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MISS LINE HOLM ANDERSEN (Orcid ID : 0000-0003-4001-0046)

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Turnover and change in plant species composition in a shielded salt marsh following variation in precipitation and temperature

Line Holm Andersen[1], Anna Sofie Krag Skærbæk[1], Thomas Bo Sørensen[1], Jeppe Storgaard Knudsen[1], Cino Pertoldi[1,2], Simon Bahrndorff[1], Dan Bruhn[1]

[1] Section of Biology and Environmental Science, Department of Chemistry and Bioscience, Aalborg University, Frederik Bajers Vej 7H, Aalborg, DK 9220, Denmark

[2] Aalborg Zoo, Mølleparkvej 63, DK-9000 Aalborg, Denmark.

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Correspondence

Line Holm Andersen, Section of Biology and Environmental Science, Department of Chemistry and Bioscience, Aalborg University, Aalborg, Denmark

Email: lha@bio.aau.dk

ORCID ID: 0000-0003-4001-0046

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Abstract

Questions: Temperature and precipitation variation between years may affect plant species composition directly or indirectly. We wish to investigate whether salt marsh edaphic conditions and plant species composition changed as a result of climatic variation. Further, whether areas with the largest edaphic variations also experience the largest change in species composition and turnover. Finally, did temperature and precipitation variations change the way the plant community was able to respond to natural edaphic gradients?

Location: Bygholmengen, a shielded salt marsh in Vejlerne, Denmark, Northern Europe.

Methods: Botanical surveys were conducted and soil samples collected from 40 plots during a wet and dry summer to register changes in vegetation cover, species richness composition and edaphic factors (moisture, nutrients, salinity). These data were used to calculate dissimilarities in species composition, temporal turnover and environmental dissimilarity between years. A linear mixed effects model was used to link species richness with the measured edaphic factors.

Results: We found that the precipitation and temperature variations altered the edaphic conditions; furthermore, the vegetation cover and species richness decreased when conditions were dry whereas the number of salt marsh species increased. Further, species composition changed significantly between years, and sampling plots that experienced the least edaphic change also retained more species between years. Species richness responded more to changes in nutrient availability during wet than dry conditions.

Conclusion: Our results pointed towards the climatic variations, and subsequent change in edaphic conditions, being responsible for the significant change in species composition as areas with the least change in edaphic factors retained most species between years. Dry conditions favored salt marsh adapted species and the extent to which increased nutrient levels led to a higher species richness decreased in dry compared to wet conditions.

Key words: Salt meadow, vegetation, species richness, biodiversity, temporal turnover, environmental dissimilarity, Denmark, coastal habitat

1 Introduction

The salt marsh, a threatened coastal habitat, is estimated to decline on a global scale due to sea level rise (Craft et al., 2009; Blankespoor, Dasgupta, & Laplante, 2014; Crosby et al., 2016; Spencer et al., 2016), and is also vulnerable to interannual precipitation and temperature variation (Dunton, Hardegree, & Whitledge, 2001; Osland et al., 2016; Hanson et al., 2016). Interannual variation in the climate can result in changes in the species composition as abiotic stressors like flooding, warming and increased salinity affect the biodiversity, species composition and distribution of coastal plant communities (Hook, Buford, & Williams, 1991; McKee, Mendelssohn, & Materne, 2004; Gedan & Bertness, 2009). Dunton et al. (2001) showed that an increase in precipitation changed the species composition and increased the biomass on a salt marsh, while droughts in estuaries are associated with dieback of salt marsh vegetation and a decrease in biomass (McKee et al., 2004; Alber, Swenson, Adamowicz, & Mendelssohn, 2008; Wetz & Yoskowitz, 2013; Paudel, Milleville, & Battaglia, 2018). Shifts in rainfall regimes can cause the vegetation structure to shift between salt flats, mangroves and salt marshes (Osland et al., 2016). Further, droughts alter the soil chemistry and result in more saline conditions (Chapple & Dronova, 2017; Forbes & Dunton, 2006; Palomo, Meile, & Joye, 2013). Stressful conditions not only affect the physical environment but both salt and drought stress impact plant ability to utilize nutrients (Bista, Heckathorn, Jayawardena, Mishra, & Boldt, 2018; Hu & Schmidhalter, 2005).

Historically, many salt marshes have been shielded by dams and while some dams have been removed many still remain (Zedler & Nordby, 1987; St. Omer, 1994). Dams may alter the hydrology and vegetation of the marsh area (St. Omer, 1994; Weis & Butler, 2009; Van Loon-Steensma & Slim, 2013). Despite the long-term presence of dams salt marsh species can still be present (St. Omer, 1994) and such salt marsh areas still fall under the protection by the European Habitats Directive (Council of the European Commission, 1992). Without regular tidal intrusions, dammed salt marshes are even more dependent on water gained through precipitation and a lack of precipitation can have large consequences for the vegetation (Zedler, Covin, Nordby, Williams, & Boland, 1986; Zedler & Nordby, 1987). Given that interannual climatic variations resulting in droughts and floodings are likely to become more frequent (Salinger, 2005; Jongejans, De Kroon, Tuljapurkar, & Shea, 2010), and as these extreme climatic events have shown negative impacts on plants across habitat types including coastal habitats (Ciais et al., 2005; Maxwell et al., 2019), it is important to know how the shielded salt marsh respond to climatic variation in precipitation and temperature. While multiple studies have described how salt marsh vegetation cover and biomass is affected by drought (McKee et al., 2004; Alber et al., 2008; Wetz & Yoskowitz, 2013; Paudel et al., 2018), the effects of precipitation and temperature variation on the shielded salt marsh plant communities are not yet explained. It is therefore important to determine whether shielded salt marshes respond equally to tidal salt marshes in response to precipitation and temperature variations; information, that will be of special interest to salt marsh managers. Here, we studied the effect of precipitation and temperature variation on a plant community of a shielded salt marsh in a wetter than average year in 2017 followed by a year drier and warmer than average in 2018 which created an optimal study setting, with the aim of quantifying changes in the vegetation (Cappelen, 2018a; Cappelen, 2019).

