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### ► To cite this version:

Quentin Laporte-Fauret, Ana Teresa Alonso Ayuso, Tiffany Rodolfo-Damiano, Vincent Marieu, Bruno Castelle, et al.. The role of physical disturbance for litter decomposition and nutrient cycling in coastal sand dunes. *Ecological Engineering*, 2021, 162, pp.106181. 10.1016/j.ecoleng.2021.106181 . hal-03411204

**HAL Id: hal-03411204**

**<https://hal.science/hal-03411204>**

Submitted on 2 Nov 2021

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1 Title: The role of physical disturbance for litter decomposition and nutrient cycling in coastal  
2 sand dunes

3

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14 **Author Contributions:** Conceptualization, Q.L.-F., R.M., V.M. and B.C.; Formal analysis,  
15 Q.L.-F.; Funding acquisition, B.C.; Investigation, Q.L.-F., and R.M.; Methodology, Q.L.-F.,  
16 V.M., B.C., R.M., S.B. and D.R.; Validation, Q.L.-F.; Writing—original draft, Q.L.-F.;  
17 Writing—review & editing, R.M., V.M. and B.C.

18

19 **Funding:** This research was funded by Agence Nationale de la Recherche (ANR) grant ANR-  
20 17-CE01-0014 (SONO project).

21

## 22 **Highlights**

- 23 • Physical disturbance increases ecosystem functioning in stressful costal sand dunes
- 24 • Dune geomorphology impacts ecosystem functioning when affecting sand deposition

- 25 • Plant community composition changes in response to increasing ecosystem functioning

26 **Abstract**

27 Disturbance increases ecosystem functioning in productive habitats but its effect in stressful  
28 conditions is less documented, although this is crucial for understanding the resilience of  
29 disturbed systems to natural and anthropogenic disturbances. Our goal is to assess the influence  
30 of physical disturbance for ecosystem functioning in coastal sand dunes. We set up an  
31 experimental design, including two treatments in four blocks, in a four km-long dune site from  
32 South West France. We simulated physical disturbance from marine and wind origin, digging  
33 Experimental Notches (EN), in the incipient (West EN treatment) and established foredunes  
34 (East EN treatment), respectively and compared the effects of EN to controls along transects  
35 including 13 positions from the beach to the transition dune behind ENs. We sampled litter  
36 decomposition rate, elevation variation, wind abrasion, sand grain size and vegetation  
37 composition. We also used drones to quantify sand deposition sheets during severe winter  
38 storms. Litter decomposition rate was the highest where sand accumulated the most, at the  
39 ecotone between the established foredune and transition dune and in the East EN treatment.  
40 This increase of ecosystem functioning was correlated to wind patterns. However, there was  
41 also a strong alongshore variability, with important sand deposition sheets occurring in some  
42 blocks depending on dune geomorphology. Vegetation composition was mainly influenced by  
43 shoreline distance, but also by the block and EN treatment, with a strong interaction between  
44 these three effects. We conclude that physical disturbance increase ecosystem functioning in  
45 the stressful conditions of the Atlantic sand dunes, only when sand accumulates, whereas  
46 excessive disturbances enhancing sand erosion are not favorable for ecosystem functioning.

47

48 **Keywords:** Coastal dunes, Drone surveys, Ecosystem functioning, Litter decomposition,  
49 Physical disturbance, Sand deposition, Wind abrasion.

## 50 **Introduction**

51 The role of disturbance for community structure and ecosystem functioning has fascinated  
52 ecologists for decades (McArthur and Wilson 1963; Grime, 1973; Connell, 1978; Huston 1979;  
53 Paine and Levine 1981; Pickett and White 1985). Grime (1973) proposed to separate  
54 disturbance from environmental stress to straightforwardly assessing plant species functional  
55 strategies, community richness and composition, and ecosystem functioning in natural and  
56 managed ecosystems. Disturbance can be defined as a decrease in plant biomass due to either  
57 biotic or abiotic factors (herbivory, trampling, ploughing, fire, flooding, soil erosion, sediment  
58 accumulation) and stress as a decrease in plant growth and community productivity due to  
59 mainly four environmental constraints, shade, drought, oligotrophy and sub-optimal  
60 temperatures (Grime 1973; 1974). This distinction is crucial to understand the role of  
61 disturbance for ecosystem functioning since stress is always related to a decrease in community  
62 productivity, whereas disturbance can show different relationships with productivity.

