

Experimental climate change impacts on Baltic coastal wetland plant communities

Thaísa F. Bergamo (✉ thaisa.fernandes@emu.ee)

Estonian University of Life Sciences

Raymond D. Ward

University of Brighton

Christopher B. Joyce

University of Brighton

Miguel Villoslada

University of Eastern Finland

Kalev Sepp

Estonian University of Life Sciences

Article

Keywords:

Posted Date: April 21st, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1517117/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Experimental climate change impacts on Baltic coastal wetland plant communities

T.F.Bergamo^{a*}, R.D.Ward^{a,b,c}, C.B.Joyce^b, M. Villoslada^{a,d}, K.Sepp^a

^aInstitute of Agriculture and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 13 5, EE-51014 Tartu, Estonia

^bCentre for Aquatic Environments, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton BN2 4GJ, United Kingdom

^cEscola Integrada de Desenvolvimento e Inovação Acadêmica, Federal University of Ceara, Campus do Pici, CEP 60455-760, Fortaleza, Ceara, Brazil

^dDepartment of Geographical and Historical Studies, University of Eastern Finland, P.O. Box 111, 80101, Joensuu, Finland

Abstract

Coastal wetlands provide a range of important ecosystem services, yet they are under threat from a range of stressors including climate change. This is predominantly as a result of alterations to the hydroregime and associated edaphic factors. We used a three year mesocosm experiment to assess changes in coastal plant community composition for three plant communities in response to altered water level and salinity scenarios. Species richness and abundance were calculated by year and abundance was plotted using rank abundance curves. The permutational multivariate analysis of variance with Bray-Curtis dissimilarity was used to examine differences among treatments in plant community composition. A principal coordinate analysis was used to visualize the responses of communities to treatments by year. Results showed that all three plant communities responded differently to altered water levels and salinity. Species richness and abundance increased significantly in an Open Pioneer while Lower and Upper Shore plant communities showed less change. Species abundances changed in all plant communities with shifts in species composition significantly influenced by temporal and treatment. The observed responses to experimentally altered conditions highlight the need for conservation of these important ecosystems in the face of predicted climate change.

Introduction

Coastal wetlands are considered valuable ecosystems for their biodiversity and the wide range of ecosystem services they provide, including sediment retention, storm buffering, water filtration, nutrient cycling, flood regulation, carbon sequestration, recreational activities and maintenance of productive coastal fisheries [1,2,3,4,5,6]. However, coastal wetlands worldwide are subject to various impacts resulting from natural and anthropogenic drivers, such as urbanization and residential developments, conversion to agricultural land, as well as sea level rise and related impacts of inundation and erosion [7, 8] due to climate change.

Climate change has been highlighted as one of the main risks to coastal wetlands, especially in low-lying areas [9, 10]. As global temperatures increase and warm the oceans, melting ice sheets and glaciers are expected to accelerate the rate of sea level rise [11, 12, 13] and can modify sea water salinity, alongside changes in the amount and distribution of precipitation and changes in wind speed [13, 14, 15]. The impacts of climate change vary both geographically and seasonally. For instance, projections for climate change highlight the largest increase in mean temperature in high latitudes of the northern hemisphere and particularly strong increases in heavy precipitation in the tropics as well as in high latitudes [16].

The consequences of climate change over recent decades are evident in the Baltic Sea region, with modifications in sea water circulation, temperature and salinity [17, 18]. A warmer climate results in modifications to precipitation patterns affecting runoff to the Baltic Sea. Seasonally, summer river flows are likely to either decrease or stay the same, while winter flows are predicted to increase [11]. As a result of this, the average salinity of the Baltic Sea is projected to decrease, with the greatest

reductions predicted to be in the surface waters of the Danish straits and lowest in the Gulf of Bothnia, while the water levels are predicted to increase [11]. These changes are likely to have an impact on both plant and animal assemblages [19].

In the Baltic Sea, both water levels and salinity have a strong impact on species distribution and therefore on the structure and composition of aquatic and coastal floral and faunal communities [19, 20]. It has been reported that decreases in salinity during the 1980s altered zooplankton species composition favouring freshwater species [21] and both salinity and water levels have been shown to have a strong influence on coastal plant community composition [20, 22]. The alterations to higher water level and lower salinity may facilitate the settlement of local freshwater or invasive non-native species that can adapt to lower salinities, affecting ecosystem functioning in species rich Baltic coastal wetlands [11].

As a result of water level and salinity changes, plant communities in coastal wetlands are expected to be sensitive to climate change [23, 24]. Coastal wetland communities often comprise a mosaic of vegetation patches and are classified by similarities in species composition and indicator species [25]. In temperate zones, coastal wetland plant communities are affected by microtopography [26], soil water condition [27], soil salinity [28] as well as management activities [25].

In order to assess the response of coastal vegetation to altered environmental conditions, mesocosms have been previously used to investigate vegetation richness [29], seedling establishment [30] and capacity of nutrient transformation by wetlands [31]. Mesocosm experiments enable the manipulation of specific conditions and species [32] and allow community-level responses to be evaluated by adding greater complexity at larger scales [33]. Therefore, mesocosm experiments constitute a useful tool to assess the potential impacts of climate change on coastal wetland plant communities.

Due to the high importance of coastal wetlands and the impacts of climate change on this ecosystem, it is important to determine how future conditions will influence coastal plant community functioning. Previous studies in the Baltic region assessed changes to coastal wetland plant communities related to: microtopography [24, using ecological assessment]; management and grazing [22, ecological assessment]; climate driven changes to precipitation and sea level rise [24, 34, modelling]. However, there have yet to be any studies directly measuring the influence of climate change impacts on plant community composition in Baltic coastal wetlands. The aim of this study was to examine the effects of altered water level and salinity conditions on three different coastal wetland plant communities using medium-term (3 yr.) mesocosm experiments. The objectives were:

- (i) To evaluate changes in species richness and abundance over time.
- (ii) To evaluate changes in the plant communities' composition under different treatments;

Results

Species richness and abundance

In total, 18 plant species were recorded in the Open Pioneer (2.7 species per m²), 27 in the Lower Shore (4.1 species per m²) and 49 in the Upper Shore community (7.4 species per m²). Compared to the beginning to the end of the experiment, species richness increased in the Open Pioneer community in all treatments, while in the Lower and Upper Shore communities, the species richness decreased particularly with decreased water level (Figure 1).

