

1 **Title: *Elymus athericus* encroachment in Wadden Sea salt marshes is driven**  
2 **by surface-elevation change**

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11 **Abstract:**

12 **Question:** What are the main drivers of vegetation succession and the encroachment of *Elymus*  
13 *athericus* (Link) Kerguélen in ungrazed Wadden Sea salt marshes? Is (1) elevation, a proxy for tidal  
14 inundation and thus abiotic conditions, limiting the expanse of *Elymus*. Does sedimentation increase  
15 the spread of *Elymus* by (2) leading to surface-elevation change or does it (3) add nitrogen and thereby  
16 allows *Elymus* to grow in lower elevation?

17 **Location:** salt marsh at Sönke-Nissen-Koog, Wadden Sea National Park Schleswig-Holstein,  
18 Germany

19 **Methods:** The experiment was established in 2007 in the high marsh and consisted of four blocks of  
20 12 m x 8 m. The blocks differed in surface-elevation change during the experiment. Each block was  
21 subdivided into 24 plots of 1 m x 1 m. The original elevation of all plots in relation to the German  
22 ordnance datum (NHN) was assessed at the start of the experiment. Plots within the blocks were  
23 randomly assigned to one of the three N-fertilisation treatments. Within each plot we planted five  
24 randomly chosen individuals of *Elymus*. After four years of treatment, the vegetation composition and  
25 cover was recorded in all plots and aboveground biomass was collected.

26 **Results:** Original elevation was found to be a main driver of succession favouring *Elymus* and other  
27 late successional plants. No effect of N-fertilisation, but a positive effect of surface-elevation change  
28 on *Elymus*-cover was detected.

29 **Conclusions:** We can therefore conclude that the positive effect of surface-elevation change on  
30 *Elymus* is based on the resulting higher elevation and more favourable abiotic conditions caused by  
31 sedimentation, but not the addition of nitrogen with the freshly deposited sediment. This case,

32 therefore, is an example for an ecosystem in which encroachment is driven by a natural factor, rather  
33 than anthropogenic eutrophication.

34 Keywords:

35 Biomass; *Halimione portulacoides*; N-deposition; N-fertilisation; *Puccinellia maritima*;  
36 sedimentation; succession

## 37 1. Introduction

38 The concept of succession, originally described by Clements (1916) as the unidirectional development  
39 of vegetation through a series of stages until a stable climax vegetation is reached, has been  
40 extensively studied in vegetation ecology (van Andel et al. 1993; McCook 1994). The first vegetation  
41 stage is often dominated by small pioneer plants which are then replaced by a diverse community of  
42 short herbaceous plants. These intermediate communities are then progressively replaced by later  
43 successional stages, which are often dominated by taller plants such as grasses (Berendse and Elberse  
44 1990), shrubs or trees (Eldridge et al. 2011). This replacement of small plants by tall ones in late  
45 successional stages can be driven by belowground competition for nutrients (Chapin et al. 1994;  
46 Casper and Jackson 1997) or aboveground competition for light (Olf et al. 1997; Veer and Kooijman  
47 1997). In the latter case, taller plants reduce the amount of light available for small plants, which are  
48 then outcompeted. This invasion of tall plants is sometimes also defined as encroachment (Eldridge et  
49 al. 2011) and can lead to a loss of plant species richness as only few competitive species prevail (Veer  
50 and Kooijman 1997).

51 The natural succession of the vegetation, however, can also be influenced by various other factors  
52 such as herbivory (van Andel et al. 1993). Herbivores reduce the standing biomass by grazing (Nolte  
53 et al. 2014) and can open gaps in the canopy for seedling establishment (Bullock et al. 1994; Bakker  
54 and Olf 2003). Thereby, herbivores decrease the light competition and enable small plants to persist  
55 while tall grazing-sensitive species are unable to establish or are reduced (Kuijper et al. 2005).  
56 Herbivores thus can halt or set-back vegetation succession (Kuijper and Bakker 2003). Therefore,  
57 grazing with herbivores is sometimes used in nature conservation e.g. in semi-natural grasslands to  
58 prevent encroachment of tall plants and maintain intermediate successional stages with a higher plant  
59 species richness (Bouchard et al. 2003; Rook et al. 2004; Metera et al. 2010). In contrast to this set-  
60 back of succession, the addition of nitrogen to an ecosystem, e.g. by atmospheric N-deposition, was  
61 found to speed up succession and encroachment (Berendse and Elberse 1990; WallisDeVries and  
62 Bobbink 2017). Especially in nutrient-poor habitats, a high N-availability can favour tall growing  
63 plants (Gaucherand et al. 2006) and thereby enhances light competition leading to low plant species  
64 richness (Veer and Kooijman 1997; Bird and Choi 2016; Soons et al. 2016).