By taking advantage of the between-year climatic fluctuations, we wish to investigate how the plant community responds to variations in temperature and precipitation. We aimed at answering the following questions: 1) Can precipitation and temperature variations between years change the edaphic conditions (moisture, salinity, nutrient levels) of a salt marsh? We expected a change in the abiotic environment following the drought towards more saline conditions (Chapple & Dronova, 2017; Forbes & Dunton, 2006; Palomo et al., 2013). As increased precipitation on salt marsh habitats influence plant species composition (Dunton et al., 2001), we expect species composition during a year of drought to be different from that of a wet year, leading to the questions: 2) Does species composition respond to extremes in precipitation and temperature on a year-to-year basis during current climatic conditions? We expected the species composition to change towards being adapted to drier and more saline condition during the dry year compared to the wet year. 3) Is species turnover linked to environmental dissimilarity? As both salt and drought stress impact plant ability to utilize nutrients (Bista et al., 2018; Hu & Schmidhalter, 2005), we expect plants to react differently to edaphic gradient during wet and dry years.

2 Methods

2.1 Study area

This study took place on the salt marsh Bygholmengen (728 ha), in De Østlige Vejler, Denmark, that is protected under the European Habitats Directive as a Natura 2000 site (H1330) (Appendix S1A) (Miljøstyrelsen, 2005a; Miljøstyrelsen, 2005b; Miljøstyrelsen, 2011). Bygholmengen was created in 1868 in a land reclamation project but due to repeated problems with flooding and drainage, the idea of using the land in agriculture was quickly abandoned (Riis, 2009). Today, the salt marsh is a scientific reserve (area with no access to the general public) shielded by a dam and exempt from regular tidal intrusion. The dam construction together with pump enables water level management to some extent in the salt marsh. Though dams may shield salt marshes from sea level rise and erosion (Van Loon-Steensma & Slim, 2013), shielded salt marshes may be increasingly susceptible to drought events as they do not experience the regular tidal inundations.

In 2017, 590 cattle grazed the meadow resulting in a grazing pressure of 0.81 cattle ha^{-1} while the number of cattle in 2018 was decreased to 525 corresponding to 0.72 cattle ha^{-1}.

2.2 Climate data

To quantify the climatic differences between 2017 and 2018, data on the climate of Northern Jutland from 2017 and 2018 was obtained through reports from the Danish Meteorological Institute (DMI).

2.3 Botanical surveys

Botanical surveys were conducted in order to determine the vegetation cover, vegetation density, species richness and biodiversity. A total of 40 non-permanent sampling plots were randomly distributed on the marsh, ensuring a distance of at least 200 m between plots and located using a GPS (Garmin etrex 10). These sampling plots were examined in both August 2017 and August 2018. Given the flat terrain, we believe that the plots were relocated with a high accuracy; in a different study, the GPS relocated pit fall traps dug into the ground with great accuracy.

Each sampling plot consisted of a circle with a radius of 5 meters (Nygaard, Damgaard, Nielsen, Bladt, & Ejrnæs, 2016) in which all plants were determined at the species level to create a comprehensive species list using Frederiksen, Rasmussen and Seberg (2006) assisted by graminoid literature (Schou, 2006; Schou, Wind, & Lægaard, 2010; Schou, Wind, & Lægaard, 2014). We determined total species richness as the number of species within the 5 m circle and counted the number of salt marsh species within each circular plot to obtain the salt marsh species richness. We define salt marsh species as species specific for habitat type 1330 in the NATURA 2000 framework as well as species listed as characteristic for Danish salt marshes (European Commission, 2013; Miljøstyrelsen, 2016) (Appendix S2).

At the center of each plot we positioned a pinpoint frame. Within the pinpoint frame of 0.5x0.5 m with 16 intersection points (Levy & Madden, 1933) we determined vegetation cover, height and density and registered the frequency of plant species.

2.4 Edaphic factors

To determine whether the abiotic environment changed between years, we tested the soil in both 2017 and 2018. At the circumference of each 5 m circle, four soil samples were collected. They were analyzed for content of total phosphorus (P) by extraction in HNO_3 using the ICP-OES method (Danish Standards Association, 2003) and available phosphorous (P) using the molybdate method after extraction in 1 N KCl (ISO 6878, 2004). Total nitrogen (N) was determined using a LECO model 628 (ISO 16948, 2015). Content of ammonium (NH_4^+) (Danish Standards Association, 1975), nitrite (NO_2^-) (Danish Standards Association, 1991) and nitrate (NO_3^-) (Danish Standards Association, 1991) were determined by spectrometric detection after extraction in 0.001 M H_2SO_4. Moisture content was determined by placing a soil sample at 105°C until constant weight following the Danish Standard (1980) and organic matter content was determined by adding dry samples to a muffle furnace for 4 hours (Dansk Standardiseringsråd, 1980). Soil salinity levels were determined in a 1:5 distilled water:soil solution (Hardie & Doyle, 2012). For all edaphic factors but total P, the four samples were analyzed separately and the mean was calculated, whereas for total P the four soil samples were mixed prior to analysis.