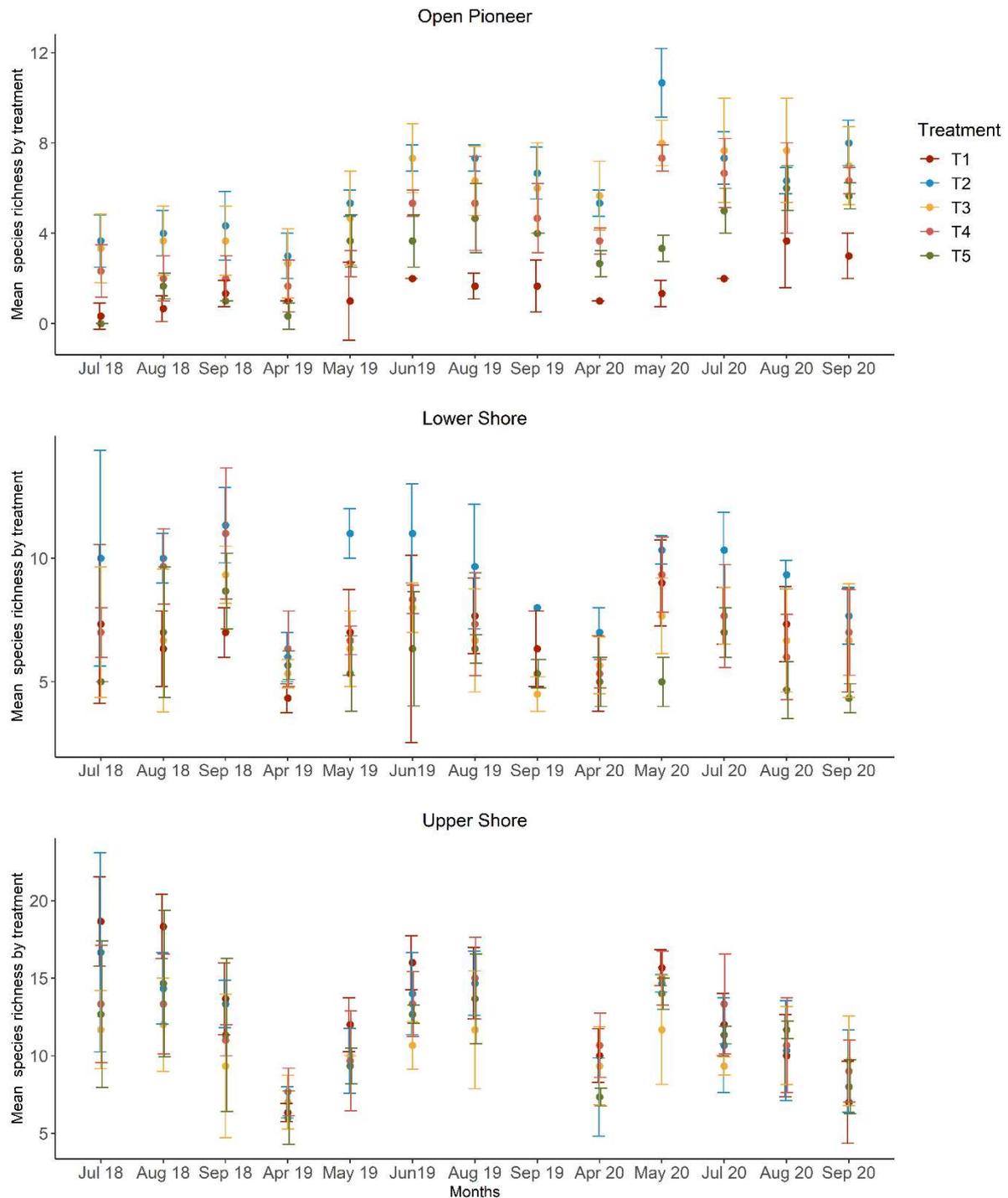


Figure 1: Mean species richness per treatment in 2018, 2019 and 2020 for Open Pioneer, Lower Shore and Upper Shore communities, respectively. The dots show the mean species richness and the bars, the standard deviation ($n=3$). Red: Treatment 1 (T1 - raised water level); Blue: Treatment 2 (T2 - lowered water level); Yellow: Treatment 3 (T3 - decreased salinity); Orange: Treatment 4 (T4 - increased salinity); Green: Treatment 5 (T5 - control). See Table 3 for treatment details.

The pairwise comparisons using Dunn's test with Bonferroni adjustments indicated that the increased water level treatment (T1) and decreased salinity (T3) presented significant richness differences ($p < 0.05$) compared to decreased water level (T2) and control treatments (T5) in the Open Pioneer community in 2018. The following year, in addition to the previous differences, treatment T1 was significantly different ($p < 0.05$) from the higher salinity condition (T4). In 2020, no other differences were observed. The Lower Shore community showed significant differences ($p < 0.05$) between treatments with altered water level in 2018 and 2019 and between lower water level and lower

salinity in 2019. In 2020, significant differences ($p < 0.05$) were present between lower water level and control treatments. The post hoc test revealed significant differences ($p < 0.05$) between T1 and T3 in the Upper Shore community in 2018 and no additional significant values (Table 1).

Table 1: Differences in species richness between treatments were examined using Kruskal Wallis followed by Dunn's post hoc test with Bonferroni adjustments in the years 2018, 2019 and 2020. Treatment 1 (T1 - raised water level); Treatment 2 (T2 – lowered water level); Treatment 3 (T3 – decreased salinity); Treatment 4 (T4 – increased salinity); Treatment 5 (T5 - control).

	2018	p-value	2019	p-value	2020	p-value
Open Pioneer	T1-T2	<0.0001	T1-T2	<0.0001	T1-T2	<0.0001
	T1-T3	<0.0001	T1-T3	<0.0001	T1-T3	<0.0001
	T2-T5	<0.0001	T1-T4	<0.001	T1-T4	<0.0001
	T3-T5	<0.001	T2-T5	<0.001	T2-T5	<0.001
Lower Shore	T1-T2	<0.001	T1-T2	<0.001	T2-T5	<0.0001
	T2-T5	<0.001	T2-T3	<0.001		
			T2-T5	<0.0001		
Upper Shore	T1-T3	<0.001				

Species-rank abundance curves were calculated for August by year and revealed a few dominating species in all three communities. All species-rank abundance curves show a long tail containing the majority of species within each community contributing to species richness. The Open Pioneer community was characterized by a large proportion of bare ground (Figure 2) and a few species adapted to relatively high salinity. The rank abundance curves showed that bare ground was the predominant characteristic during the 3 years of the experiment. *Spergularia marina* was the most abundant species in 2018 and 2019 (Figure 2) for all treatments. In 2020, the most abundant species was *Puccinellia maritima* in treatment 2 (lowered water level) and *Glaux maritima* in treatment 3 (lowered salinity) (Figure 2).

The most abundant species in Lower Shore (Figure 3) were *Agrostis stolonifera* followed by *Juncus gerardii* in 2018 in all treatments. Litter was the most abundant attribute in 2019 and 2020. Considering the species, in 2019, *J. gerardii* was the most abundant species in treatment 1 (increased water level), *Eleocharis palustris* in treatment 3 (decreased salinity) and Control, and *Juncus gerardii* followed by *Triglochin maritima* were the most abundant species in treatment 3 (Figure 3). In 2020, *A. stolonifera* was the most abundant species, except for decreased water level where *Festuca rubra* had the highest coverage. Generally, the amount of litter increased from the beginning of the experiment to the end, reducing the bare ground cover.

For the Upper Shore community (Figure 4), litter was most abundant, except in 2019 when *Carex nigra* was more abundant. *Carex nigra* was also the most common species in 2018 except in treatments 3 and 5 where *Juncus gerardii* had a higher abundance. Generally, in 2019, *C. nigra* was the most abundant species in all treatments followed by *Galium palustre*. In 2020, *C. nigra* had a higher abundance in treatments 2 and 4 (decreased water level and increased salinity), *P. annua* in the increased water level treatment (T1), *A. stolonifera* in the lower salinity treatment (T3) and *F. rubra* in the control (T5).