65 An example for such an encroachment of a tall grass species which can lead to a loss of plant  
66 diversity is the invasion of *Elymus athericus* (hereafter referred to as *Elymus*) in salt marshes of the  
67 Wadden Sea (Andresen et al. 1990; Leendertse et al. 1997; Kiehl et al. 2007; Esselink et al. 2009;  
68 Veeneklaas et al. 2013). In the Wadden Sea area, most salt marshes along the mainland coast are the  
69 result of man-made sedimentation fields, which were built to create new land (Dijkema 1987). These  
70 salt marshes are coastal, natural or semi-natural grasslands characterised by regular flooding with sea  
71 water (Adam 1990) resulting in salt stress for plants. The frequency of tidal inundation, mainly  
72 determined by the salt-marsh elevation, leads to a distinct zonation of vegetation along an elevation  
73 gradient (Suchrow and Jensen 2010). The lowest zones are flooded frequently and are thus dominated  
74 by halophytes such as *Salicornia europea* (Suchrow and Jensen 2010). The vegetation types of the  
75 lowest elevation additionally represent the early stages of salt-marsh succession (Olf et al. 1997).  
76 However, frequent tidal inundations in low elevations also deliver sediment to the marsh, thus leading  
77 to a positive surface-elevation change of the marsh platform (Nolte et al. 2013a) and consequently less  
78 frequent inundations. With higher elevation the vegetation composition shifts to intermediate and then  
79 late successional stages in the high marsh zone, the latter often being dominated by the tall grass  
80 species *Elymus*. Thus surface-elevation change was identified as a main driver of succession in salt  
81 marshes (Rupprecht et al. 2015b).

82 Salt marshes in the Wadden Sea region have been used for livestock grazing for centuries  
83 (Esselink et al. 2000). In the past decades, however, grazing has been stopped in many salt-marsh  
84 areas to allow a more natural habitat and vegetation development within the National parks (Bakker et  
85 al. 2003; Esselink et al. 2009; Stock and Maier 2016). This cessation of grazing led in many locations  
86 to the encroachment of the tall, late-successional grass *Elymus* (Andresen et al. 1990; Kiehl et al.  
87 2007; Rupprecht et al. 2015b). *Elymus* is a high-marsh species which grows in dense mono-specific  
88 stands and therefore locally reduces the plant species richness (Leendertse et al. 1997; Kiehl et al.  
89 2007; Wanner et al. 2014) and is sensitive to grazing with livestock. In the last decades it has also  
90 spread widely in areas that have never been grazed (Veeneklaas et al. 2013; Rupprecht et al. 2015b).  
91 Therefore, researchers and nature managers were wondering which factors, next to the cessation of  
92 grazing, are driving the encroachment of *Elymus* (Van Wijnen and Bakker 1999; Veeneklaas et al.  
93 2013). The elevation as a proxy for flooding frequency and therefore also for abiotic conditions has  
94 been identified as a major constriction for the distribution of *Elymus* (Bockelmann and Neuhaus  
95 1999). Yet, *Elymus* has been found to expand into lower marsh areas over the last decades (Olf et al.  
96 1997; Veeneklaas et al. 2013).

97 It has been argued that the encroachment of *Elymus* in the Wadden Sea salt marshes is driven or  
98 sped up by eutrophication (Van Wijnen and Bakker 1999). Although salt marshes are relatively rich in  
99 nutrients, the high stress environment with salt and hypoxia forces plants to respond physiologically  
100 leading to a high nutrient cost (Adam 1990). The addition of nitrogen in a fertilization experiment

101 therefore led to an increase of biomass in *Elymus* and sped up vegetation succession (Van Wijnen and  
102 Bakker 1999). Nitrogen is often added to ecosystems through anthropogenic atmospheric deposition,  
103 but in salt marshes it is also added naturally during inundations with sediment deposition. To  
104 disentangle the effects of these two deposition pathways, Veeneklaas et al. (2013) analysed time series  
105 of vegetation maps and chronosequence data of four naturally developed salt marshes varying in  
106 sediment deposition rates. They found that expansion rates of *Elymus* were highest on young salt  
107 marshes which have high sediment deposition rates. This was interpreted by Veeneklaas et al. (2013)  
108 as an indicator that *Elymus* expansion is mainly driven by spatially varying natural sediment  
109 deposition rates and not by the evenly spread atmospheric deposition. However, in this observational  
110 study it was not possible to disentangle whether the high sediment deposition rates affected the  
111 encroachment of *Elymus* by the added N, or whether the positive effect of sediment deposition on the  
112 surface-elevation change (Nolte et al. 2013a) and thus elevation caused the shift. Yet, elevation as a  
113 proxy for inundation frequency and abiotic conditions has previously been found to be an important  
114 predictor of the distribution of *Elymus* (Suchrow and Jensen 2010).

115 The aim of this study is therefore to unravel the effects of experimental nitrogen fertilization,  
116 elevation and surface-elevation change on the vegetation succession (i.e. the shift from early towards  
117 late successional plant-species composition), the cover of *Elymus* and plant biomass in an ungrazed  
118 salt marsh. We hypothesize that (1) elevation as a proxy for flooding frequency is a driving factor of  
119 succession, with a sufficiently high elevation allowing the establishment of *Elymus* and other late-  
120 successional plants with a higher biomass production. Additionally, we hypothesize that (2) *Elymus* is  
121 N-limited and therefore the experimental N-fertilisation will lower the elevation at which *Elymus* can  
122 establish. Furthermore, we expect experimental N-fertilisation to speed up the succession towards the  
123 late-successional plant communities, as it will increase the production of biomass. Finally, we  
124 hypothesize that (3) a high surface-elevation change will lead to an increase in elevation, so *Elymus*  
125 will be able to establish, even if the original elevation at the start of the experiment was below the  
126 establishment threshold. This high surface-elevation change furthermore increases the spread of other  
127 late-successional plant communities with a higher biomass.

