of the area) consists of tidal basins that are characterized by a large proportion, often >50%, of low-dynamic low-littoral ecotopes often in combination with low-dynamic sublittoral ecotopes. These tidal basins are located at both ends of the Wadden Sea, where the tidal ranges are relatively low, namely <2 m.

The second cluster (seven basins covering only 4% of the area) consists of tidal basins with over 50% low-dynamic mid-littoral ecotopes, so these are the very shallow basins. Since large basins have relatively more channels than small ones, the small basins in cluster 2 consequently have a relatively large proportion of intertidal flats.

The third cluster (five basins covering 31% of the area) is characterized by a large proportion of high-dynamic sublittoral ecotopes, or in other words, deep tidal gullies with high flow velocities. The tidal basins of the third cluster often belong to estuarine systems, such as the Eems-Dollard, Jade, Weser, and Elbe for which the basin morphology is characterized by the river channel and tidal ranges >3 m.

The fourth cluster (19 basins covering 30% of the area) is characterized by a large proportion of low-dynamic low-littoral and low-dynamic mid-littoral ecotopes in equal distribution. This cluster includes Dutch tidal basins such as Zoutkamperlaag, Eilanderbalg, Lauwers around Schiermonnikoog and Ameland in the Netherlands, as well as many tidal basins in the German Bight around Juist, Norderney, Baltrum, Langeoog, Spiekeroog, Wangerooge, Amrum and Mandø in Denmark (Baptist et al., 2019). Several tidal basins in Schleswig-Holstein are adjacent to Halligen, which formed after the flooding of a peat area around 1450 AD and are not barrier islands (Oost et al., 2017).

We try and elucidate temporal aspects of the factors and their interactions from measurements in the field, including the study of chronosequences. This synthesis consists of three parts. First, we document the geomorphological units of the model island and its surroundings. Second, we ask how, at different spatial and temporal scales, various abiotic and biotic drivers (bioengineering species) of the biogeomorphological units are at play and interact with each other to shape these biogeomorphological units (Figs. 3 and 4). We include different human interferences as a kind of unintended experiments, such as embankment, artificial sand-drift dike, livestock grazing, fisheries, that help to understand natural processes and the underlying biological and geomorphological mechanisms involved. Third we discuss the emerging knowledge gaps.

The concept of a model island (Löffler et al., 2011; Oost et al., 2012) should be completed by including the geomorphological units 'tidal
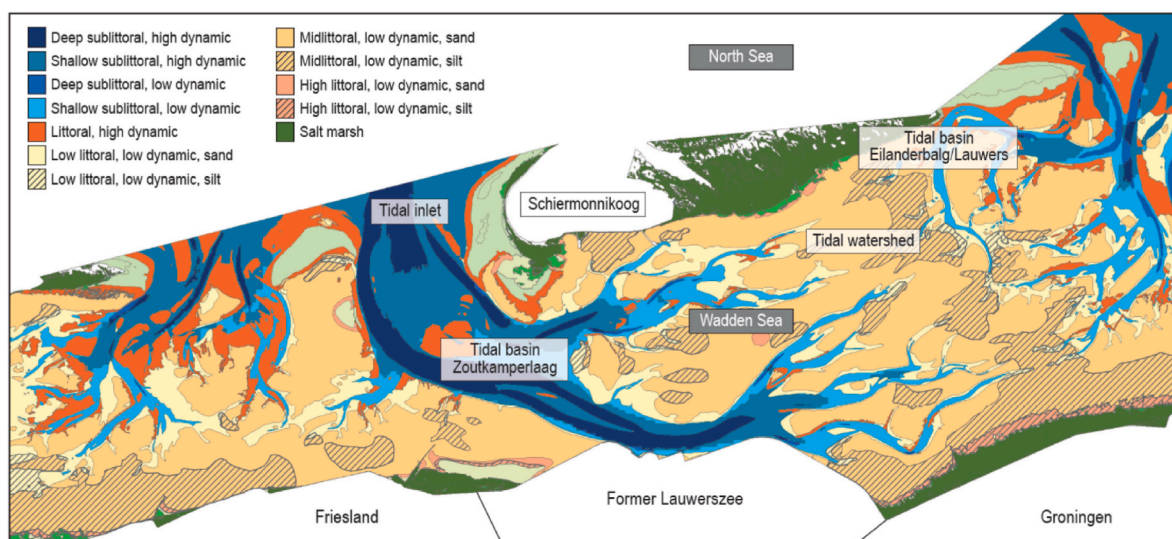

Fig. 3. Map of the (inter)tidal ecotopes around the barrier island of Schiermonnikoog (2017) with the tidal basins Zoutkamperlaag and Eilanderbalg/Lauwers, separated by the tidal watershed. The mainland of Friesland and Groningen is separated by the former Lauwerszee. Legend explanation: hydrodynamics low (max. current velocity <0.8 m s^{-1}), hydrodynamics high (max. current velocity ≥0.8 m s^{-1}), deep sublittoral (depth < −5 m Mean Low Water Springs MLWS), shallow sublittoral (−5 m MLWS ≤ depth <4% mean exposure), low littoral (4% ≤ mean exposure <25%), middle littoral (25% ≤ mean exposure <75%), high littoral (75% ≤ mean exposure <85%), supralittoral (mean exposure ≥85%) (Baptist et al., 2019) (online version in colour).
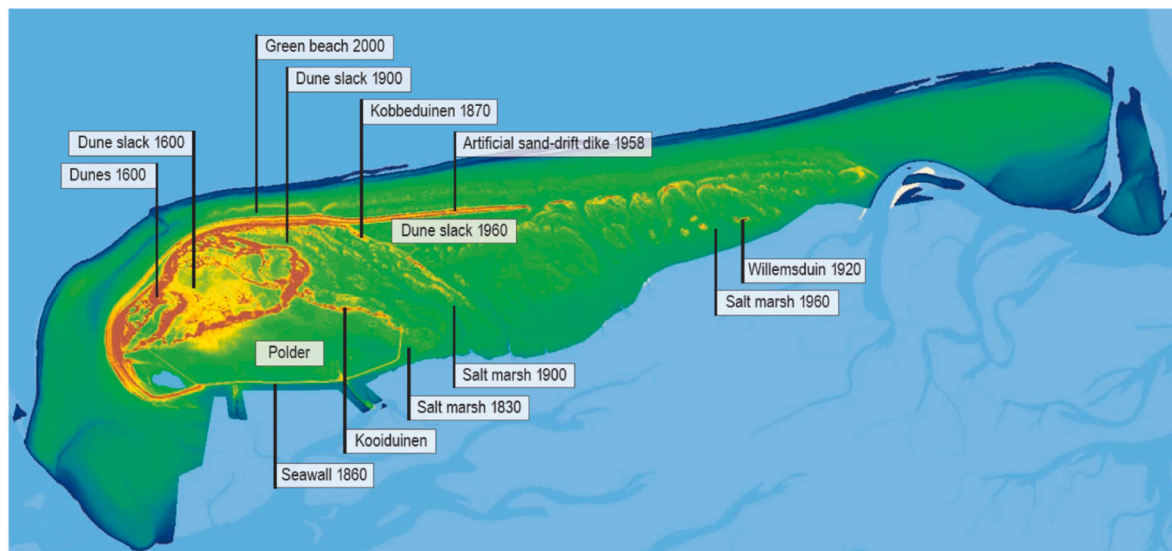
Fig. 4. Map of the barrier island of Schiermonnikoog according to Elevation Database of the Netherlands AHN 2020 with high dunes (brown), low dunes (yellow), dune slacks, salt marsh and embanked polder (green)). Estimation of establishment of dunes, dune slacks and salt marsh are indicated featuring a chronosequence (see further text). North of the island the North Sea is situated, south of the island the Wadden Sea (intertidal flats at low tide are indicated in light blue. The seawall around the polder (previously salt marsh until 1860) and the artificial sand-drift dike in middle of the island (1958) are anthropogenic structures (www.ahn.nl 2020) (online version in colour).

basin' and 'intertidal flats', thus bringing the total number of geomorphological units to seven. Hence, to understand the geomorphology of a model island, all seven geomorphological units should be taken into account. These units provide, however, not only habitats for plants, animals and micro-organisms, the biota feed back to the units by trapping sand and silt, thus (de)stabilizing the local substrate and are able to modify their own abiotic environment. Hence, we refer to them as biogeomorphological units, thus including the role of engineering biota (Corenblit et al., 2011).

The conceptual model island generalizes a barrier island, focusing on the processes on the island itself, and less on the interaction with external factors. Its geomorphological units are derived from the various barrier islands in the entire Wadden Sea area. However, recent emphasis is laid on studying individual tidal basins with respect to effects on hydrodynamics (Wang et al., 2012, 2018), on geomorphology (De Groot et al., 2017b), and on salt marshes (Esselink et al., 2017) for a better understanding of mechanisms at play. Hence, more detailed data on biogeomorphological interactions and their dynamics might be better derived from a single island. The barrier island that is perhaps best studied in the international Wadden Sea is the West-Frisian island of Schiermonnikoog, the Netherlands (Fig. 1). Its size is about 15 km × 2 km, and it is inhabited by 1000 people, it receives about 200,000 visitors each year, the polder is exploited for intensive agriculture, with high stocking density. All seven biogeomorphological units of this island have been studied intensively during the past 40 years, namely, tidal basin (Wang et al., 2012, 2018), island heads (Wang et al., 2012), dune arc complexes (Grootjans et al., 1998; Lammerts and Grootjans 1998; Rohani et al., 2014), wash-over complexes (De Groot et al., 2011b; Wesselman et al., 2019), island tails with salt marshes (Olff et al., 1997; Schrama et al., 2012), beach and shoreface (Olff et al., 1993; Van der Veen et al., 1997), intertidal flats (Eriksson et al., 2010; Engel et al., 2017). Hence, development and dynamics are quantified from long-term recordings covering several decades. Moreover, as a result of its movement during the past centuries (Isbary 1936), it is the only barrier island from which the succession and dynamics can partly be reconstructed from spatial phenomena according to a so-called chronosequence, i.e. a form of space for time substitute (Olff et al., 1997). When succession trajectories exceed the life span of investigators, temporal change can be successfully explored through the judicious use of chronosequences

(Walker et al., 2010).

2. The biogeomorphological units of the model barrier island at different spatial and temporal scales

2.1. Tidal basin: sand, silt, water, benthic organisms except for high dynamic channels

Sea-level rise during the past millennia pushed the barrier island towards the mainland and reduced the tidal basin. Human interference further reduced the tidal basin by embankments of polders along the mainland coast since 1200, and closure of the Lauwerzee in 1969. Little interaction between abiotic and biotic factors take place, except for low dynamic channels.

Tidal basins have been formed over a long geological time scale, stretching millennia. Most tidal waters flowing through the inlets between barrier islands in combination with wave- and wind-driven currents, continuously exchange enormous amounts of mainly sand sediments between the North Sea, the ebb-tidal delta, the barrier island, the inlet, the flood-tidal delta and the back-barrier basin. The Wadden coast consists of barrier islands, separated by tidal inlets and their associated ebb-tidal deltas. These ebb-tidal deltas do not interconnect. Smaller-scale morphological elements, such as isolated shore-oblique sand bars, reef-bow or saw-tooth bars at the downdrift sides of the ETDs offshore of Terschelling, Ameland and Schiermonnikoog, and elongated coast-parallel breaker bars, have been identified, although the distance between the islands is not more than 15 km. Variation in hydrodynamic conditions, shore-parallel tidal flow at Ameland Inlet vs. combined action of currents and waves at Terschelling, can explain differences in seabed patterns, namely, predominantly linear megaripples up to 0.5 m high at Ameland Inlet vs. compound, three-dimensional ripples up to 0.25 m high at Terschelling (Van der Spek et al., 2022). The Wadden Sea is characterized by 39 tidal basins separated by tidal watersheds (Baptist et al., 2019). These different basins can exist as long as the transport across the tidal watersheds is limited (Wang et al., 2012). Net sedimentation occurs in the back-barrier basin at the expense of the North Sea coast, which has been retreated a few kilometres in a landward direction as a result of sea-level rise (Chang et al., 2006) over the past 2.5 millennia (Fig. 5) (Esselink 2000; Schepers
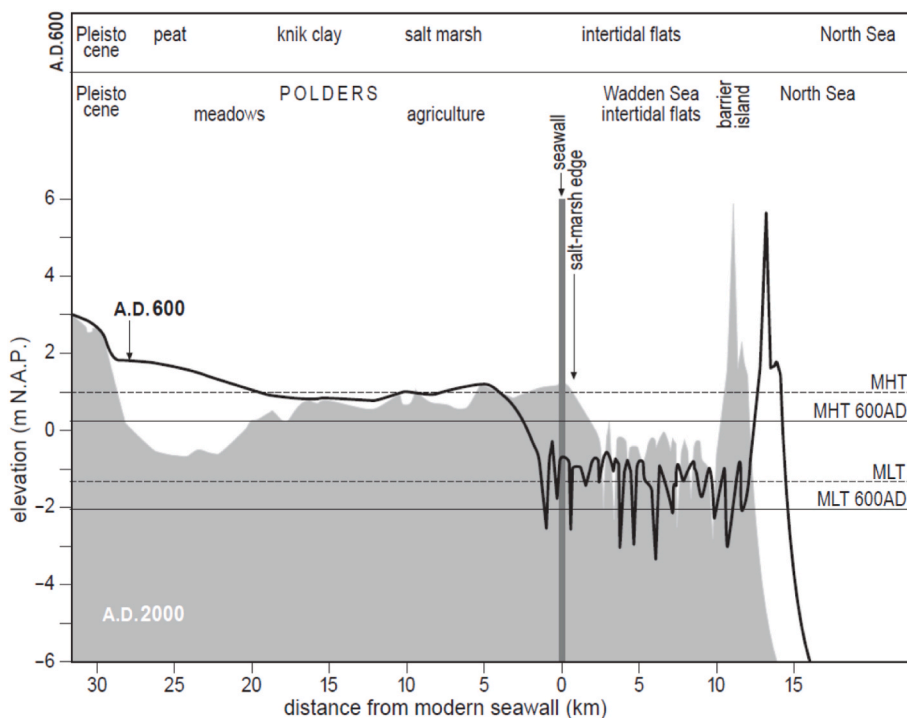
Fig. 5. (A) Schematic cross section through the Wadden Sea landscape from the Pleistocene upland up to the North Sea by about AD600, before human influence became an important factor in the geomorphological development of the coastal area, and at present. The elevation of the modern landscape (m NAP = Dutch Ordnance Level = 1 m below Mean High Tide MHT) is based on a transect that runs from SW of the City of Groningen over the eastern tip of the island of Schiermonnikoog (data provided by A. Oost) (Esselink 2000).

et al., 2021). The ebb-tidal deltas and channels within the basins consist of coarse-grained sand (grain size 0.10–0.40 mm), the intertidal flats are mainly composed of sand (90%, 0.15–0.20 mm), and fine-grained silty sediments (10%, with decreasing grain-size diameters away from the inlet (Wang et al., 2018). Locations with tidal currents with velocity at spring tide above 0.8 m s^{-1}, are highly dynamic. This allows for frequent stirring up and transporting of sediments, causing local sand redistribution exemplified by the presence of sand ripples. Along the low dynamic parts of the tidal basin, for example near the foreland coast, silt gets deposited. Both the ebb-tidal and the flood-tidal deltas are characterized by channels and adjacent shoals. The stability of a tidal inlet depends on two competing processes: the tidal current which keeps it open, and the wind waves and associated littoral drift try to close the inlet. The tidal inlet has a stable equilibrium if the tidal current (determined by the combination of tidal range and size of the basin) is sufficiently strong compared to the waves. The channels in the ebb-tidal delta and the inlet migrate from west to east under the influence of the tidal flow and the longshore eastward sediment transport by littoral drift. This process leads to a cyclic and dynamic behaviour of the channels in the inlets. Movements of hundreds of metres per year can occur (Wang et al., 2012). In natural conditions the accommodation space for the seawater is large, resulting in a large volume of water entering the Wadden Sea during the flooding tide. This volume of water has been coined tidal prism. It transports large amounts of sand and silt that settles in sediment sinks and builds channel levees (sand) and intertidal flats (sand and silt) and salt marshes (silt) (Oost et al., 2021). Grain-size fractions in tidal basins are sorted according to an energy gradient. The general trend shows a decrease with both tidal and wave energy and, hence, in grain size from the inlet to the landward side of the basin. The locations where silt settles are characterized by low-energy hydrodynamic conditions, and are in general persistent (Oost et al., 2021). Emerged salt marshes have been subsequently embanked, resulting in extension of the coastline into the intertidal flats since the 17th century (Dijkema 1987). Land reclamation resulted in major loss of sediment sinks where fine sediments naturally accumulate. Decreased tidal prism may cause increasing tidal range with increasing sedimentation rates in the mesotidal flat areas behind barriers (Oost et al., 2021). Land reclamation caused narrowing of the Wadden Sea and further

reduced the extent of the tidal basin. Moreover, the tidal basins in the entire Dutch Wadden Sea are affected by the closure of the Zuiderzee by a long seawall in 1932 (Oost et al., 2012, 2021; Wang et al., 2012, 2018). Thus, the accommodation space decreased, resulting in a decreased tidal prism. Hence, the channels became too large, which caused sand demand and filling in of the Wadden Sea over the period 1935–2005 (Wang et al., 2012).

Barrier islands not only moved in landward direction. In c. 1300, Schiermonnikoog (named Wervneraeghe at the time) was five or six km west of its present position (Fig. 6) (De Haan et al., 1983). The island of Basseaeghe, at the present position of Schiermonnikoog, moved eastward during the past five centuries. The burst of the tidal watershed of Wervneraeghe from Anjum in Friesland during the first half of the 14th century considerably enlarged the tidal basin of the Scudbalcke inlet, since the Lauwerszee and its inland tributaries were at that time not embanked. The reduction of the tidal basin area of the inlet caused an eastward shift of the tidal watershed and a subsequent large growth of the eastern part of Schiermonnikoog. This resulted in an eastward movement of the island and a new tidal watershed connecting it with the mainland of Groningen. Initially the average annual erosion of the western point of the island amounted to 12–15 m between 1350 and 1550 (De Haan et al., 1983), whereas it was later reduced to 7 m between 1550 and 1920 (Isbary 1936).