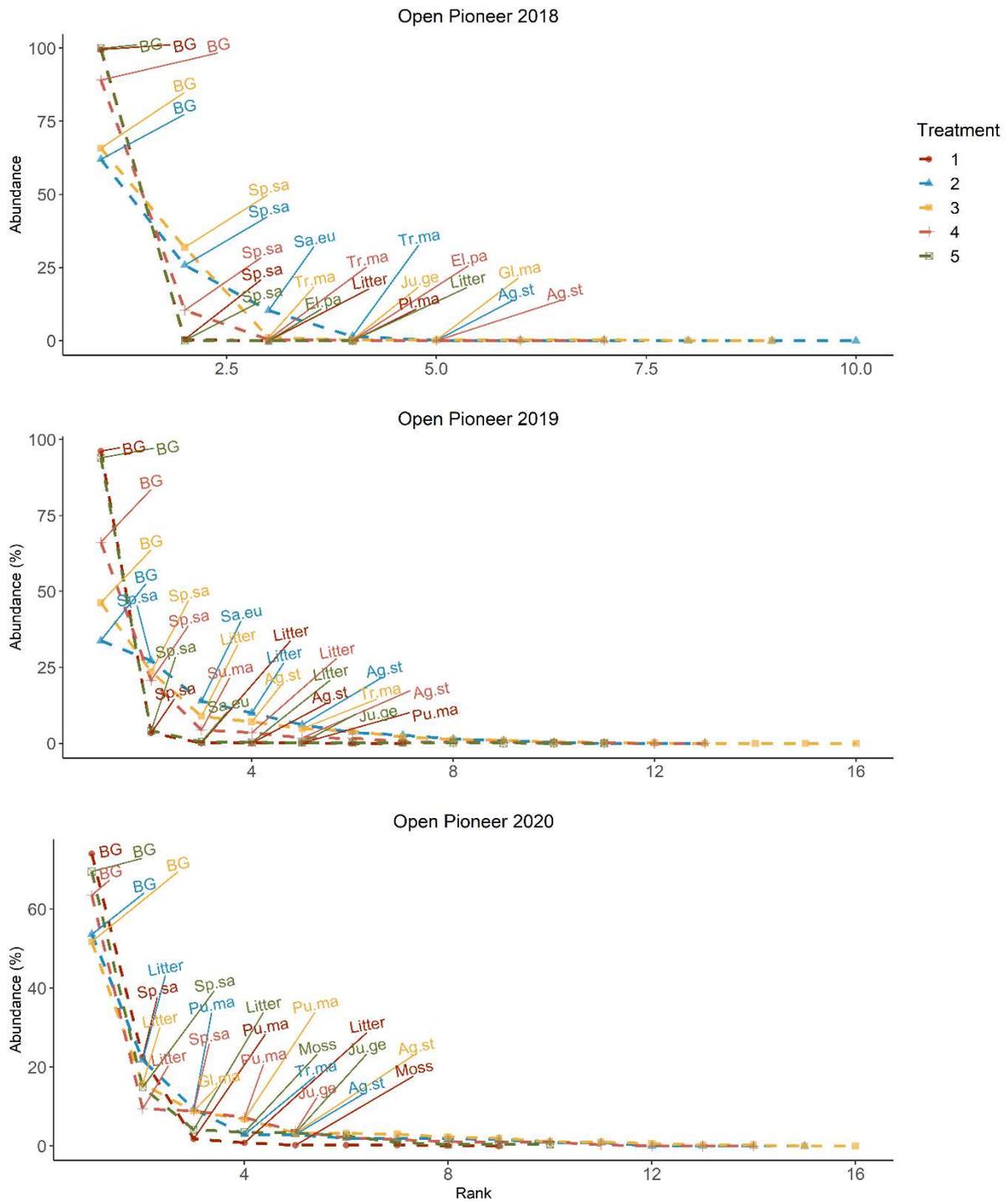


Figure 2: Rank abundance curve of Open Pioneer community. Abundance as percentage cover for August is on the y-axis, while species are ranked consecutively on the x-axis. BG: Bare Ground; Sp.Sa: *Spergularia salina*; Sa.eu: *Salicornia europea*; Tr.ma: *Triglochin maritima*; El.pa: *Eleocharis palustris*; Ju.ge: *Juncus gerardii*; Pl.ma: *Plantago maritima*; Gl.ma: *Glaux maritima*, Ag.st: *Agrostis stolonifera*. Red: Treatment 1 (T1 - raised water level); Blue: Treatment 2 (T2 - lowered water level); Yellow: Treatment 3 (T3 - decreased salinity); Orange: Treatment 4 (T4 - increased salinity); Green: Treatment 5 (T5 - control).

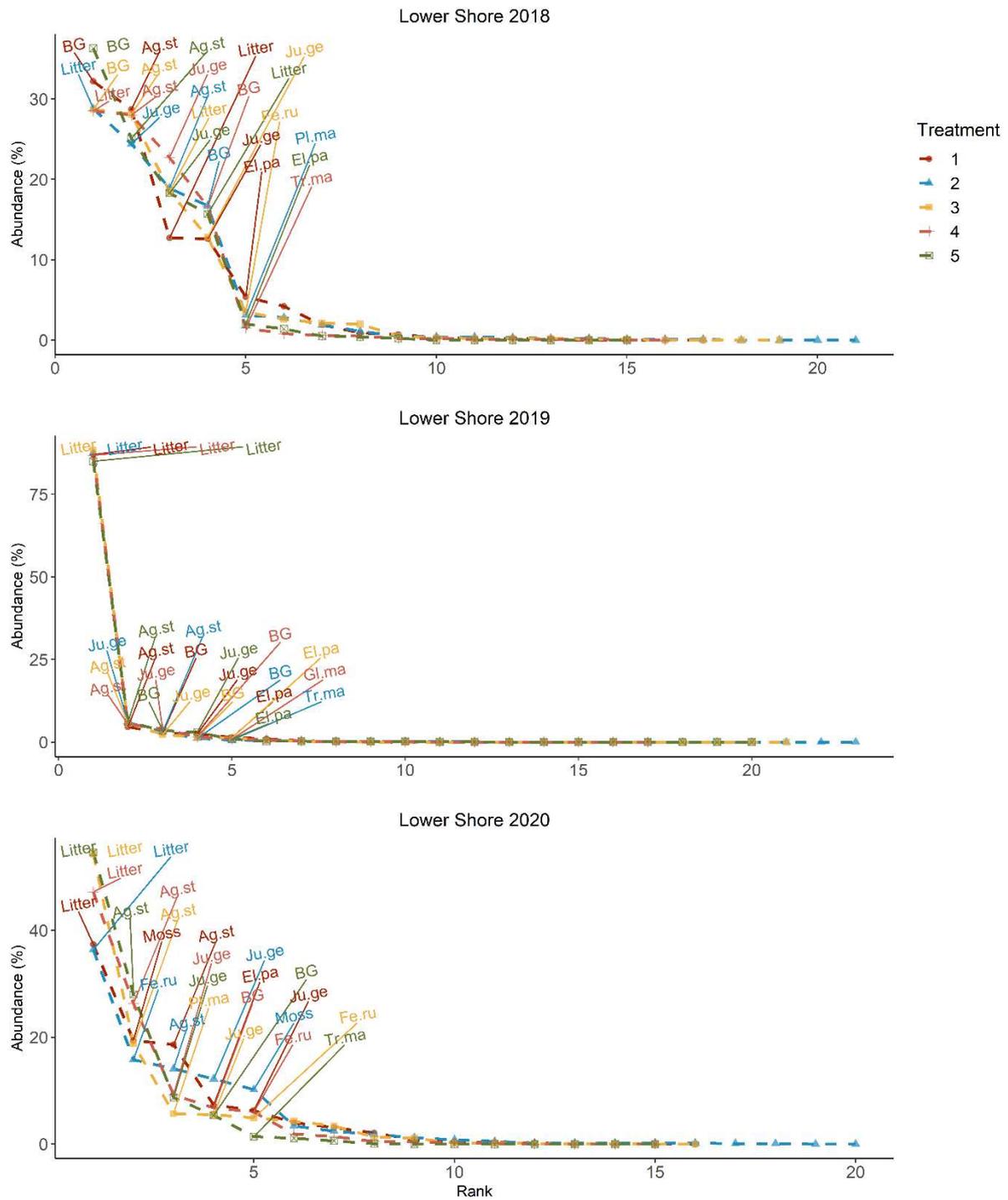


Figure 3: Rank abundance curve of Lower Shore community. Abundance as percentage cover is on the y-axis, while species are ranked consecutively on the x-axis. BG: Bare ground; Ag.st: *Agrostis stolonifera*; Ju.ge: *Juncus gerardii*; El.pa: *Eleocharis palustris*; Pl.ma: *Plantago maritima*; Fe.ru: *Festuca rubra*; Tr.ma: *Triglochin maritima*. Red: Treatment 1 (T1 - raised water level); Blue: Treatment 2 (T2 - lowered water level); Yellow: Treatment 3 (T3 - decreased salinity); Orange: Treatment 4 (T4 - increased salinity); Green: Treatment 5 (T5 - control).