2.5 Data analysis

2.5.1 Edaphic factors

T-tests were conducted to test for between-year differences in the edaphic variables. To avoid type 1 errors, we further did a Bonferroni correction of the *p*-values to account for multiple testing.

2.5.2 Vegetation cover, species richness, species composition and turnover rates

The cover was calculated as the percentage number of pins touched by any vegetation within the pinpoint frame, thereby distinguishing between ground covered in vegetation or other (incl. water, bare ground and decomposing organic materials). The vegetation density was calculated as the number of times the pinpoint pin was touched by the vegetation.

We calculated Simpson's diversity (Simpson, 1949), Shannon's diversity (Shannon, 1948) and Pielou's evenness (Pielou, 1966) as measures of biodiversity for each pinpoint frame using R package vegan (Oksanen et al., 2017). In vegan, Simpson's diversity is defined as 1- $\sum p_i^2$, Shannon's diversity (H) is defined as 1- $\sum p_i \log(p_i)$ and Pielou's evenness is defined as H/log(S). Here, p_i is the proportional abundance of species i and S is the total species count.

For all plant species present in the 5 m circle, Ellenberg values on moisture (F), salinity (S) and nutrients (N) were used to calculate average Ellenberg values for each sampling plot (Ellenberg, Weber, Düll, Wirth, & Werner, 2001).

We divided the species lists for each circular sampling plot into three groups. First, we counted how many species were present in 2017 only but had disappeared in 2018 (species lost). Second, we counted how many species appeared in 2018 that were not present in 2017 (species gained). Third, we counted the number of species present on a given sampling plot in both 2017 and 2018 (the species overlap.) We calculated the recurrence rate as the percentage of plots in which a species occurred in 2018, given it had been found in 2017; further, we determined whether the plant was annual or perennial using Frederiksen et al. (2006). This was done for the most common species (more than 10 occurrences across 2017 and 2018) as well as all species.

Aiming to determine whether species composition in the 5 m circle (presence absence) had changed significantly between 2017 and 2018 on both a larger, salt marsh scale and on a plot level scale, we followed the approach presented by Finderup Nielsen, Sand-Jensen, Dornelas, & Bruun (2019). First, a turnover matrix based on the binary Jaccard dissimilarity was created using betadisper (Oksanen et al., 2017). Next, we used a Principal Coordinate Analysis (PCoA) approach to visualize the data with a polygon symbolizing each of the years 2017 and 2018. In order to test for differences in species composition between years, we computed a PERMANOVA based on the Jaccard metric using Adonis2 in R with 999 permutations (McArdle & Anderson, 2001; Oksanen et al., 2017). Next, to determine the identity of the species that contributed most to the potential difference between years, we did an indicator species analysis using the indicspecies package in R with 999 permutations and a significance level of 0.05 (Cáceres & Legendre, 2009).

We further calculated the temporal species turnover to quantify whether the species composition had changed as (species gained + species lost)/(total number of species observed on a given sampling plot during both years) (Cleland et al., 2013; Diamond, 1969). Linear models were made between the species turnover and the total species richness on each sampling plot across years.

The environmental dissimilarity is a measure of the variability across all edaphic factors between plots (Lloyd, Mac Nally, & Lake, 2005; Qian & Ricklefs, 2012). We calculated the environmental dissimilarity between individual plots of 2017 and 2018 using the Canberra distance (Lance & Williams, 1967) on a matrix containing information on all edaphic variables. The Canberra distance internally standardizes the contributions of each variable thereby accounting for large differences in numerical values of the individual variables (Lloyd et al., 2005). We made linear models between the environmental dissimilarity and the species turnover.

2.5.4 Correlations between the edaphic factors and species richness and salt marsh richness

To test for correlations between species richness and salt marsh richness of the circular plots and the edaphic factors within and between the two years, linear mixed effects models with random slope and intercept for year was used. A model was created for each of total species richness and salt marsh species richness, each including all edaphic variables. Year was a fixed factor in the model. Plot was a random factor to account for the repeated measures. A parameter was considered significant at a 0.05 level given the t value exceeded ±1.96.

All statistical analyses described above were performed in R 3.4.1 (R Core Team, 2017). Graphs were created using ggplot2 (Wickham, 2016).

3 Results

3.1 Climate data

Since 1874, only 10 summers have been wetter than that of 2017, while the spring rainfall was among the three highest rainfalls during the past 10 years (Cappelen, 2019; Cappelen, 2018a; DMI, 2011). Meanwhile, 2018 had the most hours of sun since 1920, with spring temperatures being amongst the top ten measured since 1953 and the mean summer temperature being the highest since 1953 (Cappelen, 2019; Cappelen, 2018a).