The present tidal watershed separates the western tidal basin Zoutkamperlaag between Ameland and Schiermonnikoog with the inlet along the western point, and the eastern tidal basin Eilanderbalg, part of the larger Lauwers along the eastern point (Fig. 3). The tidal basin Zoutkamperlaag was reduced with a third by the closure of the Lauwerszee in 1969 (Oost et al., 2012, 2017). The decrease of tidal prism in the channel Zoutkamperlaag resulted in more sediment remaining in suspension and therefore higher suspended sediment concentration and thus causing sedimentation in the channel levee and intertidal flats in the basin. As a consequence, the tidal watershed between Schiermonnikoog and the mainland became muddier over the years (Oost et al., 2021). Furthermore, the tidal flow through the inlet became clearly asymmetric over time in the sense that the peak velocity during flood became clearly larger than the peak velocity during ebb. This change resulted in a net import of sediment into the basin, which can be
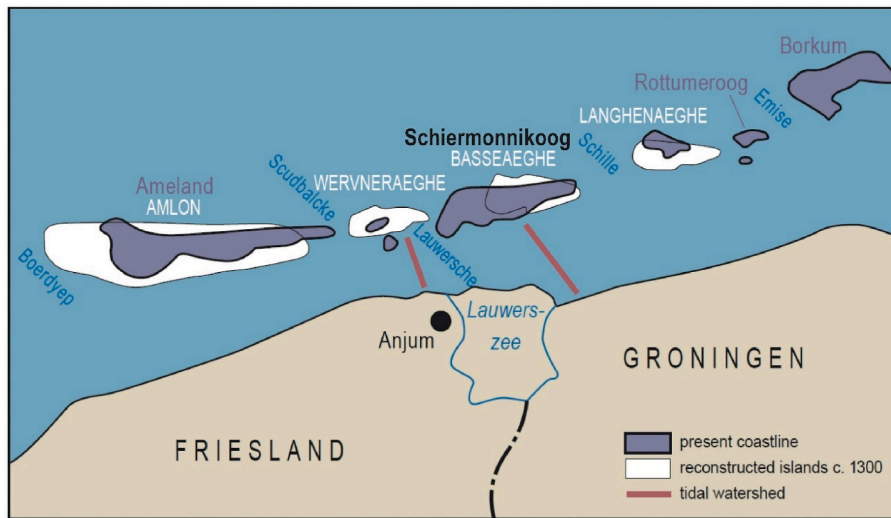
Fig. 6. Past (in white) and present (in purple) positions of islands between the North Sea and the Wadden Sea (see Fig. 1). The present island of Schiermonnikoog (black) is situated east of the former island of Wervneraeghe (white) (online version in colour).

resuspended by waves (Wang et al., 2018). The presence of mud itself also promotes its sedimentation. The reasons may be physical (related to bed roughness and erodibility of the substrate) and/or biological, namely, stickiness of benthic diatoms growing over mud beds (Oost et al., 2021). It is not known to which extent bio-engineers can fixate sediment. As a positive correlation is found between basin area and

Fig. 7. Dynamics of inlet of the tidal basin Eilanderbalg/Lauwers near the barrier island of Schiermonnikoog. There is a dynamic resulting in growth of the island at the eastern tip, at the one hand, and approach of the gully at the other hand. Position of gullies in 1988: green; in 2000: yellow; in 2007: blue. The situation in 2017 was similar to 2007 (see Fig. 3) Courtesy Rijkswaterstaat (online version in colour).

channel area, closing the Lauwerszee must have resulted in reduction of the channel area. At present, both the tidal basins Zoutkamperlaag and Eilanderbalg/Lauwers include 10% area above MHT (salt marsh + pioneer vegetation), 70% low dynamic and part of each tide emerged (intertidal flats), including 2% high-, 35% mid- and 35% low littoral, and 20% high dynamic sublittoral tidal channels) (Fig. 3). (Baptist et al., 2019). Most silt is found along the mainland coast and tidal watershed with low dynamics. Forty percent of the low dynamic areas are silty, 60% is sandy (Fig. 3).

The tidal inlets near the island tail of Schiermonnikoog were very dynamic during the past decades (Fig. 7). Currently, the inlet at the eastern point is inching closer to the island, which might in turn cut off the tail thus preventing any further extension of the salt marsh to the east. This seems to happen, considering its position in 2020 (Fig. 3).

Interaction between abiotic and biotic factors. Most benthic organisms cannot survive in the very dynamic part of the tidal basin. These organisms play, however, an important bio-engineering role in low dynamic parts of tidal basins (Baptist et al., 2019). Benthic fauna plays a role in bio-destabilization, bio-deposition and bio-stabilization. Bioturbation-induced sediment mixing and bio-destabilization may result in net sediment export out of an embayment, whilst bio-deposition and bio-stabilization by filter/suspension feeders tend to alter an embayment toward a net sediment import environment. Hence, bioengineering benthic fauna is able to modify large-scale hydro-morphology (Arlinghaus et al., 2022). Also Stal (2010) indicates the role of microphytobentos in intertidal sediment stabilization.

2.2. Island head: sand, water, benthic organisms except for high dynamic channels

The island head consists of sandbanks of the flood-tidal and ebb-tidal deltas without human interference.

The tidal current in the inlets between barrier islands results in a flood- and an ebb-tidal delta, consisting of sand banks separated by channels. These channels and sand banks migrate from west to east under the influence of the tidal flow and the longshore sediment transport by littoral drift (Wang et al., 2012).

The flood-tidal delta sandbanks joined up with a large sandbank south of Schiermonnikoog. The flood-tidal delta shift towards the axis of the tidal inlet initially replaced the channel towards the southwestern point of the island, with subsequent erosion of dunes and salt marshes. Later, during the period 1825–1840, the sandbanks grew together which resulted in the 1960s in a single huge sandbank (Fig. 3) (De Haan et al., 1983; Bakker et al., 2005b).

The closure of the Lauwerszee reduced the water movements of the tidal inlet with a subsequent contraction of the ebb- and flood-tidal delta. The ebb-tidal delta sandbanks moved eastward and one after the other became attached to the island. Along-shore currents from west to east govern sediment supply. The periodic supply of sediment from the ebb-tidal delta to the down-drift island results in a highly fluctuating coastline of the island head at the northwestern point of Schiermonnikoog. About every 25 years the beach width suddenly increased by 300 m, and gradually decreased again by 150 m. Hence, the position of the coastline showed a seaward trend in the period 1880 to 1990 (Wang et al., 2012). The width of the beach between dune foot and low tide increased from 200 m in 1880 to nearly 1000 m in the 1980s (Wang et al., 2012). Its area increased from 4 km^2 in 1860 to 13 km^2 in 2010 (De Groot et al., 2017b).

When sandbanks approached the western part of the island, a narrow inlet was formed close to the island. This resulted in erosion of the northwest point in the 1920s. When the sandbanks grew together with the island in c. 1960, a broad beach developed at the northwest point, and new dunes established. The arrival of a new sandbank in the 1980s resulted in the current wide beach along the west coast in the 2000s (Fig. 3).

Interaction between abiotic and biotic factors. Most benthic

organisms cannot survive in the very dynamic part of the flood- and ebb-tidal deltas. A small salt marsh of deposited silt with the help of benthic organisms and plants developed in the shelter of a large sandbank attached to the island in the 1990s.

2.3. Dune arc complex: sand, wind, groundwater, plants, animals

Sand and wind build dunes together with bioengineering plants. Once dunes have stabilized, a continuous interaction between abiotic and biotic factors starts resulting in accumulation of organic matter and natural succession to forest. In the meantime de calcification occurs as a result of leaching. Development of new dune arcs created a chronosequence of 400 years. Human interference by introduction of rabbits and especially livestock grazing at the one hand retards succession and increase biodiversity. At the other side intensive farming in the polder results in atmospheric deposition and enhances succession. In dune slacks succession can be prevented by a plant species. Human interference by groundwater extraction reduces seepage into the dune slacks.

Coastal dunes show a particular development due to the interaction between sand, wind, groundwater, plants and animals. The first step in dune formation is sand fixation. Dunes are typical examples of biogeomorphic systems that are strongly shaped by the interaction between sand transport by wind and water and plants that can trap and stabilize sand particles. On a broad (~300 m) sandy beach, which allows for sufficient wind-driven sand transport, the pioneer plant species Sand couch (*Elytrigia juncea*) can establish and trap sand to initiate embryonic dune formation (Van Puijenbroek et al., 2017). It spreads horizontally over a large area and hence builds low but wide embryonic dunes. Marram grass (*Ammophila arenaria*) can establish on embryonic dunes or on higher elevated sandy beaches. In contrast to *E. juncea*, *A. arenaria* has a more patchy and dense growth strategy, which leads to the formation of more hummocky embryonic dunes (Reijers et al., 2019b). Combined with its ability to develop vertically expanding rhizomes it can tolerate sand deposition of up to 100 cm yr^{-1} (Huiskes, 1979; Keijsers et al., 2015), and hence build high coastal dunes which allow the species to escape seawater flooding. Seawater flooding negatively influences plant growth by increasing osmotic stress and physical drag forces (Baye 1990). However, occasional seawater flooding can also be beneficial for plant growth by depositing marine derived nutrients. By accreting sediment and building high coastal dunes, *A. arenaria* is also adapted to grow under very low nutrient availability (Kooijman and Besse, 2002; Reijers et al., 2020)

Over time, the individual embryonic dunes can merge together resulting in the formation of large fore- or yellow-dune complexes. If the beach is wider than 300 m (Van Puijenbroek et al., 2017), another range of embryonic dunes may develop on the seaward side of the yellow dunes. When finally the dunes have grown so high and wide that sand transport no longer reaches over the dune crest, sand accumulation stops (Durán and Moore, 2013). *Ammophila arenaria* then becomes vulnerable for root-attacking nematodes in aging sand layers (Van Der Putten et al., 1988). Decreased vitality of *A. arenaria* initiates succession to grey dunes (Van Der Putten and Peters 1993). On the Wadden islands the grey dunes have eventually formed a large dune arc which protects most of its inhabitants. The initial parabolic shape emerges when the central part of the dune is stabilized by for example vegetation while constant winds cause sand to drift up to the eastward or westward edge of the dunes (Hesp, 2002; Baas and Nield 2007). Parabolic dunes can also form on non-vegetated small embryonic dunes, and can easily be blown away. The fresh sand from the sand banks that built Schiermonnikoog at the present position is rich in CaCO$_3$. Hence, dynamic yellow dunes of Schiermonnikoog are calcium rich, especially the embryo and yellow dunes (CaCO$_3$ content 0.5–3.5%) (Bakker 1976). The eastward spreading of the island is reflected in the CaCO$_3$ content of the dune sand. Once sand has been deposited, its amount of CaCO$_3$ decreases as a result of leaching. Old dunes (formed around 1600) in the western part contain 0.1–0.9% CaCO$_3$, dunes (formed around 1870) in the middle part

0.5–1.0% CaC0$_3$ and the young Willemsduin (formed around 1920) in the eastern part 1.3–1.8% CaC0$_3$ (Leertouwer in Sival 1997). In other sites on Schiermonnikoog 0.1% CaC0$_3$ (250 yr), 0.50% CaC0$_3$ (120 yr), 0.75% CaC0$_3$ (20 yr) was measured for the top soil 0–5 cm, and 0.05% CaC0$_3$ (250 yr), 0.1% CaC0$_3$ (120 yr) and 0.5% CaC0$_3$ (20 yr) at deeper soil 10–20 cm, respectively. The organic matter content increased to 3% of the soil dry weight after 250 years of dune soil development (Rozema et al., 1985). This series of dunes represents a chronosequence. Schiermonnikoog has a small part of old leached dunes, as a result of the eastward spreading of the island, compared to other barrier islands with fixed positions (Westhoff and Van Oosten 1991).

The original beach plain gets shielded by the dune arc from intensive winds. Low lying places are affected by fresh water from the surrounding dune ranges. A large fresh water body is present underneath the island, with a maximum depth of 85 m, and a maximum elevation of 3.2 m NAP (Dutch Ordnance Level) (Beukeboom 1976; Grootjans et al., 1996). The water level of the fresh water body in the dune massif is higher than the heavier sea water. As a result, the generally calcareous groundwater begins to flow and wells up in low-lying dune slacks, promoting the establishment of calciphyte pioneer communities (Grootjans et al., 1996; Lammerts et al., 1999). The oldest dune slack on Schiermonnikoog developed in the shelter of the original dune arc. Later new slacks developed after formation of younger dune ridges, both north-east and north-west of the dune arc. Although the position of dune slacks over the island is different, they show similar data with respect to amounts of CaCO$_3$, namely, 0–0.2% in an old slack of 400 year, 0.1–1.1% in an intermediate slack of 100 year and 0.8–2.9% in a young slack of 30 year (Lammerts and Grootjans 1998). Soil pH in dune slacks decreased from 6 in a 10-year old slack to 4 in a 150-year old slack (Rohani et al., 2014). This suggests that the different dune systems of the island represent a chronosequence, featuring stages of increasing age, with the caveat that no disturbance with set-back takes place. Most basiphilous dune-slack plant communities show an optimum after 25 years, decline after 35 years and disappear within 100 years with ongoing succession. With mowing they can, however, maintain themselves longer (Lammerts and Grootjans 1998). In case of a steady supply of groundwater throughout the year, basiphilous pioneer plant communities can persist much longer. Some cases have been reported that pioneer stages with basiphilous vegetation can persist for more than 100 years (Adema et al., 2001, 2005), even without regular mowing. In such cases a pioneer plant Shoreweed (*Litterella uniflora)* can prevent accumulation of organic matter in the soil as long as it is capable of keeping up a positive-feedback mechanism, by creating an oxic-anoxic gradient in the rhizosphere resulting in a combination of nitrification and denitrification. By doing this the small species can outcompete rapid growing grass species, such as *Calamagrostis epigejos*. *Littorella* keeps its own rootzone very poor in dissolved nutrients by oxygenation of its own root zone, by radial oxygen loss (ROL). When the groundwater has passed the root zone of *Littorella uniflora*, the environment becomes anoxic again and the dissolved nitrate is denitrified and is escaping into the atmosphere.

Soil Organic Matter (SOM) may establish during succession. Accumulation rates within soils in relation to ROL of the same successional stage were studied in several diachronic chronosequences. Two 50 to 60 year-old sites were sampled on Schiermonnikoog that developed around 1600 (Fig. 3): site-1 and -4. They are located in the same slack and have not been managed since ca. 1964, when sod removal took place. These sites were sampled 4 times with intervals ranging from 5 to 10 year. In 2010, site-1 was still in a pioneer stage, while site-4 was in a late-successional stage with scrubs and trees up to 5 m tall. Rates of SOM accumulation were remarkably different between sites. The 4 showed a steep trend during the last 20 years and had a high SOM content (15.8 kg m^{-2}) in 2010. Late-successional plant species, especially shrubs, dominated the vegetation. In contrast site 1, which was situated 50 m away in the same slack, showed a very low organic matter build-up of only 3.5 kg m^{-2} after 50 years. The vegetation was still in a pioneer stage, dominated by *Littorella uniflora*, showing the effect of ROL (Fig. 8)
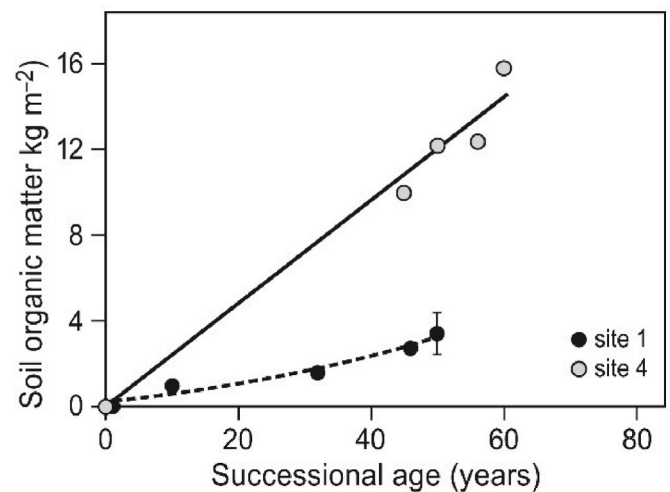

Fig. 8. Soil Organic Matter accumulation trend from diachronic chronosequences (50 and 60 years, respectively) of two sites within the same dune slack on Schiermonnikoog (Rohani et al., 2014).

(Rohani et al., 2014). The maximal accumulation of 17.5 kg m^{-2} was found in a slack of 150 years and this stage was dominated with trees (*Betula pubescens*). This suggests that SOM accumulation slowed down after 60 years.

The land side of the dune arc is influenced by surface water from the Wadden Sea, that initiates the formation of a salt marsh. Until c. 1850, the Kooiduinen formed the coastal defense at the eastern part of Schiermonnikoog, enclosing the salt marsh area south of it (Fig. 4). This salt marsh has been embanked in 1860, and transformed into the Banckspolder. Around 1850, the whole island east of the Kooiduinen was a vast bare sand flat with a few low dunes. After c. 1870, a great deal of sand probably became available for the creation of the parallel Kobbeduinen dune ridge, after the joining together of a sand bank from the ebb-tidal delta and the island. The landlocked beach plain between the two dune arcs received fresh seepage water from the adjacent dunes and transformed into a brackish marsh at the seaside and fresh marsh with Common reed (*Phragmites australis*) at the landside.