63 Concerning plant species richness, Huston (1979) proposed that physical disturbance  
64 decreases species richness in stressful environments but promotes it in favorable ones due to  
65 decreasing competition. Thus, Grime (1973), Huston (1979) (see Huston, 2014 for a synthesis)  
66 proposed the occurrence of a unimodal (i.e., highest diversity at mid-position along the  
67 gradient) relationship between plant species richness and stress, disturbance, and community  
68 biomass. This hypothesis has been supported by a number of empirical studies, for example  
69 Ross et al. (2019) and Maalouf et al. (2012) for productive herbaceous communities and  
70 stressful calcareous grasslands, respectively. However, this relationship has been recently  
71 debated (Adler et al., 2011; Fraser et al., 2015).

72 Ecosystem functioning refers to the ecological processes that control the fluxes of  
73 energy, nutrients and organic matter through an environment (e.g., decomposition, primary  
74 production and nutrient cycling) (Cardinale et al., 2012). It is also widely acknowledged that

75 the absence of disturbance in low stress conditions leads to a progressive decline in ecosystem  
76 functioning. For example, Wardle et al. (2004) studying the long-term evolution of six forest  
77 ecosystems from tropical, temperate, and boreal biomes, showed that litter decomposition,  
78 biomass, and decomposer microbe activity decreased over time in absence of major disturbance,  
79 mainly due to increasing phosphorus limitation. Fortunel et al. (2009) also found an overall  
80 decrease in ecosystem functioning, measured by litter quality and decomposition, with  
81 decreasing disturbance for herbaceous systems from ten European sites exhibiting moderate to  
82 low stress conditions. Finally, Peltzer et al. (2010) reviewed the findings from studies of long-  
83 term chronosequences assessing nutrient cycling for systems spanning the boreal, temperate,  
84 and subtropical zones. Although they also found an overall decrease in ecosystem functioning  
85 through time, they stressed the occurrence of exceptions in arid climates with no ecosystem  
86 retrogression or slower depletion in nutrients. The depletion of nutrients through time is highly  
87 dependent on climate drainage (Huston, 2012; Delgado-Baquerizo et al., 2013), with increasing  
88 phosphorus limitation and decreasing productivity during succession in wet climates only. This  
89 explains why nutrient cycling is improved by disturbance in wet climates.

90         However, if disturbance (e.g., wildfires, grazing) is essential to maintain ecosystem  
91 functioning in low stress conditions, its role in stressful systems is less known, with contrasting  
92 results, either increases or decreases of ecosystem functioning, depending on disturbance type  
93 (Deng et al., 2013; Dimitrakopoulos et al., 2006; Wardle et al., 1997). Additionally, even in wet  
94 climates, changing and intensifying disturbance regimes has been shown to drive positive  
95 feedback loops between vegetation composition, structure, and ecosystem function that could  
96 reduce ecosystem resilience and trigger ecosystem collapse (Lindenmayer et al., 2016; Bowd  
97 et al., 2019). Such effects are even more likely to occur in stressful systems with lower resilience  
98 to natural and anthropogenic disturbances (Kéfi et al., 2007). Thus, the role of disturbance for  
99 ecosystem functioning is not clearly established in stressful systems and its occurrence might

100 be more dependent on the frequency and intensity of disturbances than in wet climates. The  
101 resilience of ecosystems to natural and anthropogenic disturbances is highly dependent on the  
102 ability of plant species to recolonize disturbed habitats and, thus, to plant growth and ecosystem  
103 functioning. If disturbance is decreasing ecosystem functioning and, thus, plant growth and  
104 community biomass in stressful systems, this may induce a collapse of ecological communities  
105 and ecosystem services (Michalet et al. 2006; Kefi et al. 2007). This will support the CSR model  
106 of Grime (1974) that consider there is no viable strategy for plant in highly stressed and  
107 disturbed systems. Therefore, increasing our knowledge on the role of physical disturbance for  
108 ecosystem functioning in stressful systems is key for managing and restoring disturbed stressful  
109 ecosystems, such as arid ecosystems or coastal sand dunes.