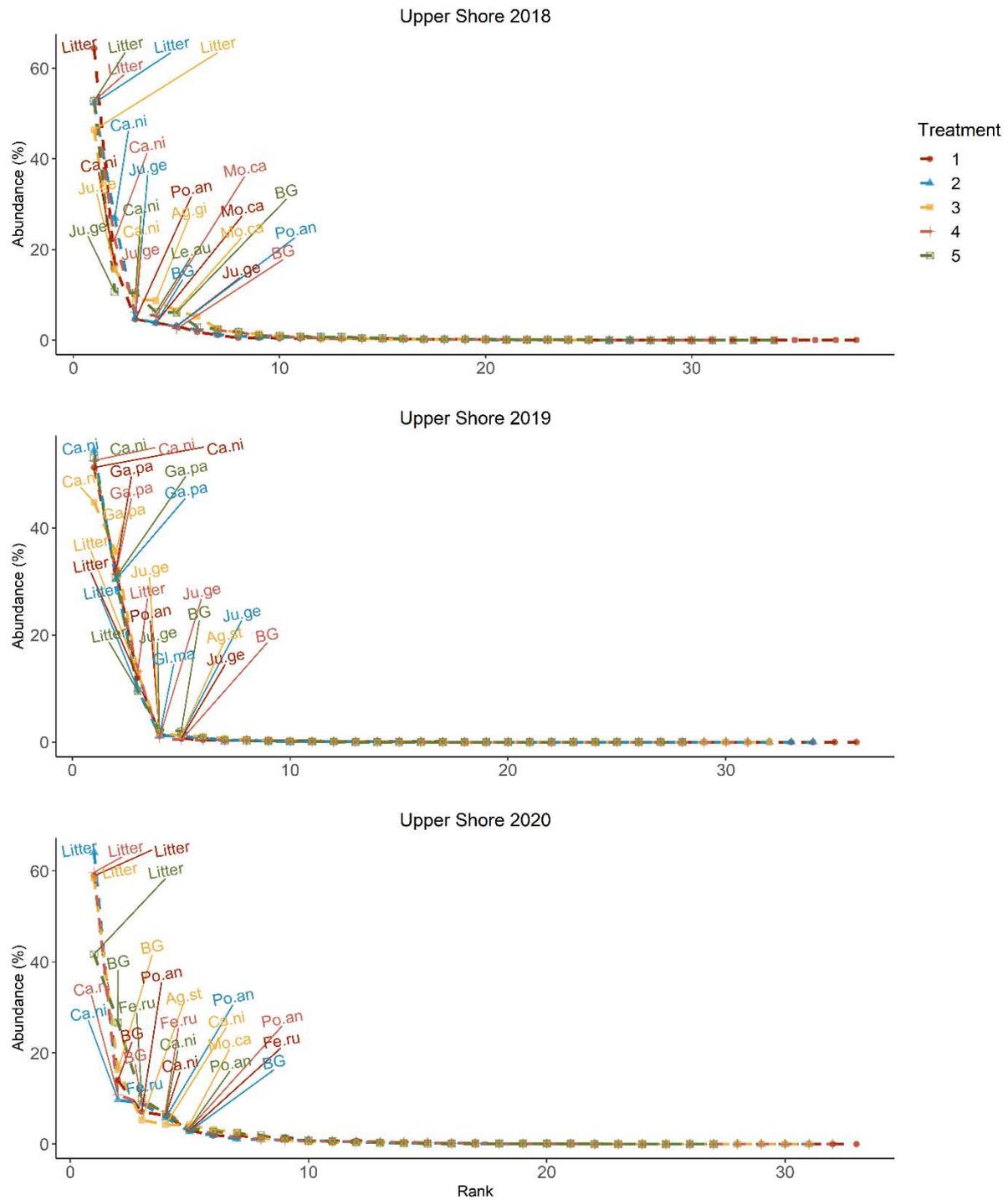


Figure 4: Rank abundance curve of Upper Shore community. Abundance as percentage cover is on the y-axis, while species are ranked consecutively on the x-axis. Ca.ni: *Carex nigra*; Ju.ge: *Juncus gerardii*; Po.an: *Poa annua*; BG: Bare ground; Mo.ca: *Molinia caerulea*; Le.au: *Leontodon autumnalis*; Ag.gi: *Agrostis gigantea*; Ga.pa: *Galium palustre*; Ag.st: *Agrostis stolonifera*; Fe.ru: *Festuca rubra*. Red: Treatment 1 (T1 - raised water level); Blue: Treatment 2 (T2 - lowered water level); Yellow: Treatment 3 (T3 - decreased salinity); Orange: Treatment 4 (T4 - increased salinity); Green: Treatment 5 (T5 - control).

Plant Community Composition

All factors (year, treatment and their interaction) significantly influenced plant community composition (Table 2). Based on factor effects, the treatment and year explained most of the variation for Open Pioneer. Year explained the most variation for the Lower Shore community, followed by treatment. For Upper Shore, treatment vs year explained most of the variation (Table 2).

Table 2. PERMANOVA results based on Bray-Curtis dissimilarity from species importance values obtained from the percentage cover of each quadrat. The results show the effects of experimental factors on plant community composition (August of 2018, 2019 and 2020).

Source of variation		Df	MeanSqs	F. model	R2	<i>p</i> (perm)
Open Pioneer	Treatment	4	25.72	337.9	0.15	<0.001
	Year	2	51.42	675.56	0.15	<0.001
	Treatment x Year	8	9.53	125.4	0.11	<0.001
	Residuals	4860	0.07		0.56	
	Total	4874			1	
Lower Shore	Treatment	4	11.7	112.21	0.07	<0.001
	Year	2	30.04	228.14	0.09	<0.001
	Treatment vs Year	8	2.65	25.49	0.03	<0.001
	Residuals	4835	0.1		0.79	
	Total	4849			1	
Upper Shore	Treatment	4	4.47	69.8	0.05	<0.001
	Year	2	5.57	87.08	0.03	<0.001
	Treatment vs Year	8	0.99	15.6	0.24	<0.001
	Residuals	4485	0.06		0.88	
	Total	4499			1	

The results of Principal Coordinate Analysis (PCoA) shows the first 10 species given by the rank abundance curve for each community and year (in August) (Figure 5). Changes in species composition between years confirmed by PERMANOVA testing can be visualized on the PCoA.

For the Open Pioneer community, differences between treatments are shown by the PCoA plots in the second and third years. Plant community shifts were already observed in the second year of the experiment. *Puccinellia maritima* together with *Suaeda maritima* were visibly clustered, associated with high salinity and water levels. In the third year, differences between treatments were more pronounced. The presence of *Spergularia marina* was strongly associated with conditions of increased salinity, whereas *Eleocharis palustris*, together with moss and *Juncus gerardii*, appeared in conditions of increased water levels. A third cluster of species (*Triglochin maritima*, *Glaux maritima*, *Puccinellia maritima* and *Agrostis stolonifera*) was observed in conditions of decreased water and decreased salinity.

Species were more clustered in Lower Shore and Upper Shore communities compared to Open Pioneer, but changes were still noted. The small spread of species throughout the years in ordination space in Lower Shore and Upper Shore suggests a higher degree of similarity between communities across treatments. Lower Shore in the third year shows species separated along a water level gradient, with a lower influence of salinity. As in Open Pioneer, *Eleocharis palustris* was present in conditions of increased water level, whereas *Plantago maritima* and *Festuca rubra* shifted towards conditions of relatively lower water level and salinity. Moss also appears in higher moisture and lower salinity conditions.

Upper Shore showed a response to variations in salinity in the second year. Species were spread along the salinity gradient, with *Molinia caerulea* in lower salinity and relatively higher water level, and *Linum catharticum* and *Triglochin maritima* in higher salinity. The treatment separation developed further in the third year, with a community shift across both the water level and salinity gradients. *Molinia caerulea* and *Leontodon autumnalis* appeared in higher water level conditions, whereas *Poa pratensis* and *Poa angustifolia* appeared in relatively higher salinity and lower water levels.