Natural forest developed on the dry dunes of Kooiduinen and Kobbeduinen with Rum cherry (*Prunus serotina*), Hawthorn (*Crataegus monogyna*), Pedunculate oak (*Quercus robur*), and Sycamore (*Acer pseudoplatanus*). The dune slacks showed low scrub with Creeping willow (*Salix repens*), later tall scrub and forest with Downy birch (*Betula pubescens*), Willow (*Salix* spp.) and Alder (*Alnus glutinosa*). Close to the village a pine forest (*Pinus nigra*) was planted since the 1910s and this had impact on natural processes by preventing wind erosion, and causing severe acidification of the top soil. Heavy storms and management created more variation due to spontaneous establishment of deciduous trees and a transition to mixed forest (Bakker et al., 2005c).

Rabbits are (introduced) natural grazers in dune systems. Livestock grazing in dunes was common practice in dune systems along the mainland coast and barrier islands. Apart from farmers, many individual people had a cow for own milk production. Dune and dune-slack formation can be delayed/altered/modified due to livestock grazing. Due to intensive grazing no forest over 100 year is found, despite the age of the oldest part of the dune arc. The first aerial photograph of Schiermonnikoog (1927)revealed large areas of bare soil in the central dune area, likely as a result of overgrazing by livestock and subsequent wind erosion. In the early 1970s still much bare soil was found, mainly in the western part of the island, due to natural wind erosion (Westhoff and Van Oosten (1991). Later, deliberate blow out of sand after removal of the vegetation was re-introduced, locally to groundwater level, which created new wet dune slacks (Bakker et al., 2005c). In the central part of the island, succession continued with sandy-grassy vegetation

decreasing from 95% coverage in 1959 to 60% in 1990, whereas low- and tall-shrub vegetation increased from 5% to 40% coverage (Van Til et al., 2000). A strong decrease of rabbits due to diseases may have played a role. Myxomatosis had a significant outbreak in 1956 and decimated rabbit density. Rabbit numbers recovered from it, but decreased again since the start of Rabbit Haemorrhagic Disease (RHD) around 1990.

Livestock grazing was re-introduced to prevent further establishment of tall-grass and scrub encroachment, and allowed wind erosion. Eutrophication due to atmospheric nitrogen deposition can cause grass encroachment and acceleration of vegetation succession (Sival 1997; Provoost et al., 2011), resulting in decreased area of wind-blown bare soil. Within the Netherlands, atmospheric deposition values increase in the Wadden Sea area from west (Texel) to east (Schiermonnikoog). Here they amount to 17 kg N ha^{-1} yr^{-1} in 2015 (De Groot et al., 2017b), most likely related to local sources such as intensive farming. Dune habitats are vulnerable to high nitrogen deposition rates, with critical loads set at 10–15 kg N ha^{-1} yr^{-1} for nutrient-poor habitats such as coastal (grey) dunes (Van Dobben et al., 2014). Groundwater extractions affect the hydrological system on the Wadden Sea islands by (locally) lowering groundwater tables and reducing seepage (Grootjans et al., 1996). This may have strong negative effects on dune-slack vegetation (Grootjans et al., 2002). In the 1950s, more and more tourists started to visit the Wadden Sea islands, resulting in a growing need for drinking water. Since then, the amount of groundwater extracted increased very fast until the mid-1980s (De Groot et al., 2017b).

2.4. Island tail with salt marshes: silt, water, plants, animals

Silt and water build salt marshes together with bioengineering plants in the shelter of the dune arc, thus creating gradients for many other biota. Abundant sand supply and strong easterly alongshore transport caused spit development at the eastern end of the barrier. The enabled to study a chronosequence covering 150 years with increasing thickness of sedimented silt, including autocompaction. Human interference reduced the salt marsh by embankment of the polder for coastal protection in 1860, that is now exploited for intensive farming. The salt marsh is used for cattle grazing that reduces the dominance of a single tall grass with natural succession. It allows dynamics with geese and hares, thus enhancing biodiversity. Trampling cattle results in reduced accretion by biocompaction of the soil, interfering with bioturbation by a bioengineering invertebrate animal.

Initially the island tail is a bare, dynamic sandbar. The relationship between sandbar and barrier island can be bi-stable. Plants can trap sediment and have to grow fast enough to build a salt marsh and survive storms, otherwise the systems returns to a sandbar (Vinent and Moore 2015). The wind transports sand to form low embryonic dunes. The beach dunes will broaden and eventually join together to form a coastal dune strip breached by depressions. During storm floods, seawater flows through these lower areas, which are in fact small wash overs. In the lee of the dune strip, a salt marsh will be formed. Salt marshes are typical examples of biogeomorphic systems that are strongly shaped by the interaction between sand and silt transport by water and plants that trap suspended sediment during inundation at high tides. The result may be a stepwise increase in height above sea level (Vinent and Moore 2015). Once the embryo dunes become grown together, they offer shelter from wave action from the sea and allow the establishment of salt-marsh plants that can trap sediment. In the first stage geomorphological processes dominate, fine sediment is deposited, creeks are formed due to tidal action, influenced by the topography of the intertidal sand flats and the presence of establishing pioneer plants, especially Glasswort species (*Salicornia* spp.) and Cord grass (*Spartina anglica*). In the second stage, vegetation increasingly affects creek formation. Seawater flows into and out the salt marsh through creeks every tide. The water flow is redirected by vegetation clumps, especially of *S. anglica* which enhances flow velocity and erosion in the lower parts. On the higher parts concurrently,

vegetation cover increases, enhancing the sediment fixation and reinforcing the incision of creeks in the lower parts. Especially Common saltmarsh grass (*Puccinellia maritima*) is important in trapping silt. With increasing surface elevation of the marsh in the third stage, the creeks deepen, and expand by head-ward erosion, the flooding frequency decreases, and the vegetation shifts to late-succession stages. Dominant plant species in this third stage are Red fescue (*Festuca rubra*) and Sea couch (*Elytrigia atherica*). In the fourth stage, the formation of levees may induce poorly drained depressions. Although these depressions may have a high surface elevation, the poor drainage conditions may cause the reestablishment of pioneer vegetation at the expense of late-succession vegetation types (Esselink et al., 2017). Salt-marsh plants protect the surface from vertical erosion (Friedrichs and Perry 2001). The higher sedimentation in the seaward parts results at some stage in the formation of a high marsh ridge, and eventually a marsh cliff will develop (Van de Koppel et al., 2005). Sediment trapping at the marsh edge is enhanced by plants causing wind wave attenuation (Möller 2006). Once deposited on the salt-marsh surface, the fine-grained sediment consolidates due to auto-compaction. It can be misleading to measure salt-marsh accumulation by means of level change alone. On the Skallingen back-barrier marsh in the Danish Wadden Sea, a constant accumulation can give half of its initial value of accretion (thickness change/time) after about 70 years of sedimentation (Bartholdy et al., 2010). Fertilization experiments showed that N and P are limiting for plant production on back-barrier salt marsh with a thin layer of silt (Van Wijnen and Bakker 1999), in contrast to mainland marshes with a thick layer of silt (Nolte et al., 2019). This makes back barrier-island salt marshes vulnerable for atmospheric deposition.

Closure of the Lauwerszee in 1969 still seems to influence the erosion of the salt-marsh edge of Schiermonikoog. Locally, it might have resulted in erosion of about 50 m of the oldest part of the salt marsh and cliff formation in the 1970s (Bakker 1989). The cliff existed, however, already in the 1950s (Den Hartog 1952), suggesting a longer-term process of erosion and lateral accretion of the salt marsh at its edge (Van De Koppel et al., 2005). Indeed, a former cliff at the edge of the salt marsh between 1800 and 1850 (Fig. 9) seems to exist about 100 m further inland from the present edge. It might be the result of the embankment of the Banckspolder in 1860.

The barrier island of Schiermonnikoog extends eastward with spreading of salt marshes in the shelter of dunes towards the east thus featuring a chronosequence (Olff et al., 1997). The comparison of old maps and aerial photographs on which the establishment of vegetation could be recorded, revealed the increase of the salt-marsh area during the past two centuries (Fig. 9) (De Groot et al., 2015). The border between the coarse-grained sandy base layer and the fine-grained silty top layer can easily be discovered using a narrow auger (Fig. 10). The thickness of the silt layer depends on the position in the salt marsh. Detailed measurements of silt-layer thickness on the salt marsh of Schiermonnikoog (near creek 7, see Fig. 24) show thicker layers near the sediment supply routes, namely the edge of the salt marsh and the creeks (Fig. 11). This might give the impression that further from the edge of the marsh a 'bath-tub' depression can develop. The hindered sediment supply from the North Sea by sand-drift dikes is not compensated everywhere by extra input from fines from the Wadden Sea. This leads to relative deepening of the areas directly landward from the sand dike (Oost et al., 2017).

The salt marsh showed an elevational gradient from the low dunes into the salt marsh (Fig. 12). The thickness of the silt layer is related to the elevational gradient: thin at the higher marsh and thicker at the lower marsh. Moreover, the age of the salt marsh is reflected in the thickness of the silt layer: thin at the young marsh and thicker at the older marsh along the chronosequence (Fig. 13). Surface elevation change (SEC) varies along the chronosequence. Cumulative SEC over 24 years amounted to 8 cm (3.2 mm yr^{-1}) in the young marsh (established 15 and 30 year before start of measurements), to 3.5 cm (1.4 mm yr^{-1}) in the intermediate aged marsh (55 year), and was negative −1.7 cm
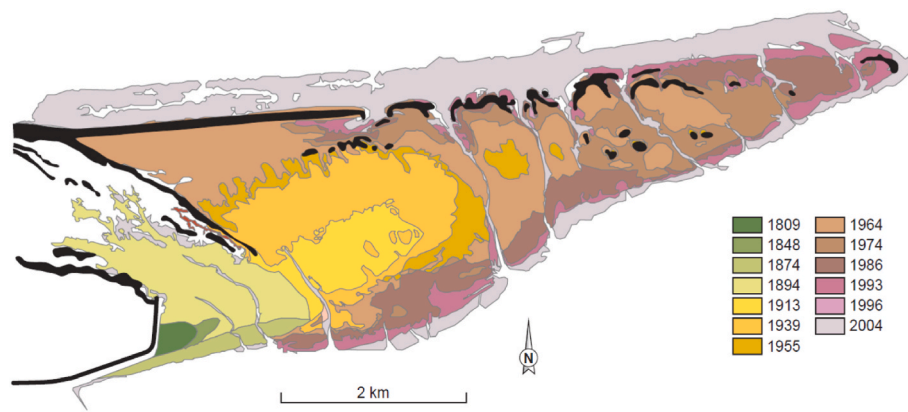
Fig. 9. Eastwards expansion of the salt marsh on the eastern part of the barrier island of Schiermonnikoog (colour key shows successive stages). On the north side the salt marsh is protected from the sea by dunes and a sand-drift dike (black). On the south side the Wadden Sea can daily inundate lower parts of the salt marsh, whereas the polder is protected by the seawall (black) (De Groot et al., 2015) (online version in colour).

(-0.07 mm yr^{-1}) in the old marsh (120 year) in the chronosequence, likely as a result of autocompaction of older salt-marsh locations (Fig. 14).

Along this chronosequence, plant species succeed each other from Common saltmarsh grass (*Puccinellia maritima*), Common sea lavender (*Limonium vulgare*), Red fescue (*Festuca rubra*), Sea wormwood (*Artemisia maritima*) and finally the tall grass Sea couch (*Elytrigia atherica*). Repeated detailed measurements on young (first vegetation colonization in 1996) and older marshes (first vegetation colonization in 1974) illustrate the spread of the late-successional plant species *E. atherica* in space and time (Fig. 15). The coverage of this species over the entire salt marsh of Schiermonnikoog strongly spread from 1 ha in 1958 to 354 ha in 2016 (Veeneklaas et al., 2013) (Table 1). Importantly, *E. atherica* is not always the final succession stage. It can locally disappear and be replaced by communities with Saltmarsh rush (*Juncus gerardii*) and Common reed (*Phragmites australis*) far away from the intertidal flats. This is likely related to seepage of fresh water from the adjacent low dunes (Veeneklaas et al., 2013).

Fresh sediment contains nutrients, such as organic and inorganic nitrogen, resulting in a positive correlation between the thickness of the silt layer and the total N pool (Olff et al., 1997) and N-mineralization (Bakker et al., 2005a) on back-barrier marshes. Hence, the chronosequence represents a productivity gradient. Early in succession, on bare sandy soil, external input from marine sources such as macroalgae and sea bird guano plays an important role (Schrama et al., 2012). In this early stage, large numbers of Diptera, especially the Seaweed fly (*Fucellia maritima*) occur under decaying algae, as well as microbivores and their predators. This stage thus harbours a food web dominated by detritivores (i.e., the so-called brown web) and a low plant standing biomass. Stable isotope analyses revealed that marine-derived N is not only found in the various trophic groups of the brown web, but also in the pioneer plants at this stage (Schrama et al., 2013a). Fungal (Dini-Andreote et al., 2016) and microbial soil communities revealed a transition gradient from initially marine-driven to a terrestrial driven system (Dini-Andreote et al., 2018). Soil organic matter (SOM) increased significantly with age, and bacterial and fungal community sizes increased through soil development (Dini-Andreote et al., 2018). Intermediate succession stages are characterized by a strong increase in above-ground standing live plant biomass, hence, a dominance of the green web. This is accompanied by a strong increase in the biomass of small plant-feeding insects and intermediate-sized herbivores e.g., geese and hares. Late-successional stages show increase in dead biomass in the form of plant litter. Beach hopper (*Orchestia gammarellus*), a litter-feeding terrestrial crustacean becomes dominant in the final stages of succession (Schrama et al., 2012), which is characterized by dominance of the brown web. This bioturbator creates oxic conditions by

digging in the upper layer of the sediment. This increases redox potential and net N-mineralization and promotes dominance of the tall grass *E. atherica* (Schrama et al., 2015). *Elytrigia* and *Orchestia* occur in both high (50 cm + MHT) and low (25 cm + MHT) salt marsh. Local environmental conditions, such as elevation affect the bacterial communities in external sources, here plant litter and soil, which in part determine digestive tract composition of the host microbiome, i.e. *Orchestia*. However, the enrichment of specific potential symbionts is constant and in high abundance regardless of the local environmental conditions. The outcome of this stable proportion might determine the success in the performance and distribution of *O. gammarellus* at contrasting salt-marsh elevations (Garcia Hernández et al., 2021).

Grazing by large herbivores, such as livestock is a common practice on salt marshes. They cause soil compaction by trampling, with subsequent reduced soil elevation, increased bulk density, reduced pore volume, reduced air-filled porosity, increased water-filled porosity, increased water content, less oxygen in the soil, reduced redox potential, and hence reduced rates of net N mineralization on grazed sites compared to ungrazed sites (Schrama et al., 2013b). Reduced pore size in a compacted soil increases the water holding capacity, because the fraction of small pores becomes much larger in a fine-textured soil. This is the case for silt in a salt marsh when measured as the relative fraction of the amount of pores (Schrama et a. 2013c). During inundation events, fresh sediment is deposited on top of litter, resulting in a layer consisting of alternating thin layers of sediment and buried litter on top of a soil column consisting of silt (Lagendijk et al., 2022) (Fig. 16). This coincides with a strong decline in the abundance of *O. gammarellus* and a resulting decrease in bioturbation and litter degradation. Such differences were particularly found on salt marsh with fine-grained sediment. Barnacle geese (*Branta leucopsis*) were found to depend on the facilitation by livestock (Bos et al., 2005), and hares also profit from the enhanced foraging conditions created by livestock on older salt marshes (Kuijper et al., 2008). High densities of livestock, hares, geese, and herbivorous invertebrates turn the brown web back to a green web (Schrama et al., 2012; Bakker et al., 2015). In the oldest part of the salt marsh, livestock together with intermediate-sized herbivores reduces vegetation height, increases bulk density and shows 1 cm lower surface elevation than the ungrazed site during a 22 years experiment, whereas sediment input is similar in both sites (Elschot et al., 2013). A 46 years experiment revealed 4–7 cm lower surface elevation in grazed compared to ungrazed sites. This long-term experiment revealed that trampling by livestock affected the biotic component by increasing root density, and the abiotic component by increasing bulk density of the fine-grained silt layer, and together the resistance against erosion despite the lower surface elevation compared to ungrazed sites (Fig. 17) (Marin-Diaz et al., 2021).
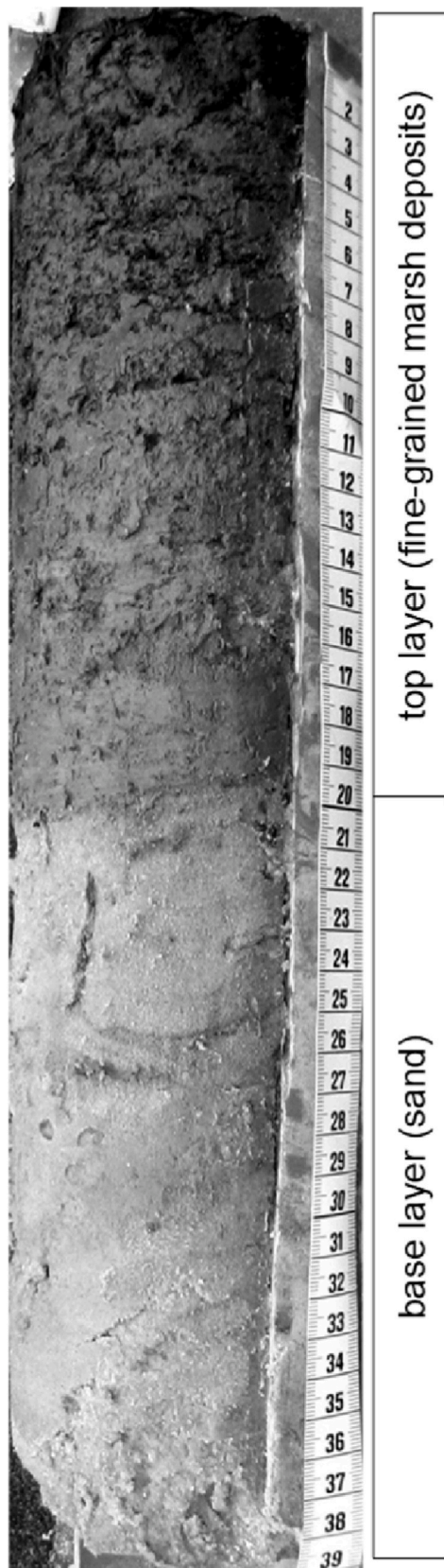
Fig. 10. Example of a core of salt-marsh sediment from Schiermonnikoog. The sediment consists of a layer of fine-grained, predominantly mineral salt-marsh deposits (dark) on top of sand (light). Scale in cm. (De Groot et al., 2011a).