110 We choose to assess in coastal dunes the role of physical disturbance for ecosystem  
111 functioning in stressful environments since community structure and ecosystem functioning are  
112 known to be mainly driven by these two environmental constraints in these systems (Maun,  
113 1998; Forey et al., 2008). Coastal dunes are generally occurring along coasts having sufficient  
114 sand supply, prevailing onshore winds and the presence of vegetation, or other obstructions, to  
115 trap the sand transported by the wind (Nordstorm, 2015). They are subjected to wave action,  
116 likely to induce drastic coastal erosion during storms (Castelle et al., 2015; Guisado-Pintado  
117 and Jackson 2017). Additionally, coastal dunes are highly influenced by wind processes,  
118 transporting sand from the beach to the dune (Hesp and Walker 2013), and the presence of  
119 plants limiting wind erosion by trapping sand with their aerial parts (Zarnetske et al., 2012).  
120 Interactions between these physical and biotic processes can lead to the formation of blowouts  
121 in coastal dunes (Hesp, 2002), promoting sediment transfers from the beach to the back dune  
122 by wind acceleration in the blowout (Hesp and Walker, 2013).

123 Plant communities in coastal dunes are subjected to a large range of environmental  
124 stresses such as saline spray, swash inundation (principally in the beach and incipient foredune),

125 drought, nutrient deficiency (Hesp, 1991; Hesp and Martinez, 2007; Martinez and Psuty, 2004).  
126 However, in dunes from wet temperate climates where salt can be washed from plants and  
127 through soils during heavy rain events, disturbance by sand deposition has been shown to be  
128 the crucial factor driving plant community zonation before salinity (Moreno-Cassola, 1986;  
129 Maun, 1998; Forey et al., 2008). Maun (1994) also showed that partial sand burial, for some  
130 species, stimulated growth of ramets, stolon, roots and leaves leading to an increase of total leaf  
131 area, number of tillers and total dry biomass. Moreover, sand deposition also increases soil  
132 volume, soil resources and mycorrhizae activity promoting ecosystem functioning (Maun,  
133 1998; Forey et al., 2008). However, in these studies, the effects of increasing disturbance on  
134 ecosystem functioning might have been confounded by a decrease in stress also occurring  
135 towards the ocean, as observed in salt marches by Proença et al. (2019). Indeed, Forey et al.  
136 (2008, 2010) have documented a beneficial effect of the ocean spray for plant growth and  
137 survival in the incipient foredune, with lower vapor pressure deficit values and maximum  
138 temperatures than in the inland transition dunes protected by the incipient foredune and the  
139 established foredune. In order to assess the potential role of disturbance for ecosystem  
140 functioning in stressed environments, we have to control for variation in stress.

141         Recently, scientists and coastal dune stakeholders have been attempting to reintroduce  
142 a certain dynamic in stabilized coastal dunes characterized by high plant cover and biomass  
143 (Creer et al., 2020; Pye et al., 2020; Arens et al., 2020). This is particularly the case in Northern  
144 Europe where some remobilization projects are attempting to restore a dynamic of sediment  
145 transport from the beach to the back of the dune by removing vegetation or foredune notch  
146 excavation (Eamer et al., 2013; Konlechner, et al., 2015; Arens et al., 2013; Kuipers 2014). In  
147 these low-stress coastal dunes, these methods have been shown to be successful in increasing  
148 sand transport and thus disturbance in the dunes (Ruessink et al., 2018), leading to an increase  
149 in diversity, by reducing competition, and a rejuvenation of the soils (Brunbjerg et al., 2015;



150 Nordstrom et al., 2007), confirming the CSR model (Grime, 1974). In contrast, sand  
151 remobilization in dunes from southern latitudes with lower summer rainfall and, thus, higher  
152 stress may reduce ecosystem functioning and diversity, consistent to Huston (1979). To the best  
153 of our knowledge, there has been no experimental study assessing the impact of sand  
154 remobilization on ecosystem functioning in more stressed coastal dunes. These impacts are  
155 crucial to assess in the context of changing management paradigms.