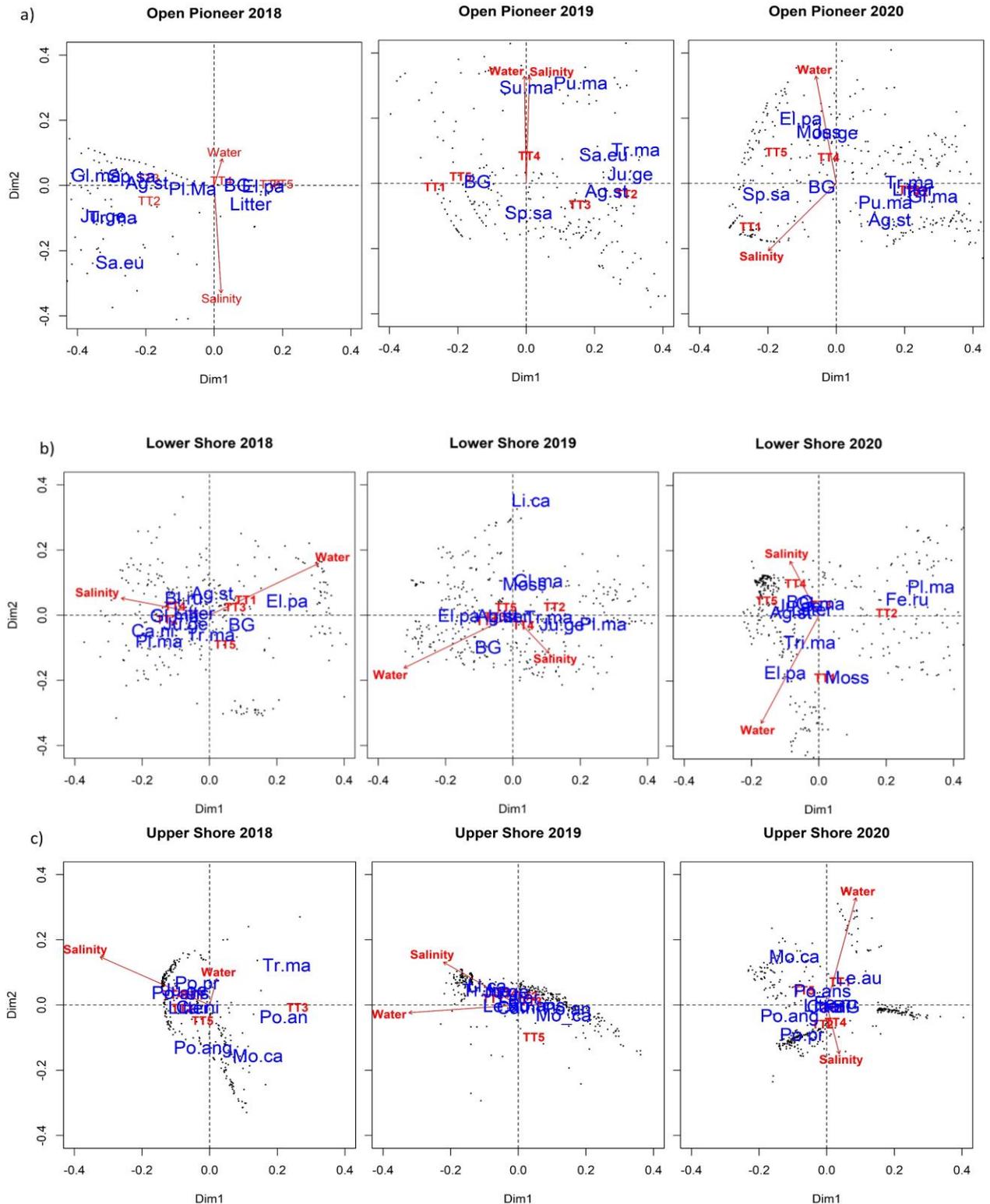


Figure 5: Principal Coordinate Analysis (PCoA) plot of plant community composition (% cover from August) based on Bray-Curtis dissimilarity matrix. a) Open Pioneer; b) Lower Shore; c) Upper Shore. BG: Bare ground; Gl.ma: *Glaux maritima*; Ju.ge: *Juncus gerardii*; Tr.ma: *Triglochin maritima*; Sa.eu: *Salicornia europaea*; Sp.sa: *Spergularia marina*; Ag.st: *Agrostis stolonifera*; Pl.ma: *Plantago maritima*; El.pa: *Eleocharia palustris*; Pu.ma: *Puccinellia maritima*; Su.ma: *Suaeda maritima*; Bl.ru: *Blysmus rufus*; Ca.ni: *Carex nigra*; Li.ca: *Linum catharticum*; Fe.ru: *Festuca rubra*; Po.an: *Poa annua*; Mo.ca: *Molinia caerulea*; Ly.vu: *Lysimachia vulgaris*; Po.pr: *Poa pratensis*; Po.ans: *Potentilla anserina*; Po.ang: *Poa angustifolia*; TT1: Treatment 1; TT2: Treatment 2; TT3: Treatment 3; TT4: Treatment 4; TT5: Treatment 5.

Discussion

All three coastal wetland communities exhibited considerable temporal changes under altered water and salinity regimes, highlighting the response of plant species to environmental variables. Results showed different responses to the treatments according to the community. The Open Pioneer (OP) community showed an increase in species richness and vegetation cover across all treatments, while Lower Shore (LS) and Upper Shore (US) underwent changes to a lesser degree (Figure 1), related to both water level and salinity.

In Baltic coastal wetlands, the Open Pioneer community appears as patches with distinctive edaphic characteristics compared to surrounding plant communities, including high levels of soil conductivity and pH, low soil moisture, and high abundance of bare ground [25], similar to sebkhas or apicum in tropical environments. Due to elevated levels of evaporation and consequently high salinity concentrations, Open Pioneer typically has a low abundance of vegetation cover, with few characteristic species able to germinate and grow in such conditions (halophytes). Changes in this community were observed in all treatments. Shore plants, which are affected by disturbances and stress such as flooding, salinity, waves and ice, may survive stressful conditions by using avoidance strategies, such as a persistent seed bank, or tolerance strategies, such as metabolic adaptations [35]. The seed bank in Open Pioneer could explain the rapid colonization of species related to new, altered conditions. In this regard, the seed bank often reflects adjacent community composition and will follow site-specific physical conditions [36]. In Baltic coastal meadows, Jutila [37] found that the total cover of vegetation was positively correlated with seedling density and negatively with open spaces of bare soil. However, this study revealed emergence and an increase in abundance of pioneer species within the Open Pioneer, including species that grow in open communities such as *Puccinellia maritima* and *Triglochin maritima*. These two species appeared in treatments characterized by lower water table and lower salinity levels. *Glaux maritima* was the most abundant species in the third year of the experiment in the decreased salinity treatment. *Glaux maritima* is classified as present in the upper saltmarsh and in brackish conditions by Ellenberg [38]. Because of the high salinity concentration in the Open Pioneer community, stress-tolerant species such as halophytes, are able to survive due to adaptations like osmotic adjustments, and antioxidant production [39]. In this community, an association of *Puccinellia maritima* and *Suaeda maritima* to raised salinity and water level was observed. This pattern may be related to the fact that these species are pioneers and dominate disturbed environments [40].

Changes in the number of species in Lower Shore and Upper Shore communities were significant but did not respond to as many treatments as those in the Open Pioneer community. The duration of the experiment (three years) may not have been enough time to observe final community shifts in Lower Shore and Upper Shore. These communities are characterised by perennial species and are subject to disturbance regimes like herbivory, common in coastal wet grasslands where extensive grazing is the main management strategy. Besides that, the main species in these communities are able to tolerate changes in water level and salinity [41] and more significant changes may only be detectable in longer-term experiments.

Plant species of coastal wetlands are adapted to saline/brackish water conditions and water level fluctuations [10]. However, accelerated sea-level rise can be a threat to coastal wetlands at different scales [42] and result in total loss where sea-level rise (including land subsidence/uplift) is greater than net elevation gain (compaction, root growth and sediment deposition) [43]. Alterations in salinity can also affect photosynthetic rate and leaf growth, causing necrosis and mortality [44] depending on species adaptation. This could explain the increase in litter and bare ground in the Lower Shore and Upper Shore communities observed within the water level and soil salinity treatments in this experiment.

Changes in soil salinity concentration due to climate change can alter soil redox potential and sulphide concentration driving shifts in species composition [29]. Salinity is the main factor controlling the species composition in the Open Pioneer community, even within soils composed of greater proportions of coarse, medium and fine sand (as is found in this plant community), which retain less

nutrients. Seeds present in the seed bank germinated under the simulated salinity changes in the Open Pioneer community. Species like *Spergularia marina* and *Glaux maritima* contributed to an increase in species richness under conditions of raised and decreased soil salinity concentration, respectively. A previous study demonstrated an inverse distribution through the Baltic coast [45], where *Spergularia marina* together with other halophytes was closer to the waterline in soils with a higher salinity, and *Glaux maritima* was associated with other species with lower soil salinity.

Overall, the Lower Shore and Upper Shore communities did not show significant changes under different salinity conditions compared to the control treatment. These communities present species occurring in both saline and brackish environments [38].

In order to assess changes in plant community composition linked to sea level rise, several studies have previously assessed and simulated the responses of plant communities and species under these conditions [29, 46]. For instance, Sharpe & Baldwin [29] found no influence of flooding conditions on species richness. On the contrary, Gough & Grace [47] observed a reduced number of species with increased flooding stress, while alleviating flooding did not have an effect on the number of species. Following a similar response as seen in the altered salinity treatments, the Open Pioneer community underwent an increase in species richness with raised water levels compared to the control. Species adapted to higher water levels such as *Eleocharis palustris* were in greater abundance in year 3 in the increased water level treatment, while species characterized by a lower requirement for water, such as *Glaux maritima* and *Centaurium littorale*, were in greater abundance in the decreased water level treatment at the end of the experiment compared to the beginning.

Lower Shore showed differences in terms of species richness in decreased water levels compared to the control. The variation of species over time was related to species with low coverage (e.g. *Carex flacca* and *Triglochin palustris*). This could be explained by the fact that Lower Shore is located in a gradient of water level between Open Pioneer and Upper Shore, with species tolerating a wide range of soil moisture conditions.

The Upper Shore community experienced a loss in species presence and consequently a decrease in species richness within the increased water level treatment, these were species with low coverage and with low water level requirement (e.g. *Stellaria graminea* and *Viola canina*).