Plants and their interactions with livestock and *O. gammarellus* facilitate a patchy vegetation mosaic. Alternating patches of short and tall vegetation are governed by the interplay of two important biotic processes: biocompaction and grazing by large herbivores locally impairs soil conditions, and promotes lawn communities without *O. gammarellus* alternating with bioturbation and by soil fauna that locally ameliorates soil conditions, promoting tall plant communities in absence of large grazers. These alternating patches also differ strongly in the composition of microbial-feeding invertebrates, due to differences in pore size distribution and microclimatic conditions governed by differences in vegetation height. The opposing and self-reinforcing mechanisms of bioturbation and biocompaction, are ultimately responsible for maintenance of the status quo: where patches are kept in a particular state that can last for decades (Howison et al., 2017). Vegetation patterns in grazed salt marsh can be induced by avoidance of unpalatable species such as Sea rush (*Juncus maritimus)*. The leaves are physically defended against herbivory through heavy structural investment and sharpened leaf tips. *Juncus maritimus* protects surrounding plants from herbivory (associational resistance). Hence, patches of tall vegetation occur in grazed salt marsh, and have a litter layer and *Orchestia gammarellus* is present, but in lower amounts as in ungrazed salt-marsh vegetation. However, soil compaction is comparable to the soil under short vegetation, as cattle trample the soil when walking through the *J. maritimus* patches (Lagendijk et al., 2022).

2.4.1. Small-scale patterns in the salt marsh: legacy of intertidal flats, ants and beach hoppers

Apart from homogeneous salt marsh, small-scale topographic heterogeneity (of a few m^2) occurs along the chronosequence on Schiermonnikoog. The salt marsh may appear homogeneous but actually has a small-scale topographic heterogeneity. It is a repetitive pattern of higher elevated hummocks surrounded by lower elevated depressions (Fig. 18). The soil consists of an elevated fine-grained sediment layer on the underlying flat coarse-grained substratum of the intertidal flats formed before salt marsh started to develop. On top a layer of fine-grained sediment is found, which formed during marsh development. During early salt-marsh development, up to 15 years, higher elevated hummocks accumulated more fine-grained sediment, thereby enhancing the elevational differences that were already present. This is followed by a period with higher marsh accretion rates in the depressions. However, as marsh development continued, the patterns stabilized and similar salt-marsh accretion rates were measured on hummocks and in depressions after 55 years. Ultimately, the patterns stabilized and were able to remain for 120 years (Elschot and Bakker 2016).

Plant species such as *Puccinellia maritima* and *Limonium vulgare* first dominated on the hummocks but were found to become dominant in the depressions only in a later stage. *Festuca rubra* dominated the hummocks from early stages onward, and was accompanied by *Elytrigia atherica*. Thus, two co-occurring succession stages within this small-scale topographic heterogeneity of a few square metres explained the increase in local plant diversity found throughout the chronosequence. Even at 120 year-old salt marsh the presence of topographic heterogeneity enhanced plant diversity (Elschot 2015). On an area of 20 m × 30 m small-scale depressions coincide with small-scale elevations with an absolute difference of about 40 cm (Fig. 19). This causes differences in soil water content, resulting in dominance of *Juncus maritimus* in depressions and *E. atherica* on elevations. Moreover, elevation-induced soil moisture differences not only cause variation in vegetation composition but also in community composition of microbivorous arthropods (Widenfalk et al., 2015) and the distribution of macrodetritivores such as the Common striped woodlouse (*Philoscia muscorum*) in depressions and the terrestrial amphipod *O. gammarellus* in elevations (Zwiggelaars 2012).

Small-scale elevational differences are not only caused by the interaction between geomorphology, plant species and, subsequently differences in sedimentation rates. Other organisms, such as soil animals contribute to small-scale heterogeneity in elevation by locally increase
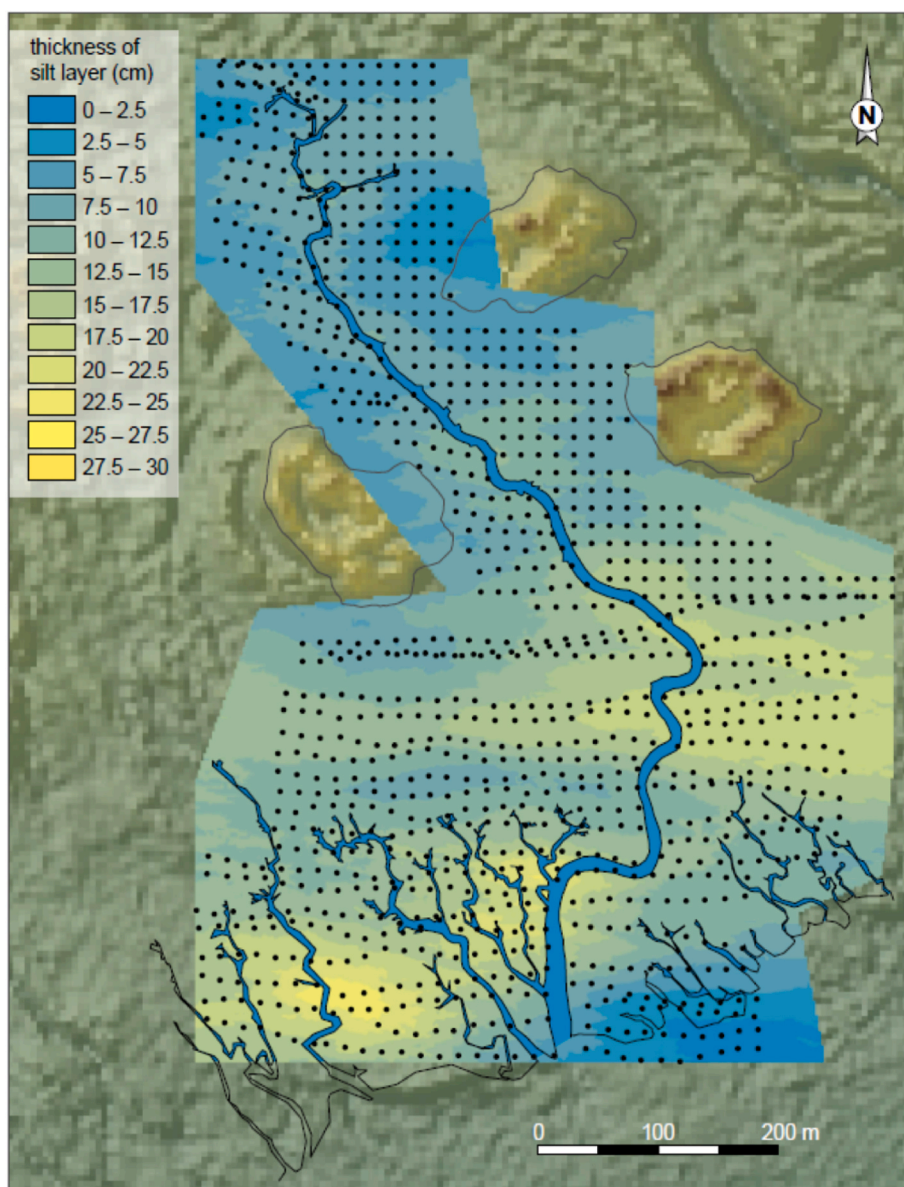
Fig. 11. Thickness of the silt layer, established since around 1974 on top of a course-grained sandy base in a catchment area around creek 7 (see Fig. 24) at Schiermonnikoog in 2010. Measuring points (dots) have been extrapolated with kriging. Individual points (dots) are indicated (Elschot et al., 2017) (online version in colour).

soil height due to nest building (Yellow meadow ants) and soil bio-turbation (Beach hoppers).

Yellow meadow ants (*Lasius flavus*) are subterranean social insects, that by digging up soil build nest mounds of 0.1–1 m in diameter, up to 0.5 m tall. Yellow ant nests are typically found in areas with a low inundation frequency, hence, on the older marsh dominated by *Elytrigia atherica* (Boomsma et al., 1987). In salt marsh developed from 1939 onwards (Fig. 9), corresponding to roughly 200 cm + MHT (Fig. 12) significant numbers of *L. flavus* nests can be found locally, from a few up to 20 mounds on a 10 m × 10 m scale. They locally alter abiotic and biotic soil properties by digging up fresh soil for their mound and in combination with differences in microclimate results under some con-ditions in a different plant community composition on and off *L. flavus* nests and hence in small-scale plant community patches (Veen et al., 2012). Mound vegetation is accessible and often preferred by hares. The interaction between subterranean *L. flavus* and hares resulted in a further shift in plant community composition, as hares specifically elected for high quality patches on ant mounds. In contrast, cattle

exerted a more homogeneous grazing pressure on and of ant mounds thereby overruling effects of ants on plant community composition (Veen et al., 2012). Moreover, in presence of cattle grazing soil compaction occurs and trampling strongly reduces the vitality of *L. flavus* colonies (Howison et al., 2017). Both factors reduce the influ-ence of *L. flavus* on soil elevation.

Next to L. flavus nest mounds, the presence of terrestrial amphipods from the family Talitridae, also known as beach hoppers, can increase soil elevation, albeit on a smaller vertical scale than *L. flavus* mounds. The dominant litter-feeding species *Orchestia gammarellus* has the ability to dig into the soil, creating pore space and elevate the soil level (Fig. 16) (Schrama et al., 2015). This species is typically found at lower elevation than the ant *L. flavus*, with its highest abundance on the border of the vegetation types dominated by plant species *E. atherica* and *Festuca rubra*. Their abundance can be as high as up to 2000 individuals m^{-2} and is positively correlated with vegetation height, while they are absent on short- grazed vegetation (Schrama et al., 2012; Smallegange and Berg 2019). In exclosures erected on the grazed marsh, excluding livestock
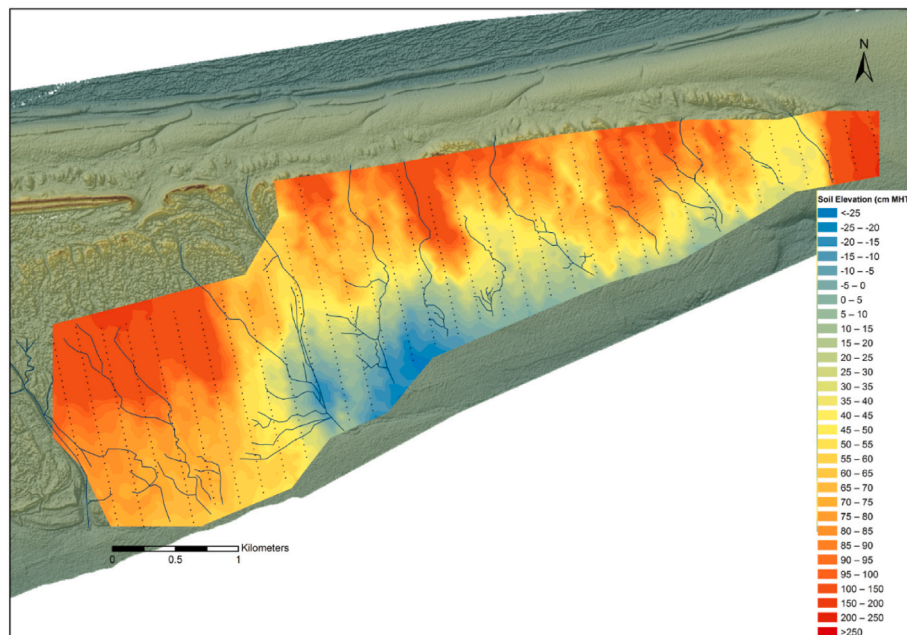
Fig. 12. Elevation (in cm Mean High Tide MHT) of salt-marsh surface of the eastern tip of the back-barrier marsh of Schiermonnikoog in 1997 (Bakker 2014). Every dot indicates a measuring point (n = 800) (online version in colour).

Fig. 13. Thickness (in cm) of the silt layer on top of the course-grained sandy base on the eastern tip of the back-barrier marsh of Schiermonnikoog in 1997 (Bakker 2014). Every dot indicates a measuring point (n = 800) (online version in colour).
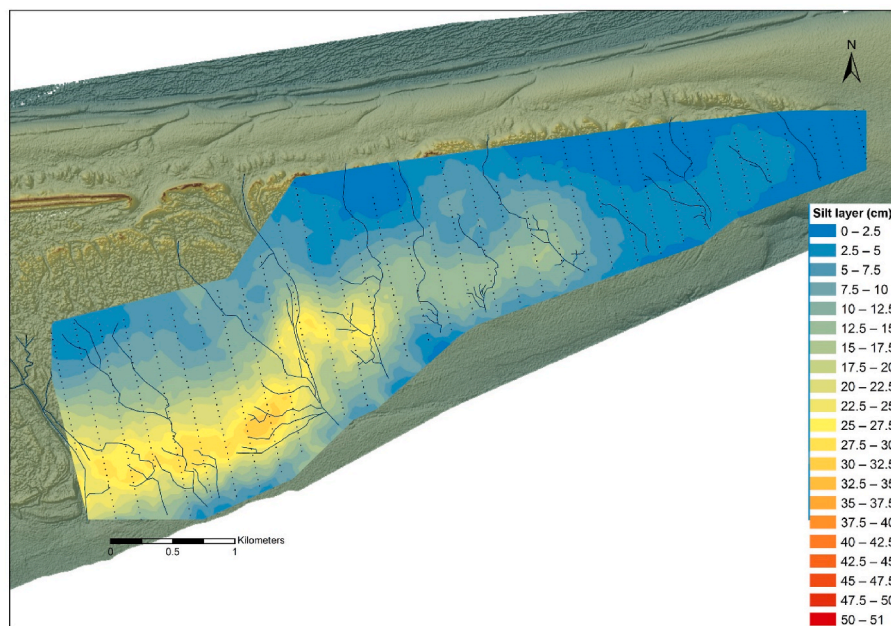
grazing and trampling for over 40 years, *O. gammarellus* is very abundant (Lagendijk et al., 2022) and it can be clearly observed that soil elevation is 7 cm higher than the surrounded grazed and trampled vegetation (Marin-Diaz et al., 2021). The combination of tall vegetation, *O. gammarellus* abundance, plant roots and litter accumulation in the ungrazed site together with soil compaction in the grazed site results in this surface elevation difference. In comparison to *L. flavus* mounds digging behaviour by *O. gammarellus* results in a more evenly rise in elevation horizontally and does not contribute to small-scale heterogeneity in height (Lagendijk et al., 2022).

2.5. Island tail with wash-over complex: sand, water, plants, animals

Storms transport sand from the beach into the adjacent salt marsh in wash-over complexes. They contribute to accretion of the salt marsh by thin layers of sand with sedimented silt. This dynamic process causes set back of salt-marsh succession, thus maintaining a dynamic biodiverse system. The building of the artificial sand-drift dike was initially meant for coastal protection, but later the by storms damaged eastern part was abandoned and left to natural dynamics. In the shelter of the sand dike, scrub developed on the low dunes. The part adjacent to the dune arc received fresh seepage water and changed into a reed marsh with bioengineering geese.
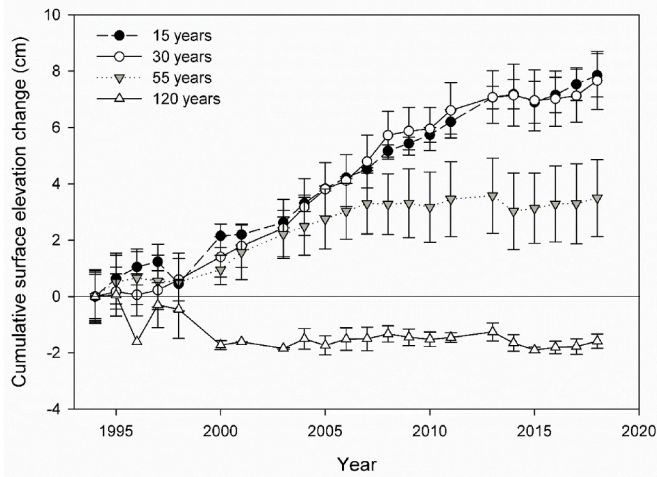
Fig. 14. Cumulative surface elevation change (cm) between 1994 and 2018 in the natural chronosequence of the back-barrier salt marsh on Schiermonnikoog. The number of years since first establishment of vegetation before 1994 is indicated. Sedimentation Erosion Bars were established at 40 cm + MHT.