156 We designed an original experiment in the coastal sand dunes of South West France,  
157 where we applied experimental disturbances simulating blowout effects from marine and  
158 aeolian origins at two positions along the complex stress/disturbance gradient. Indeed, in  
159 northern Europe, some studies have attempted to reintroduce sedimentary dynamics within the  
160 coastal dunes by blowout restoration or notches excavation (Van Boxel et al., 1997; Pye et  
161 Bolt, 2016; Ruessink et al., 2018). However, these studies have only focused on morphological  
162 changes without assessing the impact on plant communities and ecosystems. As interactions  
163 between physical and biological processes play a major role in coastal dunes evolution while  
164 evolving across many spatial and temporal scales, it is important to set up experiments able to  
165 understand these interactions across different dune habitats. We choose to quantify litter decay  
166 as good proxy of nutrient cycling and availability along transects delineated from the beach to  
167 the back dunes, along the experimental blowouts and in controls. We also measured in all  
168 treatments environmental variables (i.e., wind abrasion, elevation variation, and grain size,  
169 Forey et al., 2008) and plant species composition as indicator of community response to  
170 environmental disturbances and changes in ecosystem functioning. Additionally, in order to  
171 take into account the context-dependency of the effect of disturbance (Grime, 1974), we also  
172 assessed if community and ecosystem responses were affected by the beach dune system  
173 geomorphology (Davidson-Arnott, 2010). We aim to answer the following questions: (1) do  
174 contrasting disturbance types (e.g., marine and aeolian) have different effects on ecosystem

175 functioning and (2) does dune geomorphology (e.g., foredune elevation, oceanward slope and  
176 width, transition dune elevation) alter the effect of disturbance on ecosystem functioning.

177

## 178 **Material and methods**

### 179 *Study area*

180 The study site, Truc Vert beach, is a representative beach of the 110 km long Gironde sandy  
181 coast, in SW France (Fig 1.a). The climate is temperate oceanic with mean annual precipitations  
182 of 900 mm mainly during winter period (data were extracted from the website of METEO  
183 FRANCE, see supp mat 1 & 2). This open sandy beach of high energy is meso- to macro-tidal  
184 with an average tidal range of 3.7 m during spring tides (Castelle et al., 2015). Due to its  
185 remoteness, this beach represents an ideal natural laboratory that has been extensively studied  
186 for sediment transport and beach morphodynamics (Castelle et al., 2017), plant-plant  
187 interaction experiments and community composition (Forey et al., 2008, 2009, 2010; Le  
188 Bagousse-Pinguet et al., 2013). The Truc Vert beach coastline has remained stable over the past  
189 65 years, even after being exposed to major storm events (Castelle et al., 2018). It is bordered  
190 by a large coastal barrier system with significant foredune system (250 m wide and 20-25 m  
191 height) part of which was re-contoured since the 60s, after severe storms in 20s and World War  
192 II. The National Forest Office in charge of the management of the dunes has undertaken  
193 extensive dune profiling and plant species planting work to renovate the dune system until the  
194 80s. Since then, the dune has always been softly managed by vegetation planting, particularly  
195 to prevent the development of blowouts. In terms of vegetation, three dune types from the beach  
196 to the forest are distinguished, each representing a particular habitat with (1) the incipient  
197 foredune, in direct contact with the upper beach and dominated by pioneer species as *Elymus*  
198 *farctus* and *Euphorbia paralias*, (2) the established foredune, dominated by *Ammophila*

199 *arenaria* and (3) the transition dune, dominated by *Helichrysum stoechas*. Together the  
200 incipient foredune and established foredune are forming the foredune *sensu lato* (App. 1.a, b).

201

### 202 *Experimental design*

203 The experiment was carried out on a 4 km-long alongshore and 500 m cross-shore dune system.  
204 The site was subdivided into four 500 m-long alongshore blocks, guaranteeing spatial  
205 replication. Blocks were numerated from one to four from the south to the north (Fig. 1.a) and  
206 separated from each other by a 500 m-long alongshore distance. In each block, two large  
207 Experimental Notches (EN) were dug in December 2017, one in the incipient foredune (called  
208 the West EN, Fig. 1.b), to simulate the effect of wave erosion processes during severe storms,  
209 and one at the top of the established foredune (called the East EN, Fig. 1.c), to simulate the  
210 blowout initiation by wind erosion. These EN were dug with a horizontal dimension similar to  
211 the blowouts naturally present in the study area with alongshore and cross-shore distances of 7  
212 m and 15 m, respectively.