This study therefore revealed different responses of wetland communities to altered salinity and water conditions, especially noticeable in the Open Pioneer community. The higher rate of change within the Open Pioneer could be explained by the greater availability of open spaces, and possibly a diverse seed bank inherited from nearby communities. However, evidence is still needed on stabilizing processes and resilience of communities in the longer term. Field studies [48] have previously shown that some coastal plant communities can be resilient to sea level rise as a result of organic matter deposition and sediment accretion.

Plant communities and species are generally excellent indicators of environmental conditions [22]. Plants have been used to assess the status of wetland management, disturbance or abandonment [25, 32] as they are influenced by biotic (e.g. competition, facilitation and grazing) and abiotic factors (e.g. flooding, salinity and soil nutrients) [23, 49, 50]. Here, plants have shown themselves to be sensitive indicators to relatively small changes in water levels and salinity.

In coastal wetlands, hydrology and salinity are key variables that generate stress gradients for plants and consequently determine their distribution [22]. According to Rayner et al. [51], shifts in plant communities occur over a period of five years in an intertidal saltmarsh in Australia when the sea level rise rate accelerates beyond the accretion ability of the wetland. The present work revealed a rapid change in plant community composition, especially the Open Pioneer community, within two years of altered water levels and salinity, consistent with previous studies following changes in hydrological conditions [52] and salinity [53] in wetlands.

In the Open Pioneer community, the halophyte *Spergularia salina* was associated with raised salinity conditions, while species more tolerant to flooding (e.g. *Eleocharis palustris* and *Triglochin maritima*) were observed in the treatment with increased water level.

In the Lower Shore community, salinity had less influence on species composition compared to changes in water level. In the third year of the experiment, *Agrostis stolonifera* was the most abundant species in this community under the increased water level treatment, while *Festuca rubra* was most abundant at the lowered water level. Both species are moist-site indicators, with *A. stolonifera* noted as having a higher tolerance for wet soils than *Festuca rubra* [38].

For the Upper Shore community, *Poa angustifolia* and *Carex nigra* were the most abundant, however *C. nigra* was slightly more associated with the raised water level treatment. Ellenberg indicator values [38] showed that *C. nigra* is a wet-site indicator while *P. angustifolia* is a moist-site indicator. The relationship with wetter soils can be observed in species such as *Molinia caerulea* and *Leontodon autumnalis* as reported by Ellenberg [38].

The findings show that the number of species and their relative abundance in coastal plant communities was significantly affected by flooding and salinity [53]. In Estonia the predictions for sea level rise are different along the coast due to variations in isostatic uplift and sediment accretion [3]. Previous studies showed that coastal wetlands can adapt to sea level rise if sediment accumulation rates are high enough [54]. However, the rate of accretion varies according to sediment supply [55], which is related to a range of factors including catchment soil moisture, catchment development and topography, ground surface heat budget, rainfall patterns, river regulation, dredging, vegetation type and growth rate, and long-term climate anomalies [51]. This study shows the diversity of community and species level responses to the expected range of climate change hydrological impacts in coastal wetlands in the Baltic. The experimental conditions in this study took into account isostatic uplift and sediment accretion of the Estonian coast and the results demonstrated significant species and community changes over three years. Future studies should address similar impacts over longer time scales, in order to assess long term community responses.

Methods

Study Site

The Baltic Sea is one of the largest brackish water bodies in the world [56] due to its relative isolation as a consequence of the narrow connection with the Atlantic Ocean through the Danish Straits [57]. It is strongly influenced by large-scale atmospheric circulation, hydrological processes (e.g. currents and internal mixing) and restricted water exchange in its entrance [11, 58]. Salinity within the Baltic Sea is maintained by a pattern of stratification with low salinity surface waters during the spring and early summer, and high salinity bottom waters during the summer [59]. The outflow of low salinity water in the surface and the inflow of higher salinity water at depth maintains the upper layer salinity at about 6–8 psu (practical salinity units) around Estonia and a more saline deep-water layer with about 10–14 psu [58], although this varies geographically.

Coastal wetlands in Estonia have a very low tidal range (~0.02 m), and inundation is predominantly driven by atmospheric pressure and fluctuating meteorological conditions across the North Atlantic and Fennoscandia [57]. As a result, the rate and magnitude of inundation is irregular and varies throughout the coastal landscape [13]. Recent estimates of relative sea level rise from three tide gauges along the Estonian coast are: 1.5–1.7 mm yr⁻¹ at Tallinn, 1.7–2.1 mm yr⁻¹ from Narva-Jõesuu and 2.3–2.7 mm yr⁻¹ at Pärnu [3].

Along the Baltic Sea coastline, both water levels and salinity have a strong influence on species distribution and therefore on the structure and composition of aquatic and coastal floral and faunal communities [19]. Estonian wetlands cover around 25% of the territory and less than 1% comprises coastal wetlands, including grasslands, reed swamps and salt marshes [34]. The average number of vascular plants in the most diverse Estonian wetlands, such as meadows, varies between 15.2 and 26.1 per m² [60]. They support considerable biodiversity, including rare plant species, breeding and migratory birds [13, 22], influenced by topography and hydrology, and favoured by low grazing intensity [22, 25].

Experimental design

Six coastal wetland plant communities (Open Pioneer, Club-rush swamp, Reed Swamp, Lower Shore grassland, Upper Shore grassland and Tall Grass) were identified based on a phytosociological classification developed by Burnside et al. [25]. This classification was developed for the region where the mesocosm communities were collected and has proven useful to detect changes in plant community composition due to abandonment and management [61, 62]. Three coastal wetland communities were selected for the mesocosm experiment: Lower Shore, Upper Shore and Open Pioneer. These communities were selected for the narrow autecological preference of the key species such as water table level soil and salinity. The Open Pioneer community occupies small patches located in depressions and along water courses, where water evaporates in standing pools forming salt deposits at the surface. The Open Pioneer community is characterised by an abundance of bare ground and high salinity and presence of typical halophyte species such as *Salicornia europaea* and *Suaeda maritima*, considered rare for the region. The Lower Shore and Upper Shore communities are located in specific elevations and sometimes co-exist as a mosaic. The Lower Shore community is found in elevations around 30 cm and the Upper Shore community, around 38 cm above mean sea level (msl) and further away from the sea [24, 25]. The Lower Shore community is mainly indicated by *Juncus gerardii* with frequent *Festuca rubra*, *Glaux maritima*, *Plantago maritima* and *Triglochin maritima*. The Upper Shore has denser vegetation than the Lower Shore and is characterized by the dominant presence of *Festuca rubra*, as well as *Juncus gerardii*, *Leontodon autumnalis*, *Triglochin maritima*, and *Plantago maritima* [25].

Fifteen turves measuring 50x70cm and 30cm deep were collected from each of the three selected plant communities (45 in total) within the Tahu North coastal wetland. These were transplanted into 90L containers (dimensions 56 x 79 x 32 cm). The containers were filled with a 2:1:1 soil mixture consisting of commercially washed sharp sand, loam and compost [63], very similar to the deep substrate of the wetland. A rotating mixer was used to homogenize the base soil.

Each experimental treatment contained three replicate containers for each plant community. A control treatment was maintained with current Eastern Baltic Sea salinity (6.5 psu) [11] and current average water table level during the growing season below the soil surface for each community (Lower Shore: 0.15 m; Upper Shore: 0.2 m; Open Pioneer: 0.1 m) [22, 26]. The treatments simulating climate change included two different salinities used: 2.9 psu predicted salinity by 2100 in the eastern Baltic [11], and 13 psu to evaluate the effect of an increase in salinity in the event that there is greater mixing of deeper water (salinity of deep sea water in the Eastern Baltic is about 10–14 psu) and surface water as a result of increased storminess linked to climate change (Table 3). Considering the higher salinity characterising the Open Pioneer community (12.5 psu), the simulation was different for this community (5.6 and 25 psu). Salinity was controlled weekly by adding sea salt or fresh water [64].

Three different water level scenarios were simulated on the basis of three parameters, namely: Global sea level rise rates of 3.3 mm/yr [65], isostatic uplift (2.8 mm/yr on the north coast of Estonia and 0 mm/yr in the south west) and sediment accretion rates (1.9 mm/yr best case scenario) [24]. Resulting from the combination of the abovementioned factors, the future (2100) water level change scenarios were: 0.12 m below current plant community water levels (best case scenario with continued progradation) and 0.12 m above current water level (worst case scenario with inundation), plus a control (current water levels). Taps were placed in the containers at the corresponding water level and the treatments were kept constant during the growing period to simulate the limited water level variation.