On island tails the coastal dune barriers are intersected with low-elevated areas that function as wash-over complexes. Here, at spring tide, in combination with storm surges from the northwest, water from the North Sea washes over the barrier islands from north to south. Small embryonic dunes formed by the pioneer plant species *Elytrigia farctus* can be churned up. This occasional inundation event, called over-wash, deposits a considerable amount of coarse-grained sediment (i.e. wash-over deposits) on the already present wash-over plain or the back-barrier marsh (Hoekstra et al., 2009; Masselink and Van Heteren 2014). On the mesotidal (tidal range of ~2.4 m) Wadden Sea barrier islands over-wash naturally occurs during strong autumn and winter storms that generate severe wave and wind set-up (Wesselman et al., 2017; Engelstad et al., 2017). During over-wash the front-barrier environment can be eroded and sediment of the beach and dune-face can be redeposited, after which aeolian transport takes over (Nielsen and Nielsen, 2006). This natural sediment-sharing capacity of barrier islands

promotes vertical back-barrier marsh accretion and sea-level rise compensation (FitzGerald et al., 2008; Lazarus and Armstrong, 2015). The wet sandy soil in the low elevation inter-dune area is often covered with a mix of microbial mats, salt-marsh vegetation and dune vegetation, resulting from the combination of calcium-rich seepage water from the dunes and coastal over-wash. The irregular supply of salt water and fresh sand disrupts vegetation succession to tall grasses and scrub and can start anew.

On the eastern side of Schiermonnikoog a 2 km wide wash-over complex was present east of the dune arc Kobbeduinen with direct connection to the Wadden Sea through the third creek (Fig. 20).

The situation was similar to the present island of Spiekeroog (Germany). Following the North Sea flood of 1953, combined with the deepening and expansion of the third creek (see Fig. 24) in the northern direction led to the construction of a sand-drift dike for coastal protection in 1958 (Oost et al., 2012; de Groot et al., 2017a). The area was hardly vegetated in 1959 by Sea milkwort (*Glaux maritima*) and Glasswort (*Salicornia europaea*) in the plain and Sand couch (*Elytrigia farctus*) and Marram (*Ammophila arenaria*) on pioneer dunes (Van Der Veen et al., 1997). After a few large storm events and associated breaches in the end of the 1960s, active management was ceased in 1972 and the breaches were left open, which functioned as narrow funnel-like wash-over complexes connected to creeks from the Wadden Sea, as they are smaller than the natural opening before the sand-drift dike was built (Oost et al., 2012) (Fig. 21). Sediment transport across the island caused by over-wash and inundation is thus significantly reduced. Therefore, the areas located directly behind the dunes tend to become

Table 1
Cover area (ha) of the *Elytrigia atherica* community as a function of the year of vegetation establishment (Y-axis) and the successional age (X-axis).

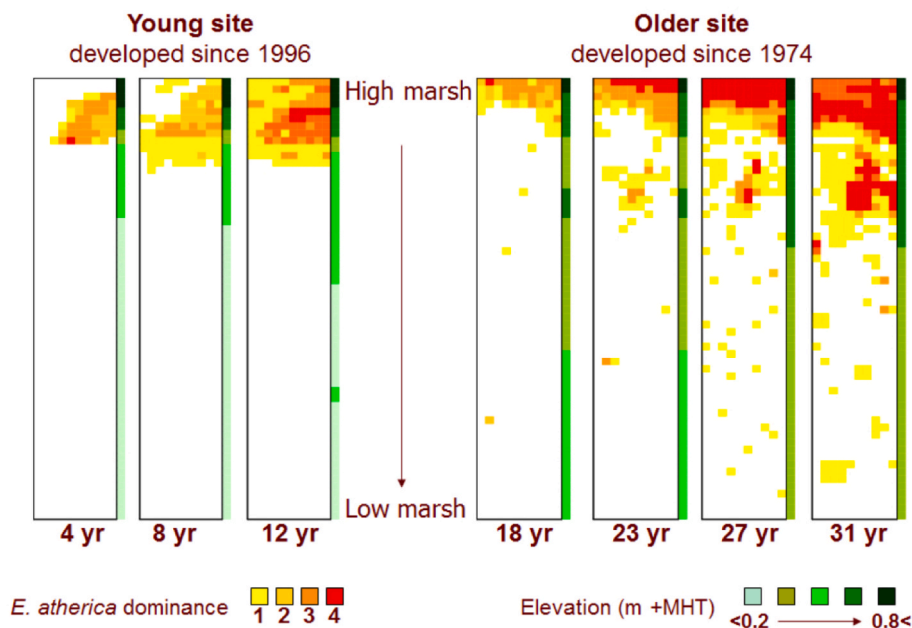|	1958	1971	1992	1997	2004	2010	2016
1955	1	21	139	109	121	185	206
1964	0	21	9	30	41	52	
1974		0	10	11	16	28	34
1986		0	3	8	23	35	41
1996		0	1	7	14	21	
Total	*1*	*21*	*173*	*138*	*197*	*303*	*354*

Fig. 15. Presence and abundance of Sea couch (*Elytrigia atherica*) over time along elevational gradients from high to low salt marsh in young and older stages of development of the back-barrier marsh on Schiermonnikoog, Each individual pixel represents 1 m² (Bakker 2014) (online version in colour).
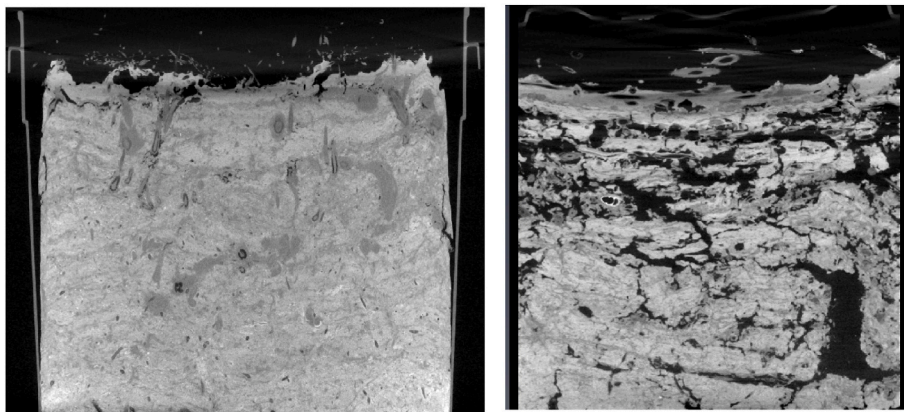
Fig. 16. X-ray CT scans from two 10 cm deep soil samples taken 2 m apart. On the left a sample from the livestock grazed salt marsh (no *Orchestia gammarellus* present, short vegetation) with strong soil compaction, on the right a sample from an 40 year old exclosure that excludes livestock grazing and trampling (100 ind. *O. gammarellus* m^{-2}, tall vegetation) with significant pore volume and pore connectivity (in black). Silt is indicated in light grey, roots are indicated in slightly darker grey, pore space in black. Also note the presence of litter in the first few cm of the right sample.
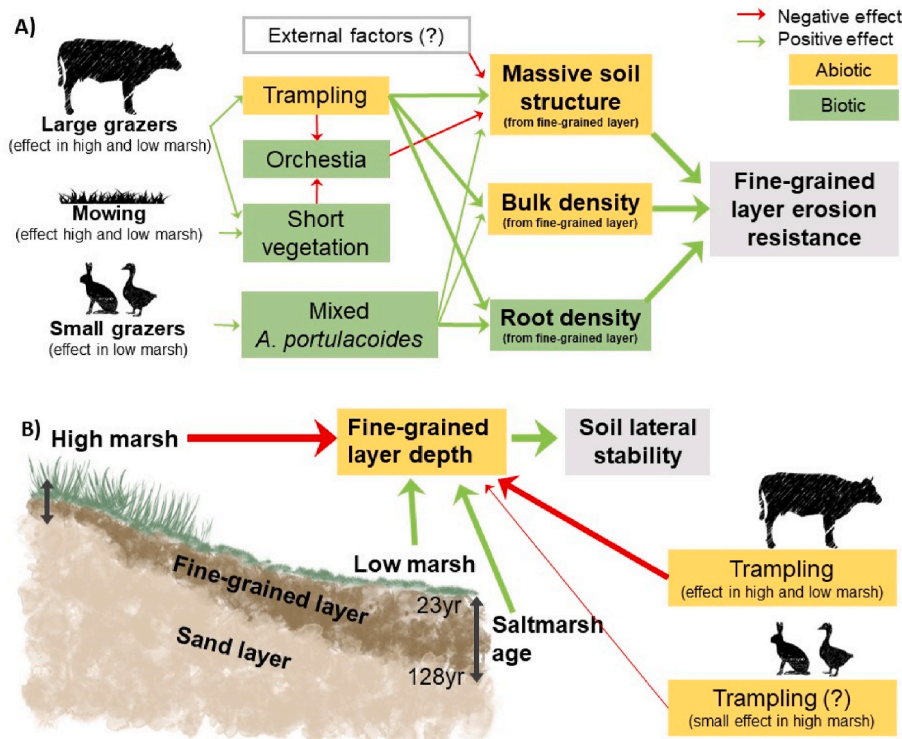

Fig. 17. Schematic representation of the interaction of biotic and abiotic components positively affecting erosion resistance (a) and negatively affecting surface elevation (b) by trampling of grazers in salt marshes (Marin-Diaz et al., 2021) (online version in colour).

lower lying relative to rising sea level (Wesselman et al., 2017). In addition, the present crest height obstructs flow from the North Sea, as many wash-over openings are ~20–30 cm higher than the beach crest. At first sight this seems to be a small difference; however, this would mean that the moderate inundation events, which in the long term lead to the most sediment transport at the island tail, do not occur at the wash-over openings (Wesselman et al., 2017), and may contribute to the 'bath-tub' mentioned in the previous section. Indeed, differences in opening height demonstrated a decrease in sediment transport by 400% for higher openings (Wesselman et al., 2019). After 2000 (Fig. 21), embryo dunes emerged on the beach and developed into a nearly closed dune system that prevents over-wash (Fig. 22) (Pranger and Tolman 2018). The formerly bare sand in the wash-over complexes showed succession from pioneer marsh (Jager 2006), via low and mid salt marsh (Pranger and Tolman 2012) into high and brackish salt-marsh communities (Pranger and Tolman 2018). Although no sand suppletion is applied at the beaches of Schiermonnikoog, the rapid succession may

not be completely natural, because remnants of the artificial sand-dike that was constructed in 1959, still interferes with a natural succession in both the dune slack development and the salt-marsh succession (Van der Veen et al., 1997).

The most eastern tip of the island is still free of vegetation and tidal inundation, and is only affected by storms when water levels are elevated, and the present wash-over system floods. Model studies suggest that net sediment transport over the beach crest is four to five times larger for severe storms than for moderate storm events; however, if net transport is combined with the frequency of occurrence (based on 25 years) the total cumulative transport is largest for less severe storms. Moderate storm inundation events (peak water levels between 1.50 and 1.75 m above MHT) typically occur several times a year, for example when a small storm surge coincides with spring tide. Severe storms (peak water levels higher than 4 m above MHT) are relatively exceptional NW storms that occur less than once a year. When the net sediment transport of each inundation class is multiplied by the frequency of occurrence,
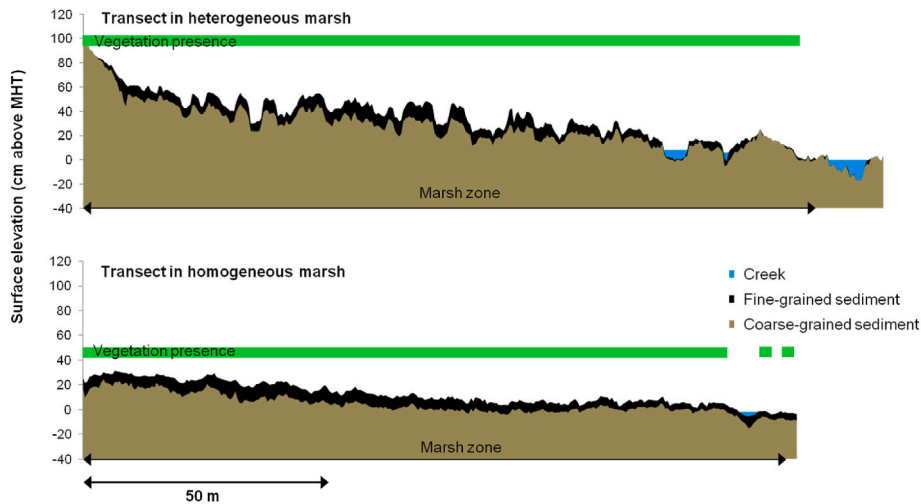
Fig. 18. Elevational transects on the salt marsh of Schiermonnikoog, perpendicular to the chronosequence. The light brown colour represents the coarse-grained sediment layer and the black colour represents the fine-grained sediment layer. In green the vegetated part of the gradient is indicated (Elschot and Bakker 2016) (online version in colour).
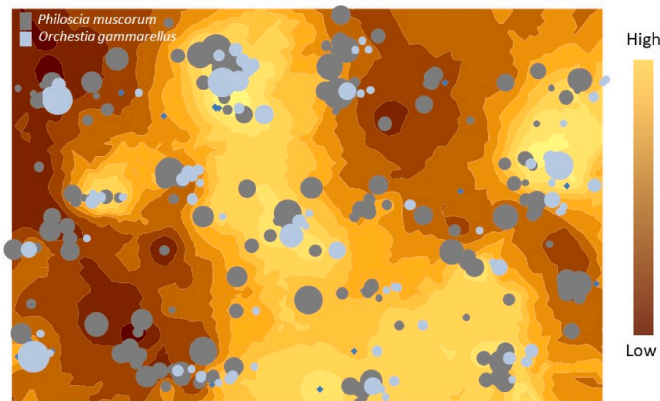

Fig. 19. Elevational heterogeneity in *Elytrigia atherica* dominated vegetation in an area of 20 m × 30 m on 120 year old marsh. Yellow high elevation, brown low elevation. Elevational differences is are about 40 cm. Low elevation areas are dominated by *Juncus maritimus* and occurrence of *Philoscia muscorum*, high elevation locations by *E. atherica* and occurrence of *Orchestia gammarellus* (After Zwiggelaars, 2012) (online version in colour).

the larger net sediment transport during larger storms is not enough to compensate for their lower frequency of occurrence. Hence, moderate storms make them the most dominant ones in terms of net sediment transport (Wesselman et al., 2017). The openings in the sand-drift dike range between 35 m and 220 m (Wesselman et al., 2019), the width is fairly constant in time, which suggests that storms do not significantly widen the openings and also that aeolian transport does not significantly influence the width, at least for the past 15 years. The wash-over elevation ranges between 2.5 and 3.1 m above MHT, which means that for normal tidal conditions they will not submerge but they can easily be inundated during storms, with peak water levels that can reach 4 m above MHT. The wash-over geometry affects sediment transport during storm events. Narrower openings result in stronger flow convergence and larger currents, but on the other hand, wider openings have more capacity to transport sediment. Both effects combined results in increasing sediment transport for wider openings, up to 800%. The patterns of sediment transport show that during inundation the wash-over opening erodes, and the area just onshore from there receives sediment, resulting in deposition. Lower and smaller openings lead to larger erosion depths, however, the total area of deposition increases for wider openings (Wesselman et al., 2019).

The sand-drift dike stopped dynamics and prevented natural
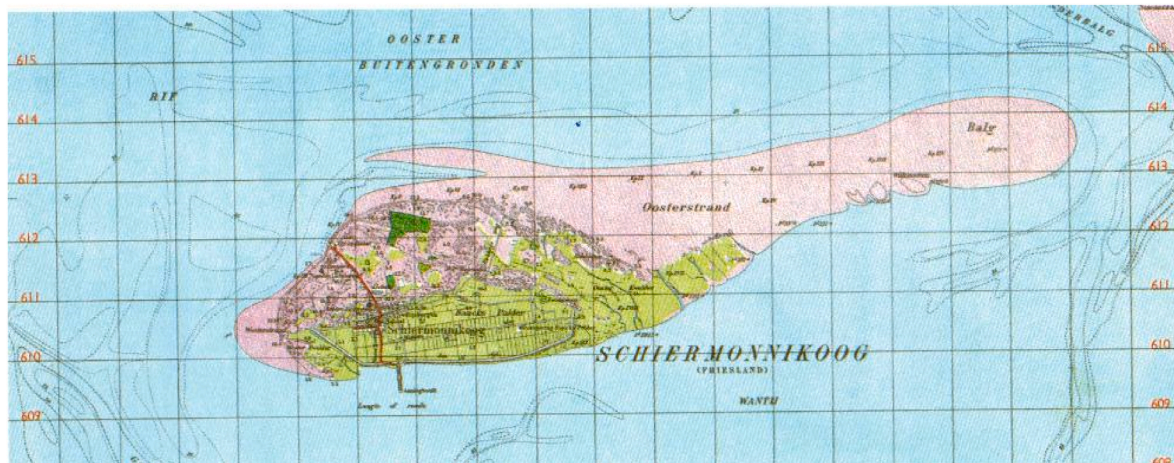