213 In order to monitor environmental parameters and plant community composition in our  
214 treatments, four cross-shore transects were placed in each block from the beach to the transition  
215 dune. Two transects were aligned along ENs, and two other transects were placed  
216 approximately 100 m further south of experimental ENs, as controls. Each transect was  
217 composed of 13 sampling quadrats distributed at the three ecotones and in the middle of each  
218 community type (e.g., incipient foredune, established foredune and transition dune) (Fig. 1.d).  
219 The quadrat number always represented the same habitat through the different transects, even  
220 if the shoreline distance can slightly differ between transects. This approach was chosen in order  
221 to better capture vegetation changes, which should preferentially occur at the ecotones. Thus,  
222 our design included four West ENs, four East ENs and height control transects and 208

223 sampling quadrats (13 positions X four transects X four blocks), for which the spatial  
224 coordinates were monitored using a differential GPS.

225

### 226 *Environmental variables and litter decomposition*

227 Several environmental variables were monitored in 2018 in order to quantify the disturbance  
228 inducted by the ENs, together with the quantification of litter decomposition that was chosen  
229 as indicator of ecosystem functioning. Elevation monitoring was carried out on the 208  
230 sampling quadrats (13 quadrats X 4 transects X 4 blocks), whereas the monitoring of other  
231 environmental variables (i.e., wind abrasive potential and grain size), and litter decomposition  
232 were carried out at five specific positions in each transect, at the ecotones (positions 7 and 11)  
233 and at the center of each dune habitats (positions 4, 9 and 13), providing a total of 80  
234 measurement points (5 positions X 4 transects X 4 blocks) (see grey plots on Fig. 1.c).

235 Sand deposition, the major factor of disturbance in coastal dunes (Maun, 1998, Forey et  
236 al., 2008), was quantified with elevation measurements at the 208 points. We used a Trimble®  
237 differential GPS and a known base, resulting in vertical and horizontal accuracy of 0.015 m and  
238 0.008 m, respectively. This monitoring was carried out just after the EN set up and during the  
239 next 3 seasons (i.e., Winter: March 2018, Spring: May 2018 and Summer: August 2018).  
240 Comparison between the elevations of each season allowed to identify the quadrats that have  
241 been subjected to erosion (negative  $Dz$ ) or accretion (positive  $Dz$ ) processes according to  
242 equation 1:

243

$$Dz = z_{Summer\ 2018} - z_{After\ ETN} \quad (1)$$

244

245 where  $Dz$  represents the elevation variation between two seasons and  $z$  the quadrat elevation at  
246 the chosen season (a  $Dz$  equal to 0 indicates that there has been no elevation change).

247 Wind abrasive potential was measured indirectly by quantifying the loss of flag material  
248 due to wind action (Rutter, 1965, Forey et al., 2008). Indeed, the cotton surface of the flag,  
249 sensitive to the sand abrasion transported by the wind, loses surface area by abrasion depending  
250 on wind intensity and frequency. The 80 flags were characterized by a length and width of 0.38  
251 m and 0.16 m, respectively (0.006 m<sup>2</sup>), attached to a bamboo pole at 0.3 m height and placed at  
252 the specific positions in each transect from mid-March to late May 2018. The remaining area  
253 of each flag was measured after exposure to the wind using a planimeter and WinFolia software  
254 (from Regent Instruments Inc®). The percentage of lost surface *Sl* (%) was expressed by  
255 equation (2):

$$Sl = 100 - \frac{Sr \times 100}{Si} \quad (2)$$

256  
257 where *Sr* is the surface remaining after exposure to the wind (m<sup>2</sup>) and *Si* the initial surface (m<sup>2</sup>).

258 Sand grains were collected in sampling tubes (0,5 x 8 cm) on the ground surface at the  
259 specific positions in each transect in mid-March 2018. They have been dried before measuring  
260 their size by a laser diffraction microgranulometer (from Malvern Panalytical®). As the data  
261 had a unimodal distribution, the median diameter of the sand grains of each sample was chosen  
262 to characterize the grain size at each position.