Over three years of the experiment, plant community responses were evaluated once a month using a 50 cm² permanent graduated quadrat (10 cm² sub-quadrats) during the growing period (April to September). Changes in the abundance of plant species present by area of ground cover were assessed [66].

Each year of the experiment, grazing was simulated by cutting the vegetation to 10 cm height two weeks after turf greening [22].

Table 3: Treatments in the mesocosm experiment. Salinity is given as practical salinity unit (psu) and water level in relation to the soil surface (m). Water level below control level is denoted with *minus* and water level above control level is denoted with *plus sign*. (*) refers to Open Pioneer.

Treatment	Control	T 1	T 2	T3	T4
Salinity (psu)	6.5	6.5	6.5	2.9	13
	12.5*	12.5*	12.5*	5.6*	25*
Water level (m)	Open Pioneer: 0.1 Lower Shore: 0.15 Upper Shore: 0.2	+ 0.12	- 0.12	Control	Control

Statistical Analysis

Plant communities were characterized using species richness and percentage cover within individual sub quadrats over three years. In order to analyse plant community data, rank abundance curves, permutational multivariate analysis of variance (PERMANOVA) and principal coordinate analysis (PCoA) were performed using R software (R version 4.0.3). The packages BiodiversityR [67], vegan [68] and ggplot2 [69] were used to examine differences between treatment in plant community composition and visualize community responses to treatment and year.

Species richness and abundance were calculated for 2018, 2019 and 2020 separately for each community. A Kruskal Wallis test was performed to identify significant differences in richness between treatments by year. When the results were significant, a post-hoc Dunn's test was used with Bonferroni adjustments to reveal the treatments which presented richness differences in each year. The abundance was plotted using rank abundance curves (RAC) on a logarithmic scale. In a rank abundance curve, the x-axis represents the most abundant species and the y-axis the relative abundance. Species evenness is reflected in the slope of the line that fits the graph. A steep gradient indicates low evenness as high-ranking species have much higher abundances than low-ranking species. A shallow gradient indicates high evenness as the abundances of different species are similar [67]. This analysis has previously been used as an indicator of the structure of a multispecies community by detailing species-level community changes [70].

The permutational multivariate analysis of variance (PERMANOVA) was used to examine differences among treatments in plant community composition and was implemented using the Adonis function in the vegan package [68]. In order to assess community composition differences with PERMANOVA, Bray-Curtis dissimilarity matrices were calculated from species importance values obtained from the percentage cover of each quadrat. Species importance values represent a measure of how dominant a species is in a given community [71]. Subsequently, PERMANOVA was run, including crossed effects of year, treatment as fixed effects, and samples as random effect (Table 2). PERMANOVA is a non-parametric multivariate test used to compare groups. It has been previously used to identify differences in plant community composition associated with environmental variables [66]. Finally, a principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity was used to visualize the responses of the communities to treatments in each year (Figure 5).

Conclusions

Baltic coastal wetlands support high biodiversity and many ecosystem services and so are important targets for conservation. Based on these mesocosm experiments, it can be concluded that the climate

change predictions for 2100 for the Baltic Sea will cause significant shifts in coastal wetland plant species richness and abundance. Both water level and salinity changes contributed to alterations in plant species composition in all wetland communities. Species richness and abundance increased in all treatments in the Open Pioneer community while in the Lower Shore and Upper Shore communities changes were not so notable, most likely because the perennial species characterising these communities are more resilient than shorter-lived species. Results suggest that relatively small changes in water level and salinity in Baltic coastal wetlands can have important consequences for species composition. Consequently, the implications of climate change could include affecting the quality of habitats for many species (e.g. wading birds) and potential alterations in the nutritional value of wetland plant communities for large grazers.

References

1. Kimmel, K., Kull, A., Salm, J. & Mander, Ü. The status, conservation and sustainable use of Estonian wetlands. *Wetlands Ecology and Management* 18, 375-395 (2008).
2. Engle, V. Estimating the Provision of Ecosystem Services by Gulf of Mexico Coastal Wetlands. *Wetlands* 31, 179-193 (2011).
3. Ward, R., Teasdale, P., Burnside, N., Joyce, C. & Sepp, K. Recent rates of sedimentation on irregularly flooded Boreal Baltic coastal wetlands: Responses to recent changes in sea level. *Geomorphology* 217, 61-72 (2014).
4. Villoslada Peciña, M. et al. Country-scale mapping of ecosystem services provided by semi-natural grasslands. *Science of The Total Environment* 661, 212-225 (2019).
5. Lima, M., Ward, R. & Joyce, C. Environmental drivers of sediment carbon storage in temperate seagrass meadows. *Hydrobiologia* 847, 1773-1792 (2019).
6. Ward, R. Sedimentary response of Arctic coastal wetlands to sea level rise. *Geomorphology* 370, 107400 (2020a).
7. Akumu, C., Pathirana, S., Baban, S. & Bucher, D. Examining the potential impacts of sea level rise on coastal wetlands in north-eastern NSW, Australia. *Journal of Coastal Conservation* 15, 15-22 (2010).
8. Ward, R. Carbon sequestration and storage in Norwegian Arctic coastal wetlands: Impacts of climate change. *Science of The Total Environment* 748, 141343 (2020b).
9. Hossain, M., Hein, L., Rip, F. & Dearing, J. Integrating ecosystem services and climate change responses in coastal wetlands development plans for Bangladesh. *Mitigation and Adaptation Strategies for Global Change* 20, 241-261 (2015).
10. Ward, R., Friess, D., Day, R. & Mackenzie, R. Impacts of Climate Change on Global Mangrove Ecosystems: A Regional Comparison. *Ecosystem Health and Sustainability* 4, 1-25 (2016c).
11. Graham, L. P. et al. Climate Change in The Baltic Sea Area Draft HELCOM Thematic Assessment (2007).
12. BACC. Assessment of climate change for the Baltic Sea Basin. (Springer, 2008).
13. Riviš, R. et al. Trends in the development of Estonian coastal land cover and landscapes caused by natural changes and human impact. *Journal of Coastal Conservation* 20, 199-209 (2016).
14. Cubasch U. et al. Projections of future climate change. In: IPCC Climate Change 2001: The scientific basis contribution of working group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press (2001).
15. Mafi-Gholami, D., Zenner, E., Jaafari, A. & Ward, R. Modeling multi-decadal mangrove leaf area index in response to drought along the semi-arid southern coasts of Iran. *Science of The Total Environment* 656, 1326-1336 (2019).
16. IPCC. Global Warming of 1.5 °C. [ipcc.ch \(2008\)](https://www.ipcc.ch/sr15/). at <<https://www.ipcc.ch/sr15/>>
17. Omstedt, A., Pettersen, C., Rodhe, J. & Winsor, P. Baltic Sea climate: 200 yr of data on air temperature, sea level variation, ice cover, and atmospheric circulation. *Climate Research* 25, 205-216 (2004).
18. Räisänen, J. (2017). Future climate change in the Baltic Sea Region and environmental impacts. In *Oxford Research Encyclopedia of Climate Science*.