Fig. 20. The island of Schiermonnikoog in 1941, before the construction of the sand-drift dike, indicating the wash over east of the dune arc. Each grid-cell represents 1 km^2 (Sonderausgabe I.1941) (online version in colour).
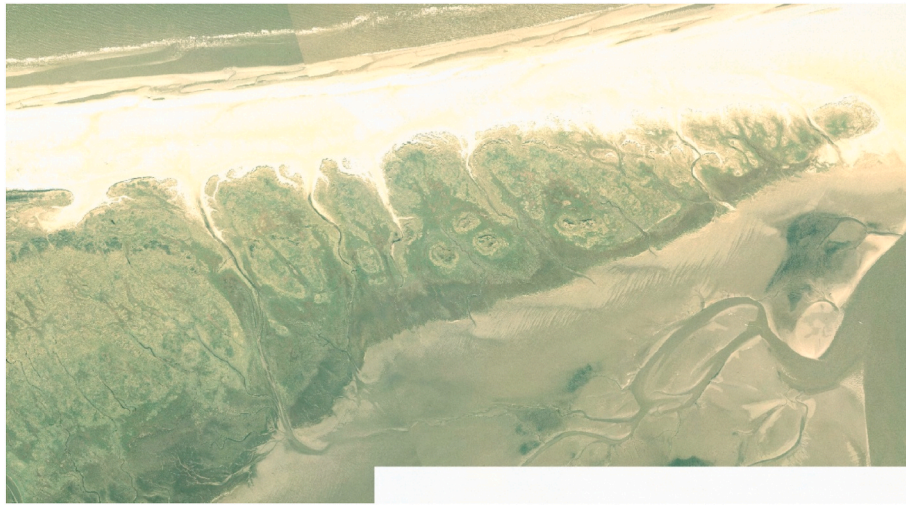
Fig. 21. Aerial photograph of the eastern part of Schiermonnikoog in 2000 with funnel-like wash overs from the beach with bare soil connected to creeks and broad wash over at the eastern tip. Courtesy Rijkswaterstaat (online version in colour).
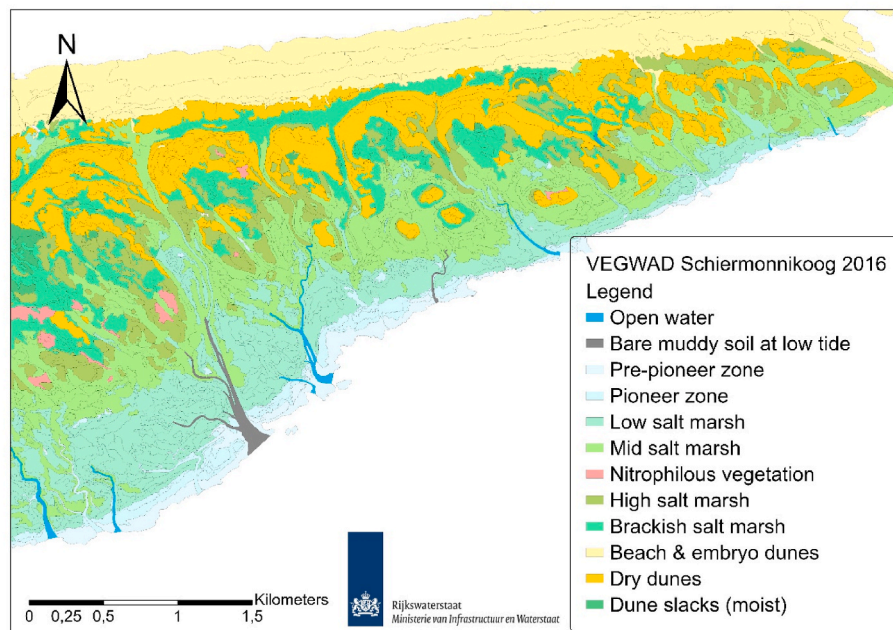

Fig. 22. Vegetation map of the eastern part of Schiermonnikoog in 2016 with dunes and brackish salt marsh, disconnecting most wash overs from the beach. Note the new dune ridge on the beach. Former wash overs are covered with brackish salt-marsh vegetation now forming the green beach (Pranger and Tolman 2018) (online version in colour).

succession. As a result of the artificial stabilization, vegetation succession was accelerated since then and made redisposition of sediment impossible (De Groot et al., 2017a). Some wash-over complexes were no longer connected to the Wadden Sea. Other wash overs were connected with creeks to the Wadden Sea until 2000 (see Figs. 19 and 20). At the younger salt marsh situated in the east of the island only few wash overs are currently connected to creeks. Hence, the chronosequence of wash overs reveals few wash overs connected with creeks in the young marsh up to 35 year, whereas older wash overs up to 50 year had been connected up to 2000 with the Wadden Sea. This might partly be due to landward incision of creeks in 'subfossil' wash overs. Currently, many wash overs in the shelter of the remaining sand-drift dike are no longer active on the island. As a result of these wash overs, locally the top layer of the adjacent salt marsh does not always consist of only fine-grained silt. It can also include thin layers of coarse-grained sand (Fig. 23).

These layers must have been deposited during high energy over-wash events, and put sand in the engine of silt sediment deposition. The recently deposited small amounts of fresh sand are rapidly stabilized by establishment of plant species Creeping bent (*Agrostis stolonifera*) and Sea milkwort (*Glaux maritima*). The occurrence of dated thin sand layers at the back-barrier marsh of Schiermonnikoog, suggests that storms capable of depositing sand in the marsh occur about every decade (De Groot et al., 2011b). Storm-related coarse-grained layers and sand deposits may occur at various locations within a salt marsh. At the back-barrier salt-marsh of Schiermonnikoog, sand layers are found on 20% of the marsh area and are partly associated with the local sources of sand, namely, marsh creeks, the salt-marsh edge and wash overs (Fig. 24). Sand layers contribute in total <10% of the volume of salt-marsh deposits on Schiermonnikoog (De Groot et al., 2011b).

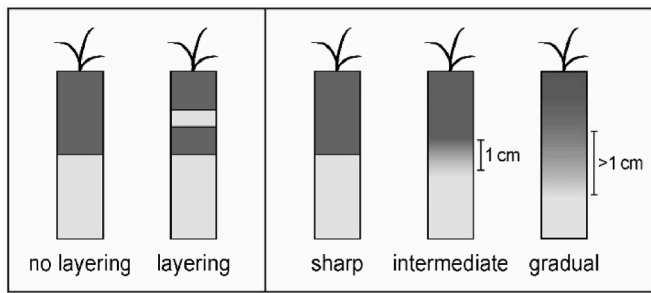The oldest wash over with small embryo dunes (established around

Fig. 23. Classification of the marsh top layer from soil cores. The figure is a cross-section of a sediment core, containing fine-grained sediment (dark colours) and sand (light colours) (De Groot et al., 2011b).

the 1870s), along the Kobbeduinen in the western part of the salt marsh is inactive since 1958 due to the construction of a sand-drift dike (Van der Veen et al., 1997). The lower lying areas were first colonized by microbial mats that prevented erosion and the nitrogen fixating bacteria allowed a mixture of dune-slack and salt-marsh species to establish (Olff et al., 1993). The vegetation of the lower plain was succeeded by *Juncus gerardii* and *Agrostis stolonifera* before it became overgrown by taller species such as Sea club rush (*Bolboschoenus maritimus*) and *Phragmites australis*, species indicating desalination of the plain (Van Tooren et al.,

1983; Olff et al., 1993; Van der Veen et al., 1997). After 30 years the tallest species (*P. australis*) dominated the lower plain (Van Tooren et al., 1993). In the meantime Greylag geese (*Anser anser*) discovered the site and increased up to 800 individuals in the 1990s with little impact on *B. maritimus* at that time (Bakker et al., 1999). Currently *P. australis* covers around 60 ha (Pranger and Tolman 2012; Reijers et al., 2019c). However, large unvegetated patches remain within the reed marsh. The heterogeneous spatial structure of the reed marsh is maintained by *Anser anser* (Reijers et al., 2019a). They forage on belowground parts of *B. maritimus* and young emerging shoots of *P. australis* in bare waterlogged soil, whereas the dense and tall structure of standing *P. australis* beds facilitate its own persistence by limiting grazer access. In addition, marsh accretion by trapping sediment or accumulating litter (1 cm yr^{-1}) can amplify this herbivore-inhibiting feedback, because *Anser anser* rely on waterlogged conditions for grubbing (Reijers et al., 2019a, Fig. 25a). Next to the ability to exclude grazers at high densities, reed can increase its persistence in coastal marshes by modifying its edaphic conditions through biogeochemical feedbacks. The occasional seawater input from large storm surges that rise beyond 2.80 m MHT can create strongly fluctuating salinity levels in the upper soil layer and promote the anoxic decomposition of the litter-rich soil layer (Reijers et al., 2019c). However, the dense *P. australis* stand can overcome the detrimental effects of salinity stress and sulfide intrusion by oxygenating the soil through radial oxygen losses and promoting a rapid infiltration of rainwater (Reijers et al., 2019c, Fig. 25b). Bush encroachment with woody *Salix*
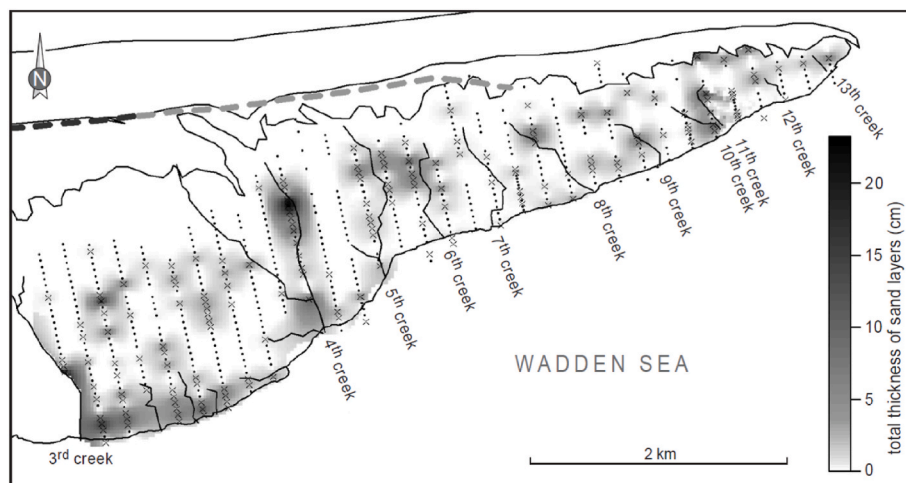
Fig. 24. Thickness of sand layers within the fine-grained top layer at the landscape scale of the island of Schiermonnikoog. The original location of the sand-drift dike on Schiermonnikoog until 1970 is given by the grey dashed line. The current location of still existing part of the drift dike is given by the black dashed line (modified after De Groot et al., 2011b).
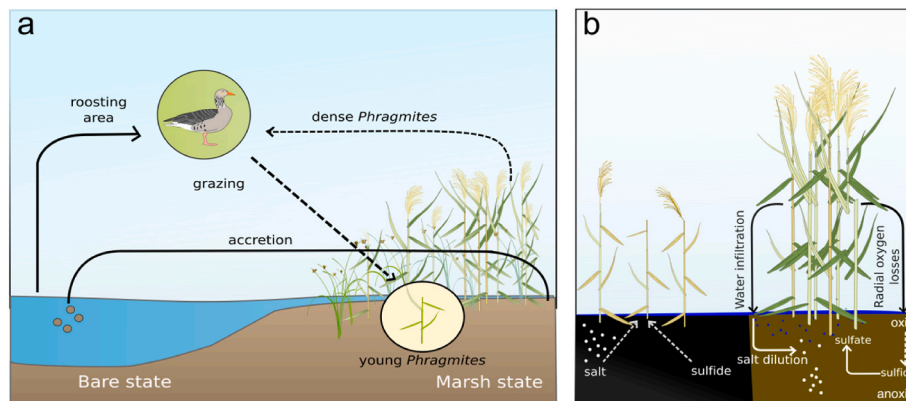
Fig. 25. Schematic representation the self-facilitative feedbacks that increase the persistence of (*Phragmites australis*) in the reed marsh behind the artificial sand-drift dike. By forming tall stands reed can inhibit grazing by geese (a) or modify soil biogeochemistry (b) (Reijers et al. 2019a, 2019b) (online version in colour).

species took place in the most western part close to the Kobbeduinen dune system with fresh seepage water (Van Tooren et al., 1993). After 20 years of spontaneous development the former small embryo dunes on the former wash over with a.o. Grass of parnassus (*Parnassia palustris*) along their edges were covered by the Sea buckthorn (*Hippophae rhamnoides*) that changed soil conditions by fixating nitrogen. The *H. rhamnoides* scrub started to die off since the establishment of Black elder (*Sambucus nigra*) after 40 years. Other woody species such as Rowan (*Sorbus aucuparia*) were found after 55 years (Janssen et al., 2019).

2.6. Beach: sand, water, wind, microbial mats, plants, animals

The beach is nourished by the shore face and sand banks grown together from the ebb-tidal delta. On the broad beach embryo dunes develop with bioengineering plants and build a new dune ridge. The beach in between this ridge and the foredune develops into a vegetated green beach. The vegetation is affected by fresh seepage water from the adjacent dune arc.

Beaches, upper and lower shoreface along the open North Sea coast of the islands are characterized by a considerable width (Oost et al., 2012). At some locations, embryo dune development is accompanied by the establishment of biodiverse pioneer dune wetland communities, which consist of a mixture of dune-slack and salt-marsh vegetation, also known as green beaches or green strands. They can be affected by freshwater seepage from the main body of the island covered by the large dune system that harbours a large fresh water body (Grootjans et al., 1996). Groundwater extraction negatively affects seepage as mentioned for dune slacks.

On Schiermonnikoog a small green beach has been formed in the 1960s harbouring a community of dune-slack and salt-marsh plants (Joenje and Thalen 1968) and soil fauna (Franken et al., 2018). In the 1990s a new sand bank became attached to the island head. This provided enough sand supply to build a ridge of low embryo dunes at the north-exposed beach, thus repairing the former erosion of the dune arc. Embryo dunes develop by the sand-trapping plant *Elytrigia farctus* Such a ridge did not establish at the lower elevated west-exposed beach, which is directly influenced by the sea. Nevertheless, vegetation started to emerge at the entire beach at the base of the old dunes, amounting to a zone of 200–400 m width between the old dunes and the new ridge and over the entire north-exposed beach toward the eastern point of the

island. It closed most of the wash overs (see Figs. 21 and 22). We refer to this vegetated beach as the green beach. Along the entire green beach salt-marsh plant species, such as *Puccinellia maritima* are found. If the level of ground water salinity drops, dune-slack vegetation can develop on green beaches. Dune-slack species, such as Black bog rush (*Schoenus nigricans*) indicate fresh water conditions. They are restricted to the green beach where low soil salinity levels are found as a result of fresh seepage water from the massive dune arc at the center of the island. When only a narrow, hence low elevation dune ridge is found adjacent to the beach, namely, the sand-drift dike east of Kobbeduinen, fresh seepage water is lacking, the salinity is higher, and dune-slack species are lacking (Bakker et al., 2005b).

In 2006 embryo dune volume differed between transects across the beach (Fig. 26). The north-exposed beach transects had an overall larger volume of embryo dunes, and thus a higher degree of shelter for emerging ~~green~~ beach system, than west-exposed beach transects with lower elevation. Between 2006 and 2016 the position of the embryo dunes shifted land inward, reducing the area of beach sheltered between embryo dunes and foredunes. Nevertheless, on most transects embryo dune volume in 2016 was higher than in 2006 (Van Puijenbroek et al., 2021) (Fig. 26).

The green beach was resistant to storms, illustrating the important role of vegetation fixing sand building embryo dunes. Thickness of the organic layer increased up to 3 cm, and salinity decreased to brackish/fresh water conditions (Franken et al., 2018). In 2006 the vegetation had a sparse coverage (28%) and mainly consisted of short herbs and grasses with a small contribution of woody shrubs. Most of the green-beach species were salt-tolerant species characteristic of salt marshes, with only a few fresh water species characteristic of young dune slacks (Van Puijenbroek et al., 2021). The soil fauna community of this stage of green beach development is dominated by the bioturbating amphipod *Orchestia gammarellus,* the Collembola *Isotoma riparia* and its associated predatory mites (Franken et al., 2018). In 2016 the average vegetation cover was much higher (90%) compared to 2006 and partly consisted of Creeping willow (*Salix repens*) and *Hippophae rhamnoides* shrubs with an average cover of 13% and highly productive grass species of later succession salt-marsh and dune habitats, such as *Festuca rubra*, *Elytrigia atherica*, and *Phragmites australis*. The green-beach species accounted for half of the total vegetation cover. As in 2006, most green-beach species where species characteristic of salt marshes, with only a few characteristic dune-slack species with a low cover (Van Puijenbroek et al.,
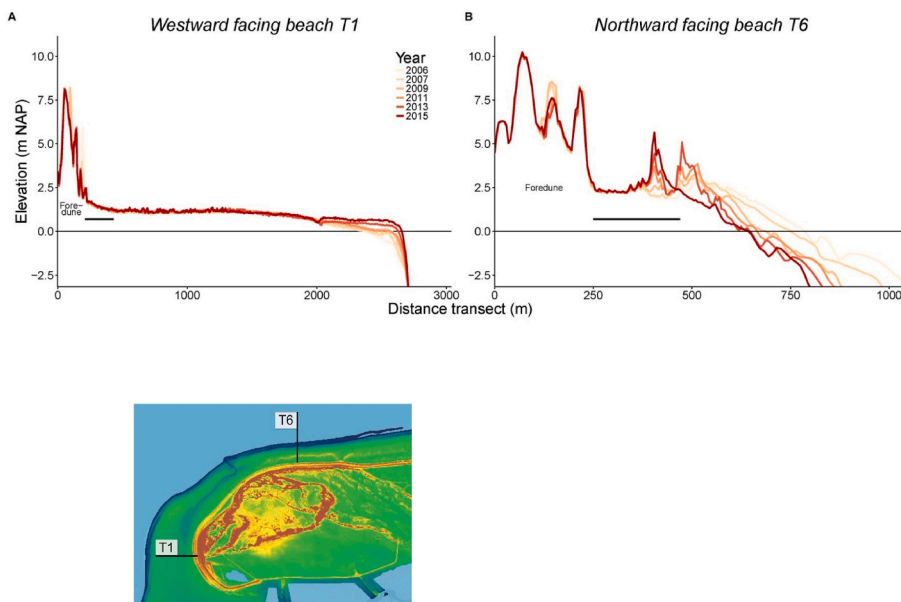
Fig. 26. Cross-shore profiles of the beach-foredune system of the island of Schiermonnikoog for the years 2006–2015 at the position of A) a west-exposed transect T1 at low elevation without embryo dune, B) a north-exposed transect T6 at higher elevation with embryo dune. The black lines below the profiles indicate the length of transects covering embryo dunes and green beach. NAP refers to Dutch Ordnance Datum, and is 1 m below MHT. The position of the transects is indicated in the accompanying map, see also Fig. 4 (Van Puijenbroek et al., 2021). (online version in colour).