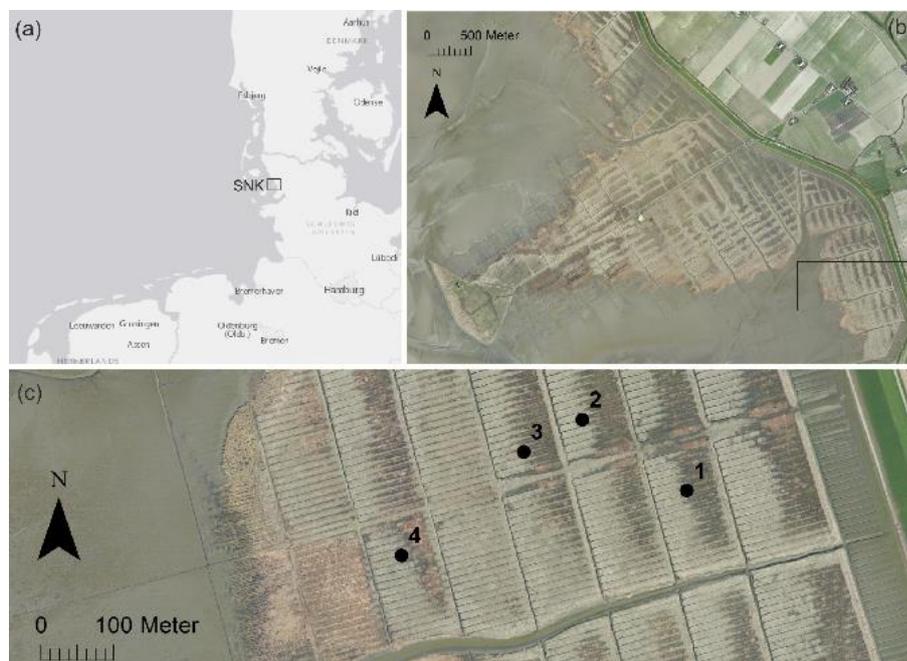
128 We carried out a field experiment in which different levels of experimental N-fertilisation were  
129 applied in blocks with a comparable range of elevation at the start of the experiment, hereafter referred  
130 to as original elevation. Additionally, the plots were positioned along a gradient of surface-elevation  
131 change, which is caused by an increasing distance of plots to the sediments source (i.e. the edge of the  
132 marsh). If the experiment shows both fertilisation and a high surface-elevation change to lower the  
133 original elevation limit for *Elymus*, we can assume that the plant is indeed nitrogen limited. If,  
134 however, no effect of experimental N-fertilisation, but an effect of surface-elevation change is found,  
135 we can conclude that the positive effect of surface-elevation change at the end of the experiment is

136 based on the resulting higher elevation, but not the addition of nitrogen with the freshly deposited  
137 sediments.

## 138 2. Material and Methods

### 139 2.1 Experimental design

140 The experiment was setup in the Sönke-Nissen Koog (SNK) salt marsh on the mainland coast of the  
141 Wadden Sea in the North of Germany (Fig. 1). The area is characterised by an artificial drainage  
142 system, but maintenance of ditches and livestock grazing stopped in 1991 after the salt marsh became  
143 part of the Wadden Sea National Park in 1986 (Stock et al. 2005). The area has been previously  
144 described in context of a grazing experiment in the Northern part of the marsh (Kiehl et al. 1996; Kiehl  
145 et al. 1997; Nolte et al. 2013b).



146  
147 Figure 1: A) Map of the German Bight with the position of the Sönke-Nissen Koog (SNK) study site indicated. B) Aerial  
148 photograph of the Sönke-Nissen Koog & Hamburger Hallig salt marsh area with the position of the experimental site. C) The  
149 experimental site with the position of the 4 plots. World Imagery - Source: Esri, DigitalGlobe, GeoEye, Earthstar  
150 Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User  
151 Community.

152 The *Elymus* experiment was established in 2007 in the high marsh and consisted of four  
153 blocks of 12 x 8 m. A rectangular shape was chosen for the blocks to exclude former ditches, which  
154 still prevail in the marsh as depressions and are evenly spaced with a distance of 10 m. Each block had  
155 a comparable mean elevation at the start of the experiment (i.e. original elevation). Within plots the  
156 prevalent micro-topography lead elevation ranges between the lowest and highest point of the  
157 respective plot of 7.0 cm to 12.5 cm. Additionally, the plots were positioned along a gradient of  
158 surface-elevation change, which is caused by an increasing distance of plots to the sediments source

159 (i.e. the edge of the marsh; Schröder et al. 2002). Blocks were positioned close to sedimentation-  
160 erosion bars (van Wijnen and Bakker 2001; Nolte et al. 2013a) previously installed by the National  
161 Park administration along a transect from the intertidal flats to the seawall to monitor surface-elevation  
162 change (Stock 2011). Measurements of surface-elevation change continued during the experimental  
163 period. From these data, mean surface-elevation change [ $\text{mm yr}^{-1}$ ] for the duration of the experiment  
164 was calculated and assigned to the blocks as surface-elevation change value. During the study period,  
165 these values for the blocks one to four are  $2.7 \text{ mm yr}^{-1}$ ,  $4.9 \text{ mm yr}^{-1}$ ,  $7.3 \text{ mm yr}^{-1}$ , and  $8.1 \text{ mm yr}^{-1}$ ,  
166 respectively. Each block was subdivided into 24 plots of  $1 \text{ m} \times 1 \text{ m}$  separated by one metre wide  
167 buffer zones. Thus while the original elevation represents the conditions at the start of the experiment,  
168 the surface-elevation change assesses the mean increase of elevation as a result of sediment deposition  
169 and soil autocompaction over the course of the experiment. The position of the plots was marked in  
170 the field using plastic sticks. The original elevation of all plots in relation to the German ordnance  
171 datum (NHN) was assessed at the start of the experiment using an optical levelling device (Nolte et al.  
172 2013a).