19. Dippner, J. W. et al. Climate-related Marine Ecosystem Change in Team, B. A. Assessment of climate change for the Baltic Sea basin. Springer Science & Business Media (2008).
20. Ward, R., Burnside, N., Joyce, C., Sepp, K. & Teasdale, P. Improved modelling of the impacts of sea level rise on coastal wetland plant communities. *Hydrobiologia* 774, 203-216 (2016a).
21. Vuorinen, I. Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. *ICES Journal of Marine Science* 55, 767-774 (1998).
22. Berg, M., Joyce, C. & Burnside, N. Differential responses of abandoned wet grassland plant communities to reinstated cutting management. *Hydrobiologia* 692, 83-97 (2011).
23. Short, F., Kosten, S., Morgan, P., Malone, S. & Moore, G. Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany* 135, 3-17 (2016).
24. Ward, R., Burnside, N., Joyce, C. & Sepp, K. Importance of Microtopography in Determining Plant Community Distribution in Baltic Coastal Wetlands. *Journal of Coastal Research* 321, 1062-1070 (2016b).
25. Burnside, N., Joyce, C., Puurmann, E. & Scott, D. Use of vegetation classification and plant indicators to assess grazing abandonment in Estonian coastal wetlands. *Journal of Vegetation Science* 18, 645-654 (2007).
26. Ward, R., Burnside, N., Joyce, C. & Sepp, K. The use of medium point density LiDAR elevation data to determine plant community types in Baltic coastal wetlands. *Ecological Indicators* 33, 96-104 (2013).
27. Goud, E., Watt, C. & Moore, T. Plant community composition along a peatland margin follows alternate successional pathways after hydrologic disturbance. *Acta Oecologica* 91, 65-72 (2018).
28. Moreno, J., Terrones, A., Juan, A. & Alonso, M. Halophytic plant community patterns in Mediterranean saltmarshes: shedding light on the connection between abiotic factors and the distribution of halophytes. *Plant and Soil* 430, 185-204 (2018).
29. Sharpe, P. & Baldwin, A. Tidal marsh plant community response to sea-level rise: A mesocosm study. *Aquatic Botany* 101, 34-40 (2012).
30. Lindig-Cisneros, R. & Zedler, J. *Phalaris arundinacea* seedling establishment: effects of canopy complexity in fen, mesocosm, and restoration experiments. *Canadian Journal of Botany* 80, 617-624 (2002).
31. Ahn, C. & Mitsch, W. Scaling considerations of mesocosm wetlands in simulating large created freshwater marshes. *Ecological Engineering* 18, 327-342 (2002).
32. Brotherton, S. & Joyce, C. Extreme climate events and wet grasslands: plant traits for ecological resilience. *Hydrobiologia* 750, 229-243 (2015).
33. Stewart, R. I. et al. Mesocosm experiments as a tool for ecological climate-change research. In *Advances in ecological research*. Academic Press 48, 71-181 (2013).
34. Kont, A., Ratas, U., & Puurmann, E. Sea-level rise impact on coastal areas of Estonia. *Climatic Change* 36, 175-184 (1997).
35. Crawley, M. *Plant Ecology*. (Oxford, 1989).
36. Eley-Quirk, T. & Leck, M. Patterns of seed bank and vegetation diversity along a tidal freshwater river. *American Journal of Botany* 102, 1996-2012 (2015).
37. Jutila, H. *Plant Ecology* 166, 275-293 (2003).
38. Ellenberg, H. *Zeigerwerte der Gefäßpflanzen Mitteleuropas*. 42-111 (Scripta Geobotanica, 1979).
39. Joshi, R. et al. Salt adaptation mechanisms of halophytes: improvement of salt tolerance in crop plants. In *Elucidation of abiotic stress signalling in plants*. Springer (2015).
40. Tessier, M., Gloaguen, J. & Lefevre, J. *Plant Ecology* 147, 193-203 (2000).
41. Hanslin, H. & Eggen, T. Salinity tolerance during germination of seashore halophytes and salt-tolerant grass cultivars. *Seed Science Research* 15, 43-50 (2005).
42. Spencer, T. et al. Global coastal wetland change under sea-level rise and related stresses: The DIVA Wetland Change Model. *Global and Planetary Change* 139, 15-30 (2016).

43. Marani, M., D'Alpaos, A., Lanzoni, S., Carniello, L. & Rinaldo, A. Biologically-controlled multiple equilibria of tidal landforms and the fate of the Venice lagoon. *Geophysical Research Letters* 34, (2007).
44. Petersen, K., Frank, H., Paytan, A. & Bar-Zeev, E. Impacts of Seawater Desalination on Coastal Environments. *Sustainable Desalination Handbook* 437-463 (2018).
45. Hulisz, P., Piernik, A., Mantilla-Contreras, J. & Elvisto, T. Main Driving Factors for Seacoast Vegetation in the Southern and Eastern Baltic. *Wetlands* 36, 909-919 (2016).
46. FitzGerald, D., Fenster, M., Argow, B. & Buynevich, I. Coastal Impacts Due to Sea-Level Rise. *Annual Review of Earth and Planetary Sciences* 36, 601-647 (2008).
47. Gough, L. & Grace, J. Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* 117, 527-535 (1998).
48. Liu, Z., Fagherazzi, S. & Cui, B. Success of coastal wetlands restoration is driven by sediment availability. *Communications Earth & Environment* 2, (2021).
49. Short, F. & Neckles, H. The effects of global climate change on seagrasses. *Aquatic Botany* 63, 169-196 (1999).
50. Engels, J., Rink, F. & Jensen, K. Stress tolerance and biotic interactions determine plant zonation patterns in estuarine marshes during seedling emergence and early establishment. *Journal of Ecology* 99, 277-287 (2010).
51. Rayner, D. et al. Intertidal wetland vegetation dynamics under rising sea levels. *Science of The Total Environment* 766, 144237 (2021).
52. Toogood, S. & Joyce, C. Effects of raised water levels on wet grassland plant communities. *Applied Vegetation Science* 12, 283-294 (2009).
53. Humphreys, A., Gorsky, A., Bilkovic, D. & Chambers, R. Changes in plant communities of low-salinity tidal marshes in response to sea-level rise. *Ecosphere* 12, (2021).
54. Krauss, K. et al. How mangrove forests adjust to rising sea level. *New Phytologist* 202, 19-34 (2014).
55. Kirwan, M. et al. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37 (2010).
56. Hannerz, F. & Destouni, G. Spatial Characterization of the Baltic Sea Drainage Basin and Its Unmonitored Catchments. *AMBIO: A Journal of the Human Environment* 35, 214-219 (2006).
57. Kont, A., Jaagus, J. & Aunap, R. Climate change scenarios and the effect of sea-level rise for Estonia. *Global and Planetary Change* 36, 1-15 (2003).
58. von Storch, H. & Omstedt, A. Introduction and Summary in Team, B. A. Assessment of climate change for the Baltic Sea basin. *Springer Science & Business Media* (2008).
59. Stigebrandt, A. Physical oceanography of the Baltic Sea. In *A systems analysis of the Baltic Sea*. Springer, 19-74 (2001).
60. Ingerpuu, N. & Sarv, M. Effect of Grazing on Plant Diversity of Coastal Meadows in Estonia. *Annales Botanici Fennici* 52, 84-92 (2015).
61. Villoslada Peciña, M., Bergamo, T., Ward, R., Joyce, C. & Sepp, K. A novel UAV-based approach for biomass prediction and grassland structure assessment in coastal meadows. *Ecological Indicators* 122, 107227 (2021).
62. Villoslada, M. et al. Fine scale plant community assessment in coastal meadows using UAV based multispectral data. *Ecological Indicators* 111, 105979 (2020).
63. Araya, Y., Gowing, D. & Dise, N. A controlled water-table depth system to study the influence of fine-scale differences in water regime for plant growth. *Aquatic Botany* 92, 70-74 (2010).
64. Koch, E. et al. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment* 7, 29-37 (2009).
65. Church, J. & White, N. Sea-Level Rise from the Late 19th to the Early 21st Century. *Surveys in Geophysics* 32, 585-602 (2011).
66. Goodwillie, C., McCoy, M. & Peralta, A. Long-term nutrient enrichment, mowing, and ditch drainage interact in the dynamics of a wetland plant community. *Ecosphere* 11 (2020).

67. Kindt, R. & Coe, R. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry | Transforming Lives and Landscapes with Trees (2005). at <<http://www.worldagroforestry.org/output/tree-diversity-analysis>>
68. Oksanen, J. et al. CRAN - Package vegan. Cran.r-project.org (2022). at <<https://CRAN.R-project.org/package=vegan>>
69. Wickham, H. Create Elegant Data Visualisations Using the Grammar of Graphics. Ggplot2.tidyverse.org (2016). at <https://ggplot2.tidyverse.org>
70. Avolio, M. et al. A comprehensive approach to analyzing community dynamics using rank abundance curves. *Ecosphere* 10, (2019).
71. Curtis, J. & McIntosh, R. The Interrelations of Certain Analytic and Synthetic Phytosociological Characters. *Ecology* 31, 434-455 (1950).

Acknowledgements

This research was supported by European Social Fund's Dora Plus Programme. The authors are grateful to Raul Sampaio de Lima and Kai-Yun Li for the help given during the data collection, and Henri Järv and Janar Raet for the mesocosm construction.

Author contributions

B., T.F. collected and analysed the data, and wrote the manuscript; W., R.D. supervised the research and revised the manuscript; J., C.B. supervised the research and revised the manuscript, V., M. revised the manuscript; S., K. supervised the research and revised the manuscript

Data availability statement

Raw data and script related to this work are available from the corresponding author upon request.