2021). It is unlikely that this green beach will be covered by scrub and tall plant *P. australis* during further succession as it is open for storms from the North Sea. In this stage of development the green-beach soil fauna is dominated by the Collembola *Sminthurinus malmgreni* and several predaceous mites and other Collembola species, such as *Xenylla maritima* and *Isotomiella minor*. *Orchestia gammarellus* is lacking from the community at this stage (Franken et al., 2018), and its place as ecosystem engineer is taken over by mount forming ants of the genus *Myrmica* and *Lasius*, as well as the litter-feeding woodlouse *Philoscia muscorum*. The increase in vegetation cover and especially the build-up of a litter layer results in a 2–3 times increase in soil fauna numbers when green beach developmental stages 2006–2016 are compared (Franken et al., 2018).

2.7. Intertidal flats: sand, silt, water, diatoms, plants, animals

The tidal basin is the sediment source for the intertidal flats. Bioengineering organisms stabilize the substrate. Human interference by bottom-disturbing fisheries prevent building of mussel-oyster reefs.

The Wadden Sea tidal basins are typified by extensive intertidal flats, including high-, mid- and low-littoral parts (Baptist et al., 2019). The eastern part around Schiermonnikoog has low dynamics and includes areas with deposition of silt (Fig. 3). During each tidal cycle, these intertidal areas are submerged during high tide, but emerge during low tide when the water drains through the system of tidal channels towards the ebb-tidal delta and the North Sea. These intertidal flats are important feeding grounds for many tidally migrating species, including many fish, crab and shrimp that forage in these areas during high tide, while they become vitally important foraging grounds for many species of wading birds during low tide (Van Gils et al., 2006; Van der Veer et al., 2011). Within the intertidal environmental range limits, a number of ecosystem engineering species can profoundly modify their environment (Reise 2002; Eriksson et al., 2010). Of these habitat modifiers, the Lugworm (*Arenicola maritima*) is by far the most prevalent species. This bio-turbating, deposit-feeding worm often occurs in densities of over 100 individuals m^{-2}, and lives in burrows with a feeding funnel on one side and a fecal mound on the other (Volkenborn and Reise, 2006; Montserrat et al., 2011). By continuously reworking the sediment via its feeding activities and creating easily erodible fecal mounds, the worms destabilize the sediment and facilitate erosion of smaller sediment particles (Van Wesenbeeck et al., 2007; Montserrat et al., 2011). Seagrass meadows, tubeworm beds, and shellfish reefs, on the other hand, are typical examples of stabilizing ecosystem engineers that can facilitate themselves and its associated community by attenuating hydrodynamic energy from currents and waves, stabilizing sediments, and providing hard attachment substrate for conspecifics or other species (Van de Koppel et al., 2008; Van der Heide et al., 2012). In addition, mat-forming diatoms can be considered another, more seasonally driven sediment-stabilizing engineer (Wiltshire et al., 2008; Weerman et al., 2010). In the Wadden Sea, diatoms bloom particularly extensive in early spring (Wiltshire et al., 2008), but their dense mats can be found throughout the entire growing season in more sheltered, silty areas, where they bind and accumulate small particles to form spatially patterned landscapes (Weerman et al., 2010). Notably, in addition to diatoms, regular spatial patterning resulting from self-organization is also observed in mussels and seagrasses (Van de Koppel et al., 2008; Van der Heide et al., 2012).

Historically, the Dutch Wadden Sea was typified by extensive seagrass beds. In the western part, Eelgrass (*Zostera marina*) covered approximately 150 km^2 in the shallow subtidal, but almost completely disappeared following an incidence of the 'wasting disease' and the workings on and effect of the closure dam of the Zuiderzee between 1927 and 1933 (Giesen et al., 1990). In the intertidal, seagrass often occurred in mixed beds of annual eelgrass and perennial Dwarf eelgrass (*Z. noltii*) throughout the entire Wadden Sea, but dramatically declined since the 1960s, most likely due to increasing eutrophication (Den

Hartog and Polderman, 1975; Van Beusekom et al., 2019). Although intertidal seagrass beds have re-established in the German north-eastern parts of the Wadden Sea (Reise and Kohlus, 2008), recovery has thus far remained absent in the southern parts. Nutrient enrichment from the rivers (Rhine, Meuse, Noordzeekanaal, IJsselmeer, Ems) since the 1950s has impacted the southern Wadden Sea ecology including loss of sea-grass, increased phytoplankton blooms, and increased green macroalgae blooms. The nutrient input of the major rivers reached a maximum during the 1980s and decreased at an average pace of about 2.5% per year for total nitrogen (TN) and about 5% per year for total phosphorus (TP), leading to decreasing nutrient levels but also increasing N/P ratios. During the past decade, the lowest nutrient inputs since 1977 were observed but these declining trends are leveling out for TP. Phyto-plankton biomass (measured as chlorophyll *a*) in the Wadden Sea has decreased since the 1980s and presently reached a comparatively low level. Nutrient loads and chlorophyll *a* were stable in the tidal inlets around Schiermonnikoog between 2009 and 2015. Benthos communities were also stable (Folmer et al., 2017b). Recent cover of thick mats of green macroalgal blooms in the uppertidal covering vast areas of tidal sediments (Reise and Siebert, 1994) have halved since early 1990s (Van Beusekom et al., 2019).

Also reefs of Blue mussels (*Mytilus edulis*), another important sediment-stabilizing habitat modifier, declined from over 4000 ha in the late 1970s to around 100 ha by the end of the 1980s due to overfishing and storms (Brinkman et al., 2002). Their habitat is characterized by exposure to air about 20–35% of the time. Below these levels, the exposure time may be too low so that there is too little time for filter feeding of phytoplankton and suspended microphytobenthos. Above these optimal exposure time levels in the intertidal mid-littoral, the hydrodynamic stress may limit the occurrence of mussel-oyster reefs (Folmer et al., 2017a). The removal of these reefs by fisheries not only homogenized the substrate, it transformed it from silty into sandy by increase of sediment erosion (Donadi et al., 2013). The average mud fraction of the intertidal flats has reduced from 2009 to 2015 with an average of 0.24% per year, hence the intertidal flats have become sandier (Folmer et al., 2017b). During the past decades, the invasive Pacific oyster (*Magallana gigas*), that was introduced in the 1960s (Reise, 1998), formed extensive reefs at sites in the western Dutch Wadden Sea that were previously dominated by mussels, while mussels recovered in the eastern parts. At present, mussels and oysters often occur in mixed mussel-oyster reefs (Van der Meer et al., 2019).

In facilitating diatom mats, mussel-oyster reefs not only stimulate an important engineering species, but also a primary producer vital for the intertidal food web. Specifically, a recent study in which 178 species were sampled at 839 locations across the entire Dutch Wadden Sea, found that diatoms are the most important energy source for the majority of consumers at higher trophic levels, including many species of worms, molluscs, crustaceans, fish, and birds (Christianen et al., 2017a). Hence, in modifying their habitat epibenthic bivalve reefs increase niche diversity through both trophic and non-trophic pathways, making these reefs, and the areas they affect beyond their boundaries, biodiversity hotspots of the intertidal (Van der Zee et al., 2015; Christianen et al., 2017b). In fact, as a consequence of their extended habitat modification effect, it has been estimated that although these epibenthic bivalve reefs currently cover only 5% (Folmer et al., 2017a), they effect around 20% of the intertidal mudflats (Nieuwhof et al., 2018).

As intertidal seagrass meadows have virtually disappeared, mussel-oyster reefs are currently the most profound biogeomorphic structures found on the intertidal flats south of Schiermonnikoog (Fig. 27). Their position is similar to that of silt in the mid-littoral zone (Fig. 3). Recent experimental work from this area revealed that, apart from dramatically altering their local environment, these reef's habitat modifying effects extend far beyond the actually size of the reefs (Van der Zee et al., 2012; Van de Koppel et al., 2015). Specifically, by attenuating hydrodynamic energy, and producing pseudofeces that settles in the surroundings, these reefs increase silt and organic matter content of the sediment up to
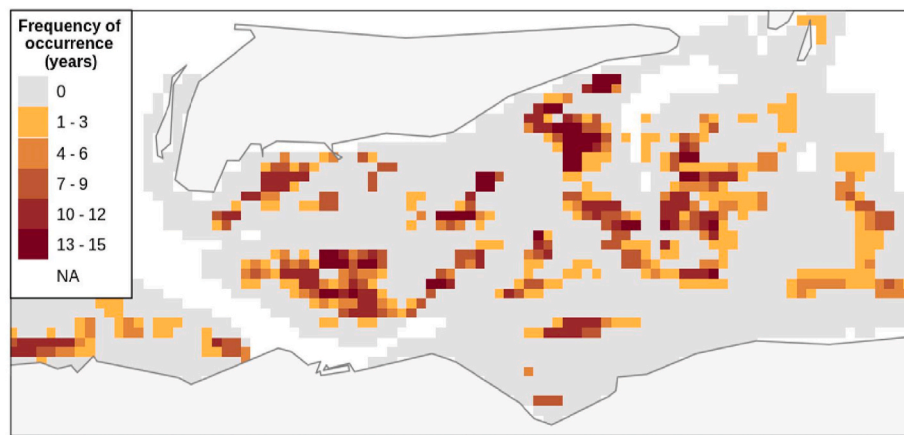
Fig. 27. Frequency of occurrence of blue mussel, Pacific oyster and mixed beds/reefs on intertidal flats south of Schiermonnikoog. The value of each pixel represents the number of times it was occupied in the period 1999–2013. A pixel is considered to be occupied if part of it contained beds/reefs (detail from Folmer et al., 2017a) (online version in colour).

hundreds of metres beyond the reef (Van der Zee et al., 2012; Donadi et al., 2013). This not only enhances the abundances of other engineering species, particularly diatoms, tubeworms and cockles (Van der Zee et al., 2012), but may also indirectly negatively affect silt deposition on land by decreasing SSC from 200 mg l^{-1} at site without musselbeds to 100 mg l^{-1} at site with musselbeds (Donadi et al., 2013). Interestingly, both tubeworm and cockle beds have also been observed to serve as important settlement substrates for mussels (Brinkman et al., 2002). In an experiment, anti-erosion mats were applied to simulate biotic attachment and substrate stabilization by commonly found tubeworm beds, were crossed with addition of adult mussels. Shrimp and crab predation were manipulated using exclosures within these treatments. Epibenthic mussel recruits were only found in treatments with manipulated substrates, attached to either the anti-erosion mat or adult mussels. These facilitation effects, however, only clearly emerged when predators were excluded, demonstrating strong synergistic effects between predation and habitat modification. These findings suggest that disturbance of trophic interactions and loss of habitat modifying species interactively affect bivalve recruitment dynamics (Van der Heide et al., 2014). This suggest that mussels may not only directly facilitate themselves, but also indirectly through community-level facilitation. Sediment stability of intertidal flats decreased by human interference by dredging and trawling and strong regulation of hydrodynamics for engineering activities, with subsequent decline of organisms that enhance sediment stability. Moreover, spatially self-organized mussel reefs create microhabitats/heterogeneity that facilitate diverse invertebrate communities. By comparing seawater filled pools with open inlets in a mussel reef, natural reef pools, emerging due to the habitat engineering of the mussels, strongly increased variation in organic enrichment and promoted beta-diversity compared to the surrounding intertidal flat. These findings significantly extend the scale of influence typically described for self-organized habitats (Van der Ouderaa et al., 2021). Shellfish reefs not only structure associated fauna but also the marine vegetation on soft bottoms by accumulating seaweeds. Blue mussels promote the development of meadow-like communities dominated by habitat forming brown seaweeds of the genus *Fucus*, with high primary biomass and high habitat complexity. In contrast, invaded invasive Pacific oysters promote bloomforming green algae communities with low primary biomass and low habitat complexity. The invasion of oysters may have dramatic effects on the structure and function of intertidal reef-communities by changing energy flow and habitat-function (Andriana et al., 2020). Eriksson et al. (2010) propose that increased sediment disturbances by human exploitation interfere with biological controls of sediment dynamics, and thereby have shifted the dominant compartments of both primary and secondary production in the Wadden Sea, transforming the intertidal from an internally regulated and spatially heterogeneous, to an externally regulated and spatially homogeneous system.

3. Concept of the model barrier island

The concept of a model island was put forward to inform policy on coastal management based on fixation of the coastline with subsequently loss of dynamics. Promoting natural processes might address current issues regarding problems related to sea-level rise and loss of biodiversity. This might allow many plant and animal species to maintain themselves by moving over the island. The best way to do this is by utilizing long-lasting processes that take place in large areas, namely, five geomorphological units (Löffler et al., 2011). We extended the concept of a barrier island based on five geomorphological units. Firstly, we included two more units, namely, tidal basin and intertidal flats, and introduced how interactions between terrestrial and marine units are of pivotal importance. Secondly, our focus was not merely on the dynamics of abiotic geomorphological units, but rather on the role of bio-engineers (both plants, animals and micro-organisms), together with the vectors water and wind, and the substrates sand and silt. We considered the spatial scale of entire units and smaller-scale entities within them. Thirdly, we tried to estimate the period of time it takes to develop the climax stage of units characterized by certain plants or animals without human interference. Here, the concept of a chronosequence was extremely instrumental to estimate the processes that take more than the life-time of an individual researcher.

In our model barrier island system of Schiermonnikoog, tidal inlets have been reduced by closing the Zuiderzee and Lauwerszee. This resulted in more sand in the ebb-tidal delta, which in turn resulted in more sand transport along the coast. Beaches became broader and a green beach could develop. Moreover, the beach crest became higher which decreased the potential for over-wash. This stops sandy sediment input into the salt marsh. Surface elevation change continues by sedimentation of silt in young salt marsh, however, slows down in older salt marsh by autocompaction. At the same time, beach hoppers and ants increase elevation by bioturbation. The salt marsh cannot spread further eastward as a result of dynamics of the tidal inlet near the island tail. Bivalve reefs enhance accumulation of silt, which subsequent lower input in salt marshes. Succession is enhanced by input of nitrogen by atmospheric deposition and nutrient loads in water from the rivers.

3.1. Barrier islands are not isolated systems

The individual biogeomorphological units of barrier islands and their

surroundings do not stand alone but are interdependent. The description of model barrier island should include the tidal basin, sand banks and intertidal flats, all three of them essential as they represent important components of the morphology and development of particular units (Fig. 28). We suggest that tidal basin affects island head with sand banks by water and sand movements, and establishment of plant ecosystem engineers, and the intertidal flats by sand, silt, diatoms and bioturbating animals. Island head affects the dune arc by sand deposition, wind and plants, and the ~~green~~ beach with sand deposition, wind, microbial mats and plants. Dune arc affects the salt marsh by shelter, water, plants and silt deposition. Intertidal flats affect the marine-terrestrial transition in the salt marsh by water, silt and animals. Island head and beach/shoreface affect the wash-over complex and salt marsh by water, sand, wind and plants. The interplay between erosion by over-wash, microbial mats and aeolian deposition of sand is poorly understood (De Groot et al., 2015).

Intertidal flats and salt marshes interact via deposition of silt. The basic morphology of the intertidal flats and its associated system of channels is abiotically driven, resulting in occurrence of silt in low-dynamic conditions along the mainland and in intertidal flats (Wang et al., 2012). Suspended matter concentration in the eastern part of the Wadden Sea is relatively high and confirms the favourable condition for sediment build up in the area. It shows, however, large variation in both space and time (Oost et al., 2021). A long-term average of around 100 mg l-1 matches the maximum value of the range considered necessary for sediment build up in salt marshes by Kirwan et al. (2016). However, mean SSC is probably not a good predictor for vertical salt-marsh accretion because most sediment originates from resuspension during storms of material deposited earlier on intertidal flats (Schuerch et al., 2014). Moreover, sediment resuspension due to the activity of bio-engineers, wave action and wind, has a strong effect on salt marshes. During inundation silt is trapped in the vegetation and deposited in the salt marsh, leading to a rise in elevation with time. Hence, intertidal flats and salt marshes seem tightly linked.

How fast a dynamic equilibrium can re-establish after disturbance depends on the magnitude of the perturbation, the sediment availability and transport capacity. At the moment it is not clear which of these prevails (Wang et al., 2018). Until now, sediment budget studies only determine total amounts of sedimentation and erosion. A budget is needed per sediment fraction at least with a distinction between sand and silt. The limits to the extent to which a tidal basin can keep up with relative SLR are one of the major focus points in trilateral sea-level rise research in the Wadden Sea (Oost et al., 2017). The role of bio-engineers in morphodynamics is not well understood (Wang et al., 2012). More

knowledge should become available on the relation between hydrodynamic energy and benthos, particularly in the shallow wave breaking intertidal zone (Baptist et al., 2019). Some smaller-scale aspects are recognized. What factors determine the branching structure of the channels in the tidal basin? What determines the cyclic behaviour of the ebb-tidal delta, and its interaction with the dynamics of the tidal basin? What factors determine the location and migration of a tidal watershed between two tidal basins? What factors determine the size, shape and bed level of intertidal flats? What determines the sediment grain size composition on these flats, and how relevant is the exchange of sediment between channels and flats? What role do extreme events such as storms play in erosion and deposition of sediment along the beach/shoreface, wash-over complexes, in intertidal flats and on salt marshes (Wang et al., 2012)?