All climatic comparisons presented below are in comparison to the 10-year average (referred to as the ‘average’). In 2017, Northern Jutland experienced 7% higher rainfall than average and 12% fewer hours of sun (Cappelen, 2018a). In contrast, both spring and summer of 2018 was significantly warmer and drier than average (Cappelen, 2018b; Cappelen, 2018c), and overall, 2018 experienced 11% more hours of sun and 25% less rainfall compared to the average (Cappelen, 2019). Comparing spring-summer rainfall of Northern Jutland it was 468 mm vs. 255

mm in 2017 and 2018, respectively (Cappelen 2018a, Cappelen 2019). These differences caused visible alterations to the landscape with more bare sand being present in the dry 2018 than in 2017 (Appendix S1B-E).

3.2 Edaphic factors

Soil moisture levels were significantly lower in 2018 compared to 2017 (Table 1). The soil nutrient levels were significantly higher in 2018 compared to 2017 for available P and NH_4^+ (Table 1). Soil salinity did not change significantly between years, neither did the organic matter content, total P or total N.

3.3 Vegetation cover, species richness, species composition and turnover

Both vegetation cover, height and density decreased significantly from 2017 to 2018 (Table 1). The vegetation height was almost halved. Across all 40 plots, total species richness was significantly higher in 2017 compared to 2018 (Table 1). In contrast, a significantly higher salt marsh species richness was found per plot in 2018 compared to 2017 and a significantly larger percentage of species were salt marsh species in the dry compared to the wet year (Fig. 1).

The total species richness was 73 in 2017 of which 46 were not seen in 2018. The total species richness in 2018 was 66 species and 39 of these species had not been found in 2017 (Fig. 2A). On average, 45.7% of the species on a given sampling plot were found in both 2017 and 2018, corresponding to 7.6 species reoccurring on any given plot. An average of 6.3 species found in 2017 had disappeared from the plot in 2018 while an average of 3.7 new species occurred on any given plot in 2018 in which it was not found in 2017 (Fig. 2B). The overall most abundant species across years were the perennial species *Juncus gerardii* (recurrence rate 96.2%), *Agrostis stolonifera* (recurrence rate 90.0%), *Glaux maritima* (recurrence rate 93.8%), *Phragmites australis* (recurrence rate 83.3%) and *Potentilla anserina* (recurrence rate 94.1%). Of all species found at least 10 times across 2017 and 2018, the perennials recurred in 65.0% (SE 8.8%) instances while annuals recurred on 50.6% (SE 15.9%) of sampling plots. However, there was no significant difference in the recurrence rate of annuals and perennials neither when considering the species occurring at least 10 times nor when considering the entire species pool (Mann Whitney U-test, $p > 0.05$).

The biodiversity did not change significantly from the wet to dry year (Table 1), but there were changes in plant community composition. The plant community had a significantly higher Ellenberg S and Ellenberg N value in 2018 than in 2017, while the Ellenberg F value remained similar between years (Table 1). Change in species composition was significant on both the small sampling plot scale (Fig. 2C, PERMANOVA, $p < 0.01$) and on the large salt marsh scale (Fig. 2C, PERMANOVA, $p < 0.01$). The indicator species analysis selected six species that were associated to either 2017 or 2018. Three were associated with wet 2017: *Juncus bufonius* (annual), *Centaurium pulchellum* (annual) and *Trifolium pratense* (perennial) and three with dry 2018: *Poa annua* (annual), *Atriplex glabriuscula* (annual) and *Carex nigra* (perennial). This means that *J. bufonius* is more likely to be found in 2017 and that if located on a given site, there is a greater probability that the site was surveyed in 2017.

The temporal species turnover ranged from 0.25-1.00 with a mean turnover of 0.54. The turnover rate and species richness had a significant positive correlation (Fig. 3, $p < 0.001$, $R^2 = 0.316$). The temporal environmental dissimilarity ranged from 0.02-0.50 and was significantly negatively correlated with the species overlap ($p < 0.01$, $R^2 = 0.38$) (Fig. 4A) while we found no significant correlation between the environmental dissimilarity and the turnover rate ($p > 0.05$) (Fig. 4B).

3.5 Correlations between the edaphic factors and species richness and salt marsh richness

From the linear mixed model, we found species richness to correlate significantly with salinity, available P and available N across years as indicated by $t > \pm 1.96$ (Table 2). The response to all nutrients were stronger in the wet year compared to the dry year (Table 2). The salt marsh richness was not explained well across years by the edaphic factors (Table 2). We did, however, find that salt marsh species responded positively to moisture in the wet year and negatively to moisture in the dry year (Table 2). Further, the salt marsh species reacted stronger to available N and total P in the wet 2017 compared to dry 2018.

4 Discussion

As drought and high rainfall are likely to become more frequent in many regions under future climate changes, it is important to know if and how these affect the vegetation in salt marsh areas. Here, we found that the climatic variations between wet and dry conditions affected the shielded salt marsh vegetation by decreasing the vegetation cover and height in dry as opposed to wet conditions as well as altering the species composition. As the study was limited to two years, however, we do not know if the trends observed here will apply in a long-term perspective and as such, are limited to make conclusions regarding how current variations in precipitation and temperature can affect the plant community within the current climate.

4.1 Edaphic factors

Following a drought, increased soil oxygen penetration may result in changes in soil chemistry (Palomo et al., 2013). Indeed, the shielded salt marsh in our study was drier and with a higher nutrient availability in low-precipitation 2018 compared to high-precipitation 2017 (Table 1). Where we found NH_4^+ levels to increase and NO_2^--NO_3^- levels to decrease, Palomo et al. (2013) found the opposite response in an experimental salt marsh experiencing drought. The increased soil available N and available P might, however, partly be a result of the plants' decreased ability to acquire nutrients during a drought (Bista et al., 2018). Soil salinity levels are known to increase during a drought (Chapple & Dronova, 2017; Forbes & Dunton, 2006), as was also the case in this study, although not significantly (Table 1).