173 A total number of 850 individual *Elymus* plants were collected close to the experimental  
174 blocks in June 2007 from an area dominated by the plant. An automatic planting device with a  
175 diameter of 8 cm and depth of 16 cm was used for extraction and individuals were transplanted  
176 together with the field substrate into pots of the same size. Pots were transported to the greenhouse  
177 where plants were cut back and cultivated for 5 weeks. In case one pot contained more than one  
178 individual the surplus individuals were removed. Only intermediate sized individuals were further  
179 used for planting. Within each plot we planted five randomly chosen individuals of *Elymus* on  
180 24.07.2007. The automated planting device was used to remove the soil in the field to create a hole, so  
181 that plants could be transplanted including their substrate. Previous to the experiment *Elymus* was not  
182 present in the blocks. Vegetation composition in blocks 1 to 3 was heterogeneous with a mix of *Aster*  
183 *tripolium*, *Halimione portulacoides*, *Puccinellia maritima* and *Spartina anglica*. Only block 4 was  
184 characterised by the dominance of *Halimione portulacoides* in most plots. Almost 50% of all planted  
185 individuals died in the autumn of 2007, probably due to extremely high precipitation. To continue the  
186 experiment dead individuals were therefore replaced in April 2008.

187 Plots within the blocks were randomly assigned to one of the three N-fertilisation treatments,  
188 namely  $0 \text{ g N m}^{-2} \text{ yr}^{-1}$  (control),  $20 \text{ g N m}^{-2} \text{ yr}^{-1}$  (N20) and  $40 \text{ g N m}^{-2} \text{ yr}^{-1}$  (N40), resulting in eight  
189 replicates per treatment per block. These Nitrogen addition treatments were chosen to be relatively  
190 high, as fertilisation treatments representing atmospheric N-input of  $4 \text{ g N m}^{-2} \text{ yr}^{-1}$  (Bockelmann and  
191 Neuhaus 1999) or  $5 \text{ g N m}^{-2} \text{ yr}^{-1}$  (Van Wijnen and Bakker 1999) were found to have no effect. A  
192 powdered slow-release N-fertilizer (Floranid® 32-0-0) was used and was dissolved in water obtained  
193 from the closest salt-marsh creek. The same volume of creek water without fertilizer was added to

194 control plots. Fertilizer was applied three times per year during the main growing season in Mai, June  
195 and July every year from the start of the experiment in 2007 to 2011.

196 After four years of treatment, the vegetation composition and cover was recorded in all plots  
197 on 30.09.2011 using the Londo decimal scale (Londo 1976). Nomenclature follows (Haeupler and  
198 Muer 2007). Additionally, total aboveground biomass was collected from a 20 cm x 20 cm subplot in  
199 each plot on 30.09.2011 as an indicator of general light competition. Biomass was stored in perforated  
200 permeable plastic bags (Sealed Air Cryovac) and air dried at 60°C for two days to constant weight.  
201 Additionally, five empty bags were weighed and the mean weight used to subtract the weight of the  
202 bag from the biomass samples.

## 203 2.2 Statistical analyses

204 To assess succession (i.e. the shift from early towards late-successional plant-species composition  
205 following Olff et al. (1997) and Petersen et al. (2014)) the effect of surface-elevation change, original  
206 elevation and N-fertilisation on plant-species composition in plots was analysed with redundancy  
207 analysis (RDA). Species cover recorded using the Londo decimal scale was recalculated as a  
208 percentage cover value,  $\log(x+1)$ -transformed and centred. As environmental factors, we added  
209 original elevation, surface-elevation change and N-fertilisation in a stepwise forward procedure to the  
210 analysis. Both surface-elevation change and N-fertilisation were treated as factors, as they had only  
211 four and three levels, respectively. Significance was tested based on Monte-Carlo permutation tests,  
212 with 499 permutations.

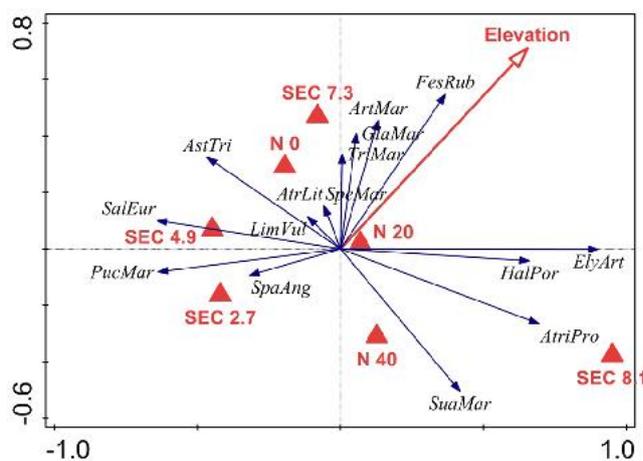
213 In addition to the RDA we tested the effect of surface-elevation change, elevation and N-  
214 fertilisation on the cover of *Elymus* at the end of the experiment using a negative binomial generalized  
215 linear model (GLM). The full model included the cover of *Elymus* as a response variable and the  
216 explanatory variables original elevation, surface-elevation change and N-fertilisation, with the latter  
217 two being factorial variables. All interaction effects were included. Overdispersion was detected and  
218 therefore standard errors were corrected using a quasi-GLM model. Backward stepwise model  
219 selection was performed using the drop1 command based on  $\chi^2$ -test (Zuur et al. 2009).