3.2. Interplay between abiotic and biotic drivers in the model island barrier system

The geomorphological units are characterized by abiotic factors, such as substrate like sand and silt, and the vectors water and wind. They are built in interaction with biota, namely, bio-engineers or ecosystem engineers, such as micro-organisms, plants and animals that make them biogeomorphological units. However, more intensive process studies are needed to elucidate the linkages between marine and terrestrial units via these engineers. For instance, when the creeks overflow due to an above-average high tide, leaf litter fragmented and mineralized by *Orchestia gammarellus* washes from the salt marsh into the creeks and is discharged onto the mud flat area when low tide sets in. This adds nutrients to the marine system. Marine ecosystem engineers, such as bivalves that form pseudo-faeces and lugworms that decrease sediment stability of the mud flat due to their bioturbating behaviour, which subsequently causes a high sediment load of the water column, which is deposited on the salt marsh as a thin layer of silt when creeks overflow due to an above-average high tide. This silt deposition not only raises the height of the salt marsh over time but also in the short term may prevent drying out of litter in summer, hence, allowing decomposition of litter by microbes to continue during the plant growing season. However, the order of magnitude is not known. In the tidal basin and island head in high dynamic channels abiotic factors sand, silt, water and wind interact without bio-engineers. In all other units biota play a role in the formation of their geomorphology and soil. For each biogeomorphological unit, an indication is given of the abiotic factors and characteristic bio-engineers (Table 2). Also the number of years for periodic events, or it takes to reach a climax stage of natural succession are indicated.

4. Possibilities for generalization

4.1. Climate change, sea-level rise and surface elevation change

An important issue for barrier islands is how they may react on effects of climate change. The question is to which extent vertical accretion of tidal basins, intertidal flats, salt marshes and wash-over complexes can keep pace with SLR. We will discuss this issue for the type of tidal basins adjacent to Schiermonnikoog. The Dutch Wadden Sea has been accreting by importing sediment from the ebb-tidal deltas and the North Sea coasts. The average accretion rate since 1926 has been higher than that of the local relative SLR. The large sediment imports are predominantly caused by the damming of the Zuiderzee and Lauwerszee rather than due to response to this SLR. The intertidal flats in all tidal basins increased in height to compensate for SLR. Barrier islands have to cope with SLR. The present vertical accretion rate (6.7 mm yr^{-1}) in the tidal basin Zoutkamperlaag is larger than the rate of SLR (2–3 mm yr^{-1}) (Wang et al., 2018). A SEC rate in the same range as the increase rate of MHT since the 1990s (2–3 mm yr^{-1}) was found in the barrier-connected salt marshes (Esselink et al., 2017). This does not automatically imply that a salt marsh has a low resilience to SLR. Marshes with a low tidal
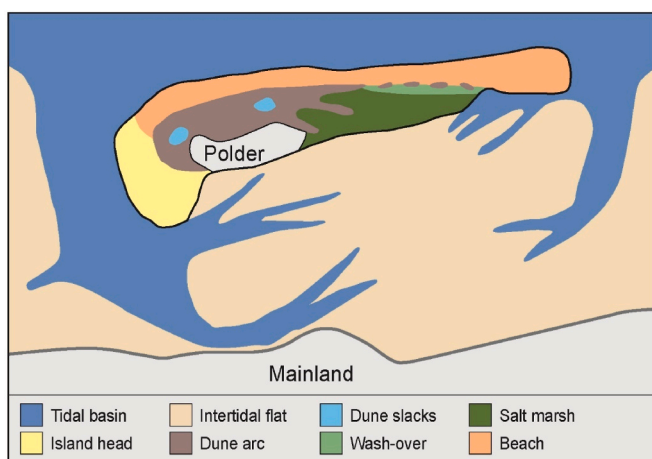
Fig. 28. The biogeomorphological units (see Table 2) of the barrier island of Schiermonnikoog and its surroundings (adapted from Oost et al., 2012, after Löffler et al., 2011) (online version in colour).

Table 2

Biogeomorphological units built and modified by substrate, vectors and biota, their climax stage and dynamics, i.e. period it takes to develop without human interference, derived from the island of Schiermonnikoog.

Biogeomorphological unit	Substrate	Vector	Biota	Climax	Timescale
Tidal basin	sand, silt	water	benthic organisms	(inter)tidal flats, channels	still dynamic, 50 yr after closure Lauwerszee
Island head	sand	water	benthic organisms	sand bank	new sand bank every 20 yr
Intertidal flats	silt	water	diatoms, sea grass, mussels, Japanese oyster, lugworms	bivalve reef	30 yr
Dune arc complex dry	sand	wind	plants, rabbits	forest	100 yr
Dune arc complex slack	sand	wind, groundwater	microbial mats, plants	forest	100 yr
Wash-over complex	sand	water, wind	plants, microbial mat	bare soil, grasses	every 10–15 yr
Island tail, salt marsh	silt	water	plants, beachhopper, hare, geese	tall grass	50 yr
Beach	sand	water, wind	microbial mat, plants	scrub	40 yr

range (below 1 m) and low SSC (<20 mg l^{-1}) are especially at risk from submergence by average SLR projections (Kirwan et al., 2016). Data indicate SECs above ~~MHT~~SLR in most back-barrier marshes. They show, however, a large range in the Wadden Sea area as they respond spatially but: 9.6 mm yr^{-1} in foreland salt marshes and 3.2 mm yr^{-1} in back-barrier salt marshes, which is still above the 2–3 mm yr^{-1} increase of MHT (Esselink et al., 2017). Some parts of older marshes (by auto-compaction) and parts away from sediment supply routes, such as salt-marsh edge and creeks, have accretion around or below SLR. As these data are recorded in ungrazed marshes, livestock grazing with subsequent soil compaction may increase the discrepancy between accretion or SEC and SLR in these marshes. The erosion resistance of the silt layer of salt marshes increased with large grazers that compacted the soil by trampling with increased bulk density and higher below-ground biomass. However, compaction by large grazers simultaneously leads to thinner silt layers and lower surface elevation, potentially leading to more inundation under SLR (Marin-Diaz et al., 2021).

Surface elevation change may be increased by extra input of sediment through over-wash. Over-wash and inundation can result in vertical growth of barrier islands (Nielsen and Nielsen 2006), and may keep pace with SLR. The water levels in the North Sea and Wadden Sea during storms are a combination of tide and storm surge and they reveal two trends. Firstly, the water level in the Wadden Sea lags behind the water level in the North Sea, which is probably a tide-induced effect as it also occurs during calm weather conditions. This results in higher water levels in the Wadden Sea than in the North Sea during the falling stages of the tide. Secondly, storm surges result in a larger increase of the mean water level in the Wadden Sea than in the North Sea side for larger storms and result in a smaller phase lag. As a result, only during part of the rising tide are water levels in the North Sea higher than in the Wadden Sea, whereas for the rest of the time Wadden Sea water levels are higher. For the severest storms, the water level in the Wadden Sea is higher than in the North Sea. This is a crucial aspect for the sediment transport across the island tail, resulting in a smaller or even reversed current and a reduced net sediment transport. Over a tidal cycle, the net sediment transport direction is still towards the Wadden Sea. When taking into account the frequency of occurrence of storms, the cumulative effect of relatively mild storms on long-term cross-shore sediment transport is much larger than that of the large storm events (Wesselman et al., 2017). Furthermore, effects must be taken into account at the locations of narrow wash overs. For example, flow contraction through an opening can accelerate currents, which enhances sediment transport. Sediment slumping from the side walls of the dunes can affect the sediment transport as well and deposition patterns behind the dunes can vary in the alongshore direction. The influence of these properties of the wash-over openings on the hydrodynamics, sediment transport and morphology change is not yet known (Wesselman et al., 2017). An alternative could be feed-back by higher flooding frequency and increasing network of creeks that transport more sediment further from the salt-marsh edge. It is not known why certain creeks are not connected to wash overs. Accretion of salt marsh by sand is relatively small. It might be higher in wash-over complexes.

4.2. Human interference and management implications

The group of tidal basins to which Schiermonnikoog is assigned (Baptist et al., 2019) is not homogeneous. Unintentional changes as those resulting from reduction of the tidal basin by closure of the Zuiderzee and Lauwerszee is characteristic for the Dutch Wadden Sea. This type of human interference cannot be restored by management. This will possibly have consequences for the resilience of the islands and the sediment sharing inlet systems as a whole. These consequences are, until now, poorly understood (Oost et al., 2012). The variation of tidal basins in the entire Wadden Sea may have repercussions on effects of climate change, and the question to which extent vertical accretion can keep pace with SLR.

Apart from indirect effects of human interference through climate change, effects of eutrophication hold for all islands. Atmospheric N deposition is above the critical level for dune systems and salt marshes with thin layer of silt. N-content in the Wadden Sea is too high. In tidal inlet stations with a long-term monitoring, summer phytoplankton levels correlate with riverine total N and total P loads but stations located closer to the coast behave in a more complex manner (Van Beusekom et al., 2019). A management implication is reduction of intensive farming in the polder to reduce atmospheric deposition.

Direct effects of human interference are also important for barrier islands. Coastal protection with sand suppletion prevents erosional coasts to develop. Their application is not related to the character of intertidal basins. They are carried out on most of the Dutch inhabited islands, half of the German Lower Saxony islands and on some of the Schleswig-Holstein and Danish islands (De Groot et al., 2017b). The ecological effects of nourishments on smaller temporal and spatial scales (i.e. years and specific beach sites) have direct negative effect due to the thick layer (3–4 m) of sand applied on the beach. Most macro-invertebrate fauna is unlikely to survive such burial of sand. Recovery of the benthic fauna takes place within a few years, but is species specific (Leewis et al., 2012). Since, at least in the Netherlands, the frequency in which sand suppletions are applied is in the same order as the recovery time, the fauna of nourished beaches are hardly ever in an undisturbed state. These processes do not take place on Schiermonnikoog where no sand suppletion is needed (Rijkswaterstaat, 2014a) (www.rijkswaterstaat.nl). A management implication for the future is sand suppletion when needed.

Currently, there are large variations in the amount of groundwater extracted per island in relation to increased tourism, with Sylt having by far most groundwater extracted. Since 2010, extractions have decreased on Fanø (Denmark), and increased on Vlieland, Terschelling, Schiermonnikoog, and Amrum (De Groot et al., 2017b). A management implication could be transport of fresh water from the mainland by a pipe.

Recent management interventions in the Netherlands on Vlieland, Terschelling, Ameland and Schiermonnikoog (Oost et al., 2017) such as creating blowouts and notches in seaward dry dunes, and sod cutting in landward dune slacks, allow more dynamics of wind and water (De Groot et al., 2017b). Increase of dynamics on salt marshes was practiced by removal of a summer dike around the salt marsh of Langeoog in Germany (Oost et al., 2017). Complete or local removal of artificial sand-drift dikes to restore wash-over complexes is discussed on islands in the Netherlands (Löffler et al., 2011), but has not been implemented yet. A management implication to maintain dynamics and thus biodiversity could be creating blowouts in the dunes and (partly) removal of the artificial sand dike.

Mechanical fisheries that disturbed the soil and bivalve reefs on intertidal flats has been reduced or stopped: mechanical cockle fisheries since 2005, blue mussel fisheries permanently closed in the Netherlands for 18% of the area with mussel beds, Lower Saxony 10% and Schleswig-Holstein in Germany 100%, and Denmark 100% (Baer et al., 2017). The recovery of mussel-oyster reefs in intertidal flats is related to cessation of mussel fisheries in the Dutch Wadden Sea (Folmer et al., 2017a). Conservation and restoration of bivalves should also focus on protecting and restoring internal facilitation mechanisms, and should simultaneously reduce excessive mesopredator predation (crabs and shrimps) by restoring natural food web dynamics, including the role of top-predators (Van der Heide et al., 2014). A management implication would be cessation of bottom disturbing fisheries.

4.3. Knowledge gaps

As illustrated above, different types of interactions play an important role in spading each of the biogeomorphological components, using insights from a the model island. Some include interactions between large biogeomorpholocal units. Others deal with the role of bioengineering plants, micro-organisms or animals in relation to abiotic conditions. From the above a number of key knowledge gaps can be identified, regarding both domains. They include the notion that individual tidal basins need measurements. Many issues deal with human interferences for which long-term experiments and monitoring will be helpful. Finally, modelling on interactions between abiotic and biotic components of the landscape, and especially the role of biological interactions is missing. This results in many questions.

Interaction between tidal basin, intertidal flats and salt marshes.

- Tidal basins have large impacts on the biogeomorphology of barrier islands. For generalizations, tidal basins should be comparable. With respect to large-scale sediment budgets, it should be noted that data from transport measurements are only partly available for individual tidal basins (Wang et al., 2018).
- How is the positive correlation between increasing tidal range and faster sedimentation in meso-tidal flats (Oost et al., 2021) related to sedimentation in salt marshes?
- How is the exchange of incoming sediment between channels, intertidal flats and salt marshes?
- How is the high vertical accretion rate of the tidal basin (Wang et al., 2018) related to lower vertical accretion rate of sites above MHT, namely, salt marshes in the framework of sea-level rise?
- How is the relationship between high sediment input in tidal basin, resuspension by waves (Wang et al., 2018) and fixation by bio-engineers such as diatom mats and mussel-oyster reefs in intertidal flats?
- Can restoration projects of seagrass meadows and bivalve reefs be performed at such scales that they also restore the important feedback mechanisms needed to promote those local abiotic conditions that are favourable for the target species (Eriksson et al., 2010)?

Interaction between intertidal flats and salt marshes.

- To which extent harbour (inter)tidal flats covered by mussel-oyster reefs more silt with subsequent higher stability after reduction of fisheries? What are effects on sediment input in salt marshes?
- To which extent do salt marshes have an impact on (inter)tidal flats via the export of fine and particulate organic matter? What is the effect of vegetation composition, in presence and absence of large grazers on organic matter transport from salt marsh to intertidal flat?
- To which extent are semi-aquatic creek food webs intertwined with salt-marsh food webs? How important is fish predation at high tides on the terrestrial food web, especially on beach hoppers, or how import is terrestrial prey for creek fishes and what is the impact of grazing on these interactions?
- Can livestock grazing be beneficial for both coastal protection and biodiversity on salt marshes? What is the role of livestock grazing on salt marshes with respect to SLR? Is there a trade-off between decreased SEC and resistance to erosion due to soil compaction during SLR?

Interaction between beach, wash-over complex and salt marshes.

- To which extent can the removal of sand-drift dikes restore wash-over complexes, and mimic the situation at Spiekeroog, the only barrier island in the Wadden Sea without an artificial sand-drift dike? It is not clear if it is possible to restore the original processes successfully, due to the massive changes in the Wadden Sea (Oost et al., 2017).
- Under which conditions will over-wash and aeolian transport of sand be important? To what extent will salt-marsh sediment being eroded with succession set back?
- On the scale of decades, sand suppletion contributes to the formation of ~~green~~ beaches and embryonic dunes (De Groot et al., 2017b). What will be the effect of long-term suppletion on the large-scale beach-dune system and its natural dynamics?
- What is the relationship between sand suppletion and wash overs?

Interaction between dunes and beach.

- To which extent will the creation of blowouts and notches in the dunes counteract stabilizing practices of dunes taken previously? Can livestock grazing enhance this process?
- What will be the effect of reduction of intensive agriculture on atmospheric deposition?
- What will be the long-term effect of increase or decrease in extraction of groundwater for dune slacks and green beaches?

Bio-engineering species.

The biogeomorphological approach with important roles for bio-engineers suggests that knowledge is needed to which extent bio-engineers can cope with climate change, especially the increase in frequency, duration and amplitude of extreme events.

- Can the micro-organisms, plants, animals, cope with sudden changes in e.g. temperature? There may be interaction between climate change and the effects of N deposition, linked to faster growth of competitive species and enhanced mineralization of soil organic matter. Indirect effects may play a role when present bio-engineers are replaced by species with a northward shift in their ranges. Invasive species may change the food web.
- What problems may happen with geomorphological units when bio-engineers cannot cope with climate change? Will they become more vulnerable? The key challenge is not only to identify the exact role of climate change, but also to determine the relative importance of climate change compared to other impacts, and how they might interact.

For purposes of environmental research, policy and conservation, it

is useful to classify ecosystems or geographic areas into distinct spatial units based on geographical and ecological criteria. An ecotope map can give a first–order estimate of the potential spatial distribution of species and communities, both bioengineering and Red List species. Further use of ecotope maps in the ecological domain is to describe habitat suitability for species of benthos, other flora and fauna. Habitat modelling is based on the preferences of plants and animals for the physical characteristics of their living environment. Biological interactions, such as competition, predator-prey relationships in food webs are usually neglected. Nonetheless, an ecotope map can give a simple first–order estimate of the potential spatial distribution of species and communities, which can be used in research and management (Baptist et al., 2019). Abiotic conditions are modelled to predict occurrence and abundance of (groups) of species in the future. Effects of biota in case of bioengineering species on abiotic conditions are, however, far from being included in predictive models. Several authors advocate to study individual tidal basins (or at least at the level of four clusters) (Baptist et al., 2019). This might offer a possible fruitful approach to including food web interactions in modelling, which could help to get to generalizations for the international Wadden Sea, which currently misses local conditions that may be of great importance to coastal conservation, management and coastal protection of Wadden Sea biodiversity.

Finally, generalizations on measures regarding coastal conservation and biodiversity are difficult as there is a large gap regarding modelling on interactions between abiotic and biotic components of the landscape, and especially biological interactions in food webs is missing. Long-term experiments and monitoring will be helpful to complete these gaps. Many resources are available for measurements and modelling of abiotic topics related to coastal protection, i.e. maintenance of barrier islands. This is in contrast with resources available for monitoring and modelling of biotic topics and finally interactions between abiotic and biotic topics. Especially such collaboration can help perspectives for future studies.

Moreover, it is essential to expand our understanding of the ways in which the natural dynamics will interact with and be affected by (i.e., coupled with) human coastal dynamics, especially as changing conditions lead to consideration of more extreme defensive measures. Perhaps most challenging, but ultimately, most important, there is a critical need to develop creative ways to maintain or re-establish the natural and essential connection among the frontal beach-dune system, the interior, and back-barrier marsh components—especially where development and protective measures have severed this connection. This will be challenging and may require a type and range of collective thinking on the part of scientists, managers, and community members that has not yet emerged, but that will become essential in years to come (Moore et al., 2018).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors are unable or have chosen not to specify which data has been used.

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