4.2 Vegetation cover, species richness, species composition and turnover

A decrease in biomass and vegetation height is a common vegetation response to drought (Zedler et al., 1986; Tilman & El Haddi, 1992; McKee et al., 2004; Forbes & Dunton, 2006; Paudel et al., 2018) corresponding to the decrease in plant cover, height and density we found during dry conditions (Table 1). Despite the increased nutrient content of the salt marsh, which commonly result in an increase in the above-ground biomass (Crain, 2007; Darby & Turner, 2008), the vegetation height and cover decreased in connection with the drought indicating that the drought stress was stronger than the increased nutrient availability. Further, as grazing pressure was lower during the dry year compared to the wet, the decreased cover, density and height cannot be ascribed to the altered grazing pressure; if anything, the lowered grazing pressure could even have confounded the effect of the drought on the vegetation cover, density and height.

Salt marsh species are adapted to coping with stressors including salt stress (Veldhuis, Schrama, Staal, & Elzenga, 2018), and the distribution of salt marsh vegetation is primarily limited by competition (Veldkornet, Adams, & Potts, 2015). At increasingly extreme edaphic conditions, abiotic stressors, such as an increased salinity, will limit the distribution of non-salt marsh vegetation due to their decreased competitive advantage compared to salt marsh species (Veldkornet et al., 2015). This could explain the increase in the number of salt marsh species during the dry conditions despite the general decrease in species richness. Further, salinity is generally known to limit species richness (García, Marañón, Moreno, & Clemente, 1993; Li et al., 2013); thus, the drop in species richness could also be caused by an increased salinity.

Salt marsh plant communities can shift in response to drought (Wetzel & Kitchens, 2007), as seen in our results by a shift towards more salt marsh species. The change in species composition and identity across the two years (Figs. 1, 2) as well as the change in Ellenberg values of the plant community (Table 1) indicate that the decline in species richness could not simply be explained by the species of 2018 being a subset of those found in 2017. Indicator species analysis found that most of the species that were linked only to one year were annuals rather than perennials. The perennial *Carex nigra* appeared more frequently during the dry year. As *C. nigra* has a seed longevity of 15-20 year, often delay germination and exploit gaps in the vegetation (Schütz, 2000), seeds in the ground were likely able to grow the altered conditions altered conditions hindered the growth of other plants. However, we did not find perennials to have a higher recurrence rate compared to annuals. Meeks (1969) found that the earlier during the spring season a marsh community was drained of water, the more rapidly perennial species would be replaced by annuals; further, that multiple years of early water drawdown would result in a plant community dominated by annuals. Therefore, the lack of water during spring might have propagated more annuals to germinate.

As individual species frequently disappear and reappear locally, the annual species turnover can be high (van der Maarel & Sykes, 1993) and several studies have found correlations of varying degrees between overall species turnover and climatic variations between years (Letten, Ashcroft, Keith, Gollan, & Ramp, 2013; Hallett et al., 2014; Noto & Shurin, 2017). Regardless of climatic conditions, the species retention is generally lower and species gain higher on salt marshes compared to other habitats (Pakeman & Lewis, 2017). The increasingly dry and saline conditions might further have made competition between species on the salt marsh harsher (Pennings & Callaway, 1992). We found temperature and precipitation variation to coincide with a significant change in species composition and a high species turnover (0.54), in accordance to Noto and Shurin (2017) who also linked the species turnover of salt marshes to precipitation. Though we did not find a significant correlation between the species turnover rate and the environmental dissimilarity, results point towards climatic variations in precipitation and temperature leading to high species turnover as more species were retained where the environment changed the least.

While a higher species richness has been associated with a higher community stability in grasslands (Tilman, 1996), the same might not apply for salt marshes (Noto & Shurin, 2017) in agreement with our results. Here, a high species richness did not increase the stability on the salt marsh given as we found no evidence that areas with more species were less prone to species loss under extreme circumstances (Figs. 3 and 4).

4.4 Correlations between the edaphic factors and respectively species richness and salt marsh richness

Both salt and drought stress alter plant ability to utilize nutrients (Bista et al., 2018; Hu & Schmidhalter, 2005). Nitrogen is a main limiting factor for salt marsh vegetation (Kiehl, Esselink, & Bakker, 1997; van Wijnen & Bakker, 1999) and in agreement with results by Morgan and Adams (2018), total species richness in our study was limited by the availability of nitrogen. Our results also showed that N availability has less influence on total species richness during dry and more saline conditions, which could be explained by results of Ryan and Boyer (2012) who found that overall species richness decrease while the dominance of a few salt marsh species increased when salinity and nitrogen levels increased simultaneously. Soil moisture affect the salt marsh plant community (Alvarez-Rogel, Ariza, & Silla, 2000) and Theodose and Roth (1999) found that species richness was highest in the most moist areas of a salt marsh.