220 The effect of surface-elevation change, original elevation and N-fertilisation on the biomass  
221 was analysed using Analysis of Covariance (ANCOVA) as assumptions of normality and homogeneity  
222 of variance were met by the data. Original elevation, surface-elevation change and N-fertilisation, as  
223 well as all possible interaction terms, were included as explanatory variables. To compare the biomass  
224 between treatments, we used a Tukey posthoc-test. No spatial autocorrelation was detected in the  
225 models when variograms of the residuals were plotted (Zuur et al. 2009). All statistical analyses  
226 except for the RDA were performed using the statistical software 'R' version 3.2.4 (R Development  
227 Core Team 2017). The RDA was performed using the statistical software CANOCO 5 (Smilauer and  
228 Lepš 2014)

229 **3. Results**

230 3.1 Plant-species composition

231 In the RDA we found that 32.2 % and 8.4 % of the variation in the plant-species composition were  
 232 explained by the first and second axis, respectively. The final model included surface-elevation  
 233 change, original elevation and N-fertilisation and was significantly different from a random model  
 234 (pseudo F = 13.5; p = 0.002). The single values of the surface-elevation change factor are organised  
 235 along the first axis, with the surface-elevation change 4.9 mm yr<sup>-1</sup> and 2.7 mm yr<sup>-1</sup> positioned  
 236 relatively close together (Fig. 2). The second axis corresponds with the single values of the N-  
 237 fertilisation factor, with N 20 being close to the centre of the plot. Original elevation lies between  
 238 axes. *Elymus* corresponds with the first axis. This indicates that *Elymus* cover is mainly explained by  
 239 surface-elevation change, with the highest percentage covers at the surface-elevation change 8.1.  
 240 Furthermore, cover of *Elymus* in plots is positively correlated with original elevation, while the N-  
 241 fertilisation seems to have little influence on the cover of *Elymus*. The same pattern can be observed  
 242 for *Halimione portulacoides*, another late-successional species. Here it needs to be noted, however,  
 243 that *Halimione portulacoides* already had a higher percentage cover in the respective block with  
 244 surface-elevation change 8.1 at the start of the experiment. Characteristic pioneer and low marsh  
 245 species such as *Salicornia europaea* L. s. I. and *Puccinellia maritima* lie close to the low surface-  
 246 elevation change values and are negatively correlated with original elevation. The typical mid-marsh  
 247 species such as *Aster tripolium*, *Spergularia maritima* and *Limonium vulgare* are clustered around the  
 248 mid-elevations and intermediate surface-elevation change value. The high N-fertilisation seems to be  
 249 positively associated only with *Suaeda maritima*, while most species cluster around the N 0 and N 20  
 250 treatment.



251  
 252 Figure 2: Biplot of the RDA analysis illustrating the effect of the environmental variables surface-elevation change (SEC)  
 253 and N-fertilisation (▲), as well as original elevation range (elevation, open arrow) on species composition. Species  
 254 abbreviations: *ArtMar* *Artemisia maritima*, *AstTri* *Aster tripolium*, *AtriPro* *Atriplex prostrata*, *AtrLit* *Atriplex littoralis*,  
 255 *ElyArt* *Elymus athericus*, *FesRub* *Festuca rubra*, *GlaMar* *Glaux maritima*, *HalPor* *Halimione portulacoides*, *LimVul*

256 *Limonium vulgare*, **PlaMar** *Plantago maritima*, **PucMar** *Puccinellia maritima*, **SalEur** *Salicornia europea*, **SpaAng** *Spartina*  
 257 *anglica*, **SpeMar** *Spergularia maritima*, **SuaMar** *Suaeda maritima*, **TriMar** *Triglochin maritimum*

258 3.2 Cover of *Elymus*

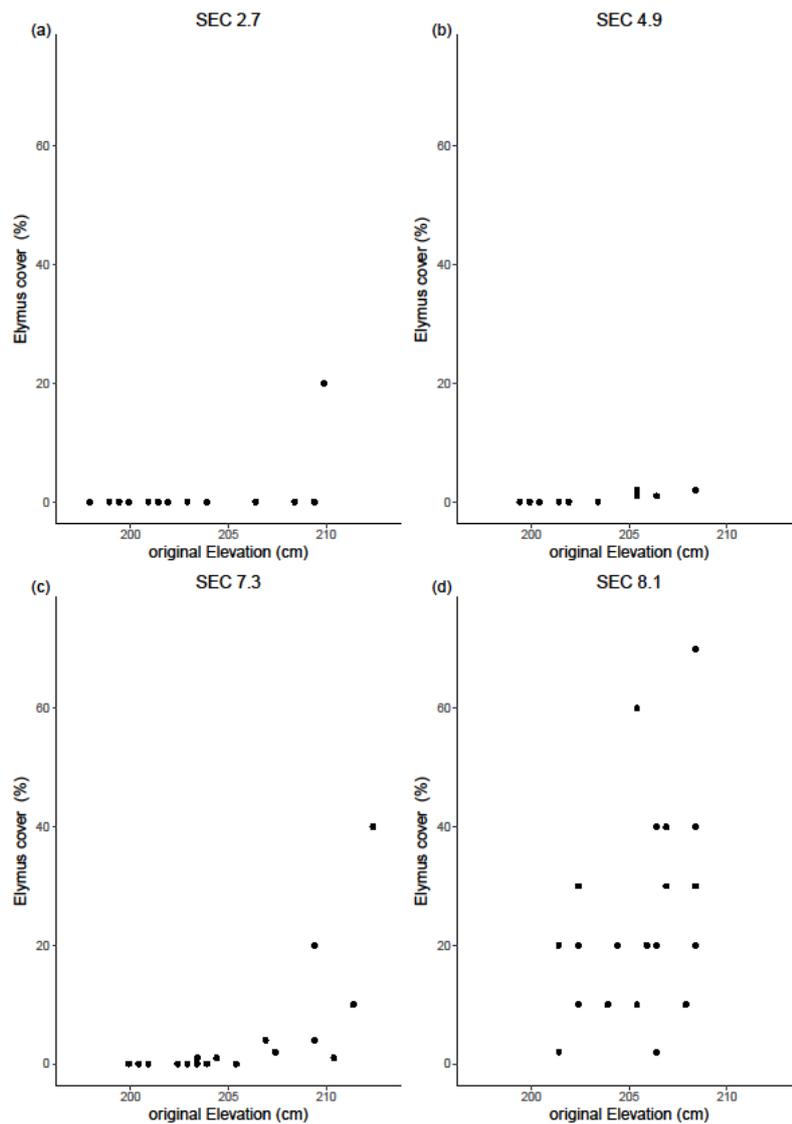
259 The final model explaining the percentage cover of *Elymus* included a significant interaction of  
 260 surface-elevation change and original elevation (Tab. 1), while N-fertilisation did not remain in the  
 261 model. If surface-elevation change is low, *Elymus* is only present with a low percentage cover at the  
 262 highest original elevation of the elevation range within the blocks (Fig. 3 A & B). With a higher  
 263 surface-elevation change of 7.3 mm yr<sup>-1</sup> *Elymus* is present more often, but cover percentage is higher  
 264 only in the highest elevation within this block (Fig. 3 C). At a high surface-elevation change of 8.1  
 265 mm yr<sup>-1</sup> *Elymus* is present at all original elevations within the plot (Fig. 3 D), and its percentage cover  
 266 increases along the elevation range within the blocks with increasing original elevation.