263 The rate of organic matter decomposition, which indirectly refers to soil fertility and  
264 therefore ecosystem functioning (Fortunel et al., 2009), was assessed using the litterbag method,  
265 with two dominant dune plant species of the study field. Half of the bags were filled with  
266 *Elymus farctus*, the species dominating the incipient foredune and the other half with  
267 *Helichrysum stoechas*, the species dominating the transition dune. Litterbags, 0.25 m by 0.15  
268 m with a mesh size of 0.001 m, were initially filled with 10 g of leaf (harvested early March  
269 2018) previously dried at 40°C during 48 hours (in order to control for moisture content without  
270 changing the palatability of the litter for decomposers). In mid-March 2018, just before the

271 beginning of the spring growing season, 80 *Elymus farctus* litterbags and 80 *Helichrysum*  
272 *stoechas* litterbags were buried at 0.1 m depth at the specific positions of each transect.  
273 Litterbags were harvested late May after 10 weeks, washed to remove the sand, dried at 40°C  
274 for 48 hours and weighed. Forey et al. (2008) have shown that this experiment duration and  
275 period of the year were adapted to assessing differences in litter decomposition rates among  
276 sand dune communities in these climatic conditions.

277

### 278 *Large-scale dune geomorphology*

279 Large scale dune geomorphology was obtained by Unmanned Aerial Vehicle (UAV) surveys  
280 covering the 4 km alongshore of the Truc Vert coastal dune. They were performed using a DJI  
281 Phantom 4 Pro quadricopter equipped with a 20 MPix camera and a set of 36 permanent ground  
282 point controls (250 m spaced pairs). The combination of UAV images and photogrammetry  
283 algorithms from the Agisoft Metashape ® software v1.5 allowed to generate and geo-rectified  
284 (using the permanent ground point controls) accurate Digital Surface Model (DSM) with a  
285 planimetric and altimetric error of 0.04 m and 0.05 m respectively and a 0.1 m resolution  
286 (Laporte-Fauret et al., 2019).

287         During the 2017-2018 winter, Laporte-Fauret et al. (2019) highlighted the formation of  
288 0.1-0.3 m thick sand deposition sheets over the transition dune, extending from the established  
289 foredune sometimes to the inland edge of the transition dune. Sand sheets have a typical width  
290 of 100-200 m, significantly affecting the vegetation (mortality by burial). In order to assess  
291 whether geomorphology played a role in these sand depositions, the cross-shore profiles of the  
292 16 transect were extracted from the DSM in order to calculate geomorphological parameters of  
293 the foredune (i.e., oceanward slope, elevation and cross-shore wide), the transition dune (i.e.,  
294 elevation) and the elevation difference between the foredune and the transition dune (see  
295 App1.a for a four km alongshore averaged profile of Truc Vert with precision about

296 geomorphological parameters). Then the large sand deposition sheets were digitized from the  
297 DSMs and a surface and volume value were assigned to each transect when they were present  
298 within 25m alongshore on either side of the transect.

299

### 300 *Vegetation sampling*

301 Plant community composition was monitored, with a seasonal frequency (Winter: mid March  
302 2018, Spring: mid May 2018 and Summer: late August 2018) at each of the 208 positions. We  
303 quantified the cover of each species using a 1 m<sup>2</sup> quadrat with a mesh size of 0.2 m (Goodall  
304 1952). Plants or their vertical projections located at the 36-line intersections were recorded to  
305 calculate their percent cover. An abundance of 0.5% was assigned to species present in the  
306 quadrat but only outside these intersections.

307

### 308 *Statistical analysis*

309 Elevation variation, wind abrasive potential and grain size were analyzed with mixed models  
310 with Treatment, Position and their interaction as fixed effects; and Treatment nested within  
311 block as random effects. Litter decay was also analyzed with mixed models with Treatment,  
312 Position, Species and their interactions as fixed effects; and Species nested within Treatment,  
313 which is nested within block as random effect. Variance analyses (ANOVA) were performed  
314 on these mixed models. Least Significant Difference (LSD) tests were used when there was a  
315 significant position effect, and sample t-tests to test for significant differences from zero values.

316 A PCA was performed to search for relationships between, litter decay of the two  
317 species, and four environmental variables (wind intensity, elevation variation, sand grain size  
318 and distance to the shoreline). We then used, a two-way ANOVA model to assess the effects of  
319 the position, EN treatments and their interaction on plot scores along the two first axes of the  
320 PCA. Vegetation data was analyzed with a Correspondence Analysis. Plots without species and

321 species with a frequency lower than four were removed before the CA. A three-way ANCOVA  
322 was conducted on plot scores along the two first axes of the CA, in order to assess the effects  
323 of the block (qualitative data), the position (quantitative data), the EN (qualitative data