4.5 Conclusions

As expected, the climate variations resulted in significant differences in several edaphic factors on the shielded salt marsh; often, but not always, responding in the same direction as edaphic factors on tidal influenced salt marshes in relation to drought. Equivalently to tidal influenced salt marshes, the drought event on the shielded salt marsh decreased vegetation cover and density compared to wet conditions and changed the overall species composition. While total species richness decreased when going from wet to the dry extreme, the salt marsh species richness increased. Perennials did not recur significantly more often than annuals. We saw a high temporal species turnover in connection with the climatic variations and found that more species recurred when the edaphic conditions changed the least. Finally, we found species richness to be better able to respond to increased nutrient availability during wet conditions. These results show that shielded salt marsh plant communities are likely to respond swiftly to a change in the edaphic conditions due to variation in precipitation and temperature; further, that extreme drought on shielded salt marshes might actually promote salt marsh species and cause a setback in the distribution of non-salt marsh adapted species.

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Author contributions

LHA, DB, CP and SB conceived the idea of the research. LHA, ASKS, JSK and TBS collected the data and assisted in the laboratory work. LHA did the statistical analysis with contributions from CP. LHA, with contributions from DB, wrote the first draft to the paper. All authors commented on the results and manuscript.

Data accessibility

All data used in this publication are stored in Zenodo, doi 10.5281/zenodo.3608523.

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List of Appendices

Appendix S1: A map of the study site along with images of the area in 2017 and 2018

Appendix S2: List of salt marsh species

Table 1. The mean, standard error (SE) and range for each edaphic and biotic factor measured in 2017 and 2018 on Bygholmengen. A *t*-test with Bonferroni correction was conducted to test for significant differences between the two years and the *p*-values for the test are provided. P > 0.1; n.s. (not significant), P < 0.01; m.s. (marginally insignificant), P < 0.05; *, P < 0.01; **, P < 0.001; ***

	2017		2018		
	mean ± SE	[min ; max]	mean ± SE	[min ; max]	*p*-value
Moisture (%)	75.7 ± 1.7	[38.5 ; 89.9]	59.3 ± 2.1	[27.8 ; 84.0]	***
Organic matter (%)	41.3 ± 2.8	[2.7 ; 83.5]	31.7 ± 2.8	[1.1 ; 68.8]	m.s.
Salinity	1.34 ± 0.13	[0.17 ; 4.40]	1.42 ± 0.15	[0.1 ; 4.83]	n.s.
Available P (mg/100g)	0.92 ± 0.10	[0.10 ; 2.94]	1.30 ± 0.10	[0.35 ; 3.51]	*
NH_4^+ (mg/kg)	33.19 ± 1.67	[17.45 ; 73.3]	61.58 ± 5.80	[23.55 ; 289.4]	**
NO_2^--NO_3^- (mg/kg)	1.24 ± 0.06	[0.80 ; 2.73]	1.02 ± 0.07	[0 ; 2.5]	n.s.
Total P (mg/kg)	742 ± 47	[150 ; 1700]	543 ± 42	[100 ; 1400]	n.s.
Total N (g/kg)	14.34 ± 0.92	[1.3 ; 26.7]	12.40 ± 0.99	[0.83 ; 25.98]	n.s.
Ellenberg N	4.83 ± 0.04	[4.14 ; 5.64]	5.41 ± 0.05	[4.5 ; 6.11]	*
Ellenberg F	7.07 ± 0.09	[5.86 ; 8.29]	7.17 ± 0.08	[6.25 ; 8.57]	n.s.
Ellenberg S	2.18 ± 0.08	[1.07 ; 4]	3.05 ± 0.13	[0.17 ; 5.40]	**
Species richness	14 ± 0.74	[6 ; 33]	11.69 ± 0.66	[0 ; 23]	*
Salt marsh species richness	5.76 ± 0.20	[2 ; 9]	7.05 ± 0.30	[0 ; 11]	*
Cover (%)	0.81 ± 0.04	[0 ; 1]	0.63 ± 0.05	[0 ; 1]	*
Vegetation density	73.8 ± 5.9	[0 ; 163]	42.5 ± 4.8	[0 ; 150]	*
Vegetation height (cm)	6.5 ± 0.9	[0.1 ; 35.5]	3.5 ± 0.5	[0 ; 21.0]	*
Simpson's diversity	0.44 ± 0.04	[0.02 ; 1]	0.54 ± 0.04	[0 ; 1]	n.s.
Shannon's diversity	0.63 ± 0.03	[0.00 ; 1.38]	0.70 ± 0.04	[0 ; 1.85]	n.s.
Pielou's evenness	0.48 ± 0.02	[0.08 ; 0.84]	0.61 ± 0.03	[0 ; 1]	n.s.

Table 2. The results of the linear mixed model with random slope and intercept for year. Regression coefficients are provided for each year for the correlations between species richness and salt marsh species richness and all edaphic factors, accordingly. Further, *t*-values are provided; a value above ±1.96 indicate a significant correlation. The significance level is noted with n.s. being not significant and * corresponding to a significant correlation.

	Species richness			Salt marsh species richness		
	2017	2018	*t*-value	2017	2018	*t*-value
Intercept	8.87	7.11	2.87 (*)	3.98	5.71	2.82 (*)
Moisture	-0.029	0.0035	-0.25 (n.s.)	0.0015	-0.0018	-0.009 (n.s.)
Organic matter	0.098	0.089	1.30 (n.s.)	0.043	0.081	1.57 (n.s.)
Salinity	-2.019	-2.007	-3.75 (*)	0.26	0.26	0.98 (n.s.)
Available P	-2.079	-1.54	-2.00 (*)	-0.30	-0.29	-0.70 (n.s.)
Available N	0.20	0.048	1.97 (*)	0.016	0.0067	0.93 (n.s.)
Total P	-0.0040	0.0026	-0.19 (n.s.)	0.0015	0.00044	0.79 (n.s.)
Total N	0.27	0.16	0.96 (n.s.)	-0.13	-0.14	-1.35 (n.s.)