267 TABLE 1 Summary statistics of GLM analyzing effects of N fertilization, original elevation and surface elevation change (SEC)  
 268 and their interactions (\*) on the percentage cover of *Elymus*  
 269

	estimate	t-value	P
N			ns
Elev	4.18 ± 1.22	3.42	<b>&lt; 0.001</b>
SEC	107.6 ± 32.31	3.33	<b>&lt; 0.01</b>
N*Elev			ns
N*SEC			ns
Elev*SEC	-0.51 ± 0.15	-3.31	<b>&lt;0.01</b>
N*Elev*SEC			ns

270

271



272

273 Figure 3: Point plots illustrating the effect of the range of original elevation within blocks on the percentage cover of *Elymus*  
 274 at four different rates of surface-elevation change (SEC) in  $\text{mm yr}^{-1}$  (A-D).

275 3.3 Biomass

276 The ANCOVA results (Tab. 2) showed N-fertilisation and surface-elevation change to be the factors  
 277 explaining the total biomass within plots. Furthermore, post-hoc tests showed biomass to be lowest at  
 278 a surface-elevation change of  $7.3 \text{ mm yr}^{-1}$  and highest at surface-elevation change of  $8.1 \text{ mm yr}^{-1}$ ,  
 279 while both low surface-elevation change values showed an intermediate biomass (Fig. 4 A). N-  
 280 fertilisation was found to have a positive effect on biomass compared to the control treatment, but the  
 281 amount of fertiliser had no effect in our experiment (Fig. 4B). Elevation had no effect on biomass (Fig  
 282 4C).

283

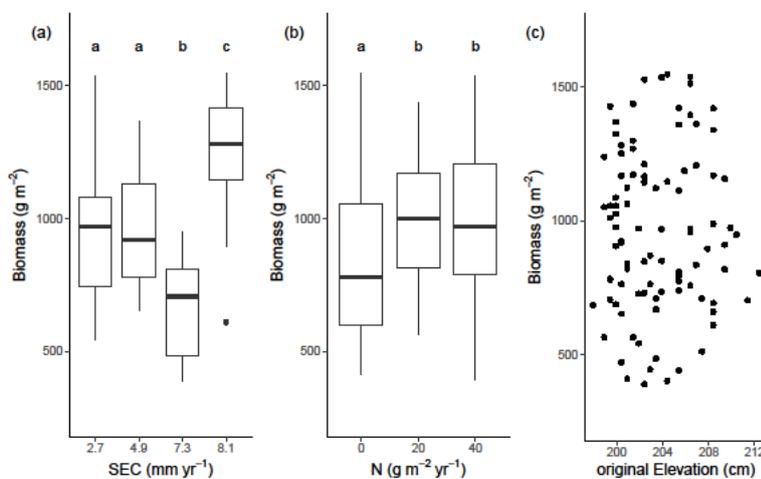
284

285 TABLE 2 Summary statistics of ANCOVA analyzing effects of N fertilization, original elevation and surface elevation change  
 286 (SEC) and their interactions (\*) on the total biomass in plots  
 287

	DF	F-value	P
N	2	4.49	< 0.05
Elev			ns
SEC	3	30.65	< 0.001
N*Elev			ns
N*SEC			ns
Elev*SEC			ns
N*Elev*SEC			ns

288

289



290

291 Figure 4: A) and B) boxplots illustrating the effect of surface-elevation change (SEC) and N-fertilization on biomass in plots.  
 292 Boxplots represent: median (middle line), interquartile range (box), 1.5 times interquartile range (bar) and outliers (dots).  
 293 Letters indicate significant differences between treatments based on PostHoc-tests. C) Point plot illustrating the effect of the  
 294 range of original elevation on total biomass.