Figure 1. Box-plot of the ratio between the number of salt marsh species (Appendix S2) and the total species richness in 2017 (green) and 2018 (grey), respectively. A value of 1 indicate that all species were salt marsh adapted species while 0 indicate that none were salt marsh adapted species. The medians are plotted together with the 25 and 75 % quantiles while the whiskers show the maximum and minimum. **** = *p*-value < 0.0001.

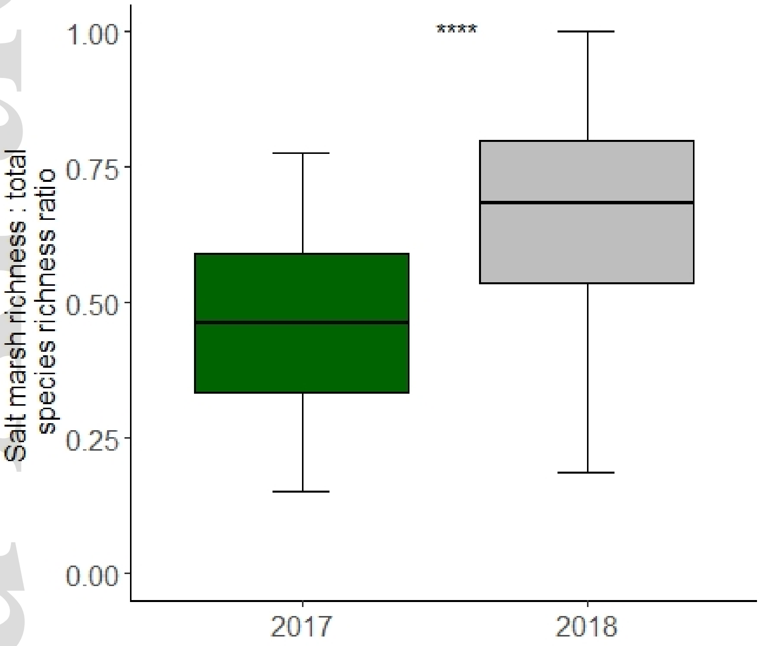


Figure 2. The species composition of Bygholmengen across 40 plots sampled in both 2017 and 2018. In A and B, the species overlap (species occurring in both 2017 and 2018) is depicted in black, the species present in 2017 only in green (species lost), those of 2018 only in grey(species gained). In A, the total number of species found across all plots on Bygholmengen is shown including both all occurrences and when excluding species that only occurred once (more than once). In B, the species distribution is shown per sampling plot, where the boxplot depict the median and the 25 and 75 % quantiles, minimum, maximum and outliers. Here, all occurrences are included. In C, species compositional change between years 2017 (green, squares) and 2018 (grey, triangles) is illustrated based on the PCoA using the Jaccard dissimilarity on binary data for 40 plots. When a line connects a green square and a grey triangle, they represent the same sampling plot in 2017 and 2018. Eigenvalues for PCoA axis 1 and 2 are 3.89 and 2.36, with 16.71% of variance explained on axis 1 and 9.49% on axis 2.

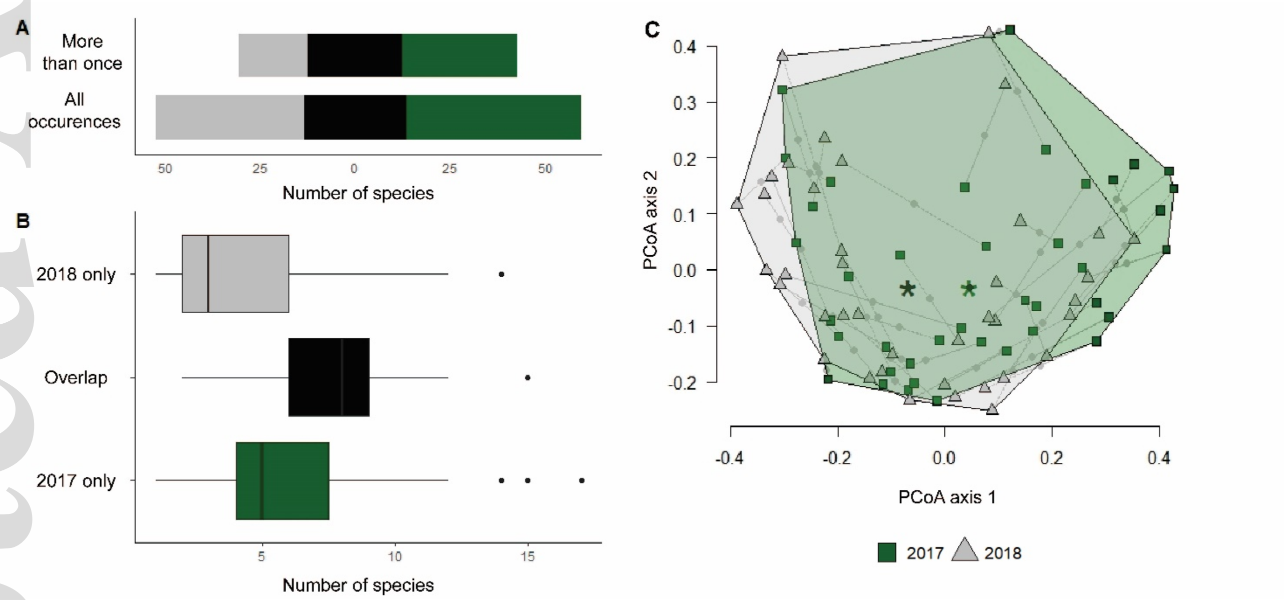


Figure 3. The temporal turnover rate plotted against total species richness. $R^2 = 0.31$.