#### 295 4. Discussion

296 In line with our first hypothesis, original elevation was found to be a main driver of succession  
 297 favouring *Elymus* and other late successional plant species such as *Halimione portulacoides*, as well as  
 298 increasing the cover of *Elymus*. Contrastingly, no effect of original elevation on biomass could be  
 299 found. N-addition increased the biomass in comparison to the control treatment, but had no effect on  
 300 succession as seen in the RDA, or the cover of *Elymus*. We therefore find no support for hypothesis 2  
 301 and conclude that *Elymus* is not N-limited. In support of hypothesis 3 we found that surface-elevation  
 302 change is a main driver of succession as seen in the RDA. The significant interaction effect of original  
 303 elevation and surface-elevation change on the cover of *Elymus* indicates that a high surface-elevation  
 304 change quickly raises the original elevation to a level, at which *Elymus* can establish. Thus as no effect  
 305 of N-fertilisation, but an effect of surface-elevation change was detected, we can conclude that the

306 positive effect of surface-elevation change on *Elymus* is based on the resulting higher elevation caused  
307 by sedimentation, but not the addition of nitrogen with the freshly deposited sediments.

#### 308 4.1 Elevation

309 Elevation is clearly one of the most important factors determining the succession and therefore also  
310 the presence and dominance of *Elymus* in Wadden Sea salt marshes (Olf et al. 1997; Suchrow and  
311 Jensen 2010; Davy et al. 2011; Rupprecht et al. 2015b). Generally, a high elevation is interpreted as a  
312 proxy for low flooding frequency and duration and therefore also for favourable abiotic conditions for  
313 high-marsh plants such as *Elymus* (Suchrow and Jensen 2010). In these less stressful parts of the  
314 marsh, the dominance of *Elymus* is often explained with its high biomass and the competitive  
315 exclusion of other species based on the limitation of light for shorter plants (Olf et al. 1997). Yet, we  
316 found no effects of original elevation on biomass which thus means that elevation might not favour tall  
317 plants and could indicate that light competition plays no role. However, the plots were chosen to be  
318 very similar in elevation and therefore only represent a small part of the entire elevation gradient in  
319 salt marshes. Additionally, biomass might not be the most suitable indicator to quantify light  
320 competition between species, because there is no clear linear relationship between biomass and the  
321 relative absorbed irradiance (Rupprecht et al. 2015a). Therefore, we cannot rule out light competition  
322 as a driving mechanism of succession in this case.

323 Furthermore, we are unable to rule out effects of belowground competition, as this study only  
324 included the assessment of aboveground biomass. An experiment using the grass species *Agrostis*  
325 *capillaris* for example, showed that the negative effect of this invasive species on the native vegetation  
326 was driven by belowground competition (Broadbent et al. 2017). Interestingly, the authors found this  
327 effect regardless of N-availability. Yet, in a mainland salt marsh in Germany with clay soil, N-  
328 availability was found to have no effect on the fine-root mass (Redelstein et al. 2018). However, the  
329 fine-root mass was significantly lower in the *Elymus*-dominated high marsh, compared to the low  
330 marsh (Redelstein et al. 2018). Both Redelstein et al. (2018) and Ford et al. (2016) found the fine-root  
331 mass to increase with plant species richness, probably because the species in the more diverse low-  
332 marsh community also represent diverse belowground space occupation strategies. Yet, the total fine-  
333 root mass of a group of species does not rule out potential belowground competition and therefore  
334 these interactions should be further investigated in salt marshes.

#### 335 4.2 N-fertilisation vs. surface-elevation change

336 We found no effect of N-fertilisation on the cover of *Elymus* and on succession. Likewise,  
337 Bockelmann and Neuhaus (1999) found no effect of N-fertilisation on *Elymus* in their study in a  
338 mainland salt marsh, thus drawing the conclusion that *Elymus* is not N-limited. In contrast, a positive  
339 effect of N-fertilisation on the succession and the relative contribution of *Elymus* to the total biomass  
340 was found by Van Wijnen and Bakker (1999) in a back-barrier island salt marsh. Thus, these

341 contrasting results might be explained by the differences between mainland salt marshes and island  
342 salt marshes, with the latter being characterised by a much shallower clay layer on top of the sandy  
343 subsoil (de Groot et al. 2011; Elschot et al. 2013). The thickness of the clay layer was found to be a  
344 good predictor of the N-pool (Olf et al. 1997). Therefore, *Elymus* might be N-limited in island salt  
345 marshes (Van Wijnen and Bakker 1999), but not in mainland salt marshes (Bockelmann and Neuhaus  
346 1999) such as in this experiment. In an indirect approach, comparing time series of vegetation maps  
347 and chronosequence data of four island salt marshes differing in sediment deposition rates, it was also  
348 concluded that *Elymus* expansion is mainly driven by spatially varying natural sediment deposition  
349 rates including the resulting N-addition, and not by the evenly spread atmospheric N-deposition  
350 (Veeneklaas et al. 2013). We can now corroborate this conclusion by the results of our experiment that  
351 sedimentation leading to a high surface-elevation change enabled *Elymus* to grow at originally lower  
352 elevation, while N-fertilisation had no effect. Sediment deposition rate in our study area is 2.8 – 8.3 kg  
353 m<sup>-2</sup> yr<sup>-1</sup> (Nolte et al. 2013b). Furthermore, we know that the N-content of the freshly deposited  
354 sediment collected using sediment traps is around 0.28% of the total mass (Mueller et al. unpublished  
355 data). Therefore the input of N via sediment deposition in the study site ranges roughly between 7.8  
356 and 23.0 g m<sup>-2</sup> yr<sup>-1</sup> and thus is representative of the lower N-fertilization treatment. For comparison,  
357 on a back-barrier island in the Netherlands sediment deposition rate was found to range from roughly  
358 1.0 to 2.5 kg m<sup>-2</sup> yr<sup>-1</sup> (Elschot et al. 2013). No data on the N-content of freshly deposited sediment is  
359 available for this specific site, but assuming similar values to those of Mueller et al. (unpublished  
360 data), the input of N via sediment deposition would range between 2.8 and 7.0 g m<sup>-2</sup> yr<sup>-1</sup>. This  
361 illustrates that natural N-input in in these island marshes is probably much lower and can thus,  
362 together with the resulting shallower clay layer, explain that *Elymus* is limited by Nitrogen in these  
363 salt marshes. Furthermore, surface-elevation change can also vary between mainland marshes. This is  
364 in accordance with a landscape scale study of succession in the salt marshes of the Schleswig-Holstein  
365 Wadden Sea coast, which found early successional stages to be more persistent in the northern  
366 Wadden Sea (Rupprecht et al. 2015b). It is argued that this is due to large scale gradients of e.g.  
367 surface-elevation change (Rupprecht et al. 2015b), which was found to be lower in the North  
368 (Suchrow et al. 2012) and might therefore reduce *Elymus* encroachment.