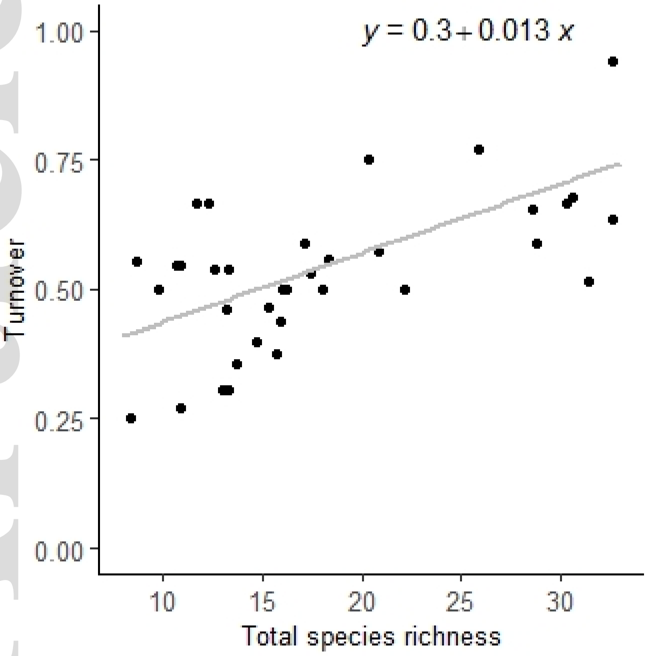
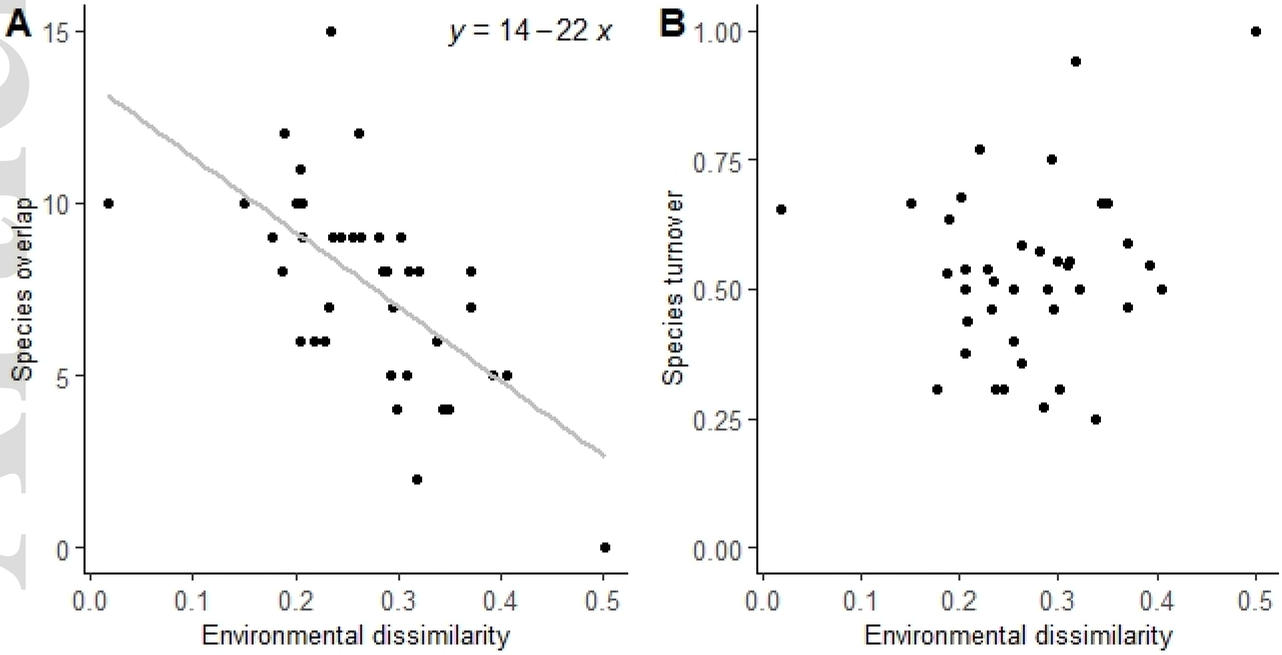


Figure 4. The environmental dissimilarity between years was significantly negatively correlated with the species overlap ($p < 0.01$, $R^2 = 0.38$) (A). No significant correlation was found between the species turnover and the environmental dissimilarity (B).



eTOC

Fluctuations in temperature and precipitation between two years resulted in a change in the edaphic environment as well as a significant change in species composition of a salt marsh flora. We linked the change in species composition to change in the edaphic environment as areas with the least edaphic change retained more species between years.