#### 369 4.3 Individual establishment vs. clonal growth

370 In this experiment planted individuals of *Elymus* were used to assess which factors drive the  
371 encroachment of the species. In natural succession, however, vegetative propagation was found to be  
372 an important pathway for *Elymus*, especially in young marshes (Veeneklaas et al. 2011). The spread of  
373 *Elymus* along the coast of Schleswig Holstein was also found to be positively affected by a shorter  
374 distance to the nearest established *Elymus* patch (Rupprecht et al. 2015b), which might also indicate  
375 the importance of vegetative spreading. Vegetative spreading can enable plants to grow into  
376 unfavourable habitats as daughter ramets can be supported by the adult plants via the rhizome

377 (Hutchings and Bradbury 1986). This physiological integration can increase the chance of survival for  
378 daughter ramets in stressful conditions (D’Hertefeldt and Jónsdóttir 1999; Zhou et al. 2014).  
379 Furthermore, clonal grasses such as e.g. *Leymus scalinus*, were found to adapt the length of their  
380 ramets under different conditions, switching to the so-called guerrilla growth form with spreading  
381 ramets in patches with low nutrient supply (Ye et al. 2006). Whether *Elymus* is also using  
382 physiological integration to invade the otherwise unfavourable low marsh, remains to be further  
383 investigated.

#### 384 4.4 Succession in salt marshes

385 Our results highlight that elevation and the change of elevation through sedimentation (i.e. surface-  
386 elevation change) is a key driver of the succession from mid-successional low marsh communities to a  
387 late successional high marsh community dominated by *Elymus*. The elevation as a key variable  
388 determining the distribution of salt-marsh plant species in Wadden Sea salt marshes (Olf et al. 1997;  
389 Schröder et al. 2002; Suchrow and Jensen 2010) and the increase in elevation over time as a main  
390 factor leading to vegetation change has been widely described here (Leendertse et al. 1997; Olf et al.  
391 1997; Veeneklaas et al. 2013; Rupprecht et al. 2015b). However, while the zonation represents the  
392 succession in mainland salt marshes (de Leeuw et al. 1993), this is not necessarily true for back-barrier  
393 island salt marshes (de Leeuw et al. 1993; Olf et al. 1997). Here the marsh elevation is a result of the  
394 underlying sand layer and the clay sediment that deposited on top of it (Olf et al. 1997; Bakker 2014).  
395 Additionally, the thickness of the clay layer in back-barrier island marshes is a good predictor of the  
396 N-pool (Olf et al. 1997). This might explain why studies with N-fertilization found much clearer  
397 effects in island salt marshes with a thin clay layer (van Wijnen and Bakker 2001), compared to  
398 mainland salt marshes with a thick clay layer (Bockelmann and Neuhaus 1999).

#### 399 4.5 Conclusions

400 We can conclude that the main driver of the *Elymus*-encroachment in the ungrazed Wadden Sea  
401 mainland salt marshes is a high surface-elevation change, raising the original elevations and thereby  
402 probably generating more favourable abiotic conditions. In contrast to many other studies on grass  
403 encroachment, N-fertilisation had no effect on the encroachment of *Elymus* in this mainland salt marsh  
404 and we therefore conclude that eutrophication by atmospheric N-deposition probably plays only a  
405 minor role. This case, therefore, is an example for an ecosystem in which encroachment is driven by a  
406 natural factor, rather than anthropogenic eutrophication. Thus, when attempting to halt or slow down  
407 grass or shrub encroachment, we suggest nature managers to assess different potential causes of the  
408 development before decisions on actions such as grazing, cutting or burning are made. In case of the  
409 Wadden Sea salt marshes, it furthermore needs to be monitored whether *Elymus* is indeed the climax  
410 vegetation. On the oldest parts of the island salt marshes, *Elymus* has been partly replaced by stands of  
411 *Phragmites australis* and *Juncus gerardii*, probably due to waterlogging and low rates of sediment

412 deposition and thus low sediment supply. Whether this development will also lead to a reduced  
413 encroachment or even reduction of *Elymus* in mainland salt marshes, remains to be seen.

414

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420

#### 421 **Data availability statement:**

422 Data is available in PANGAEA. <https://doi.org/10.1594/PANGAEA.899893>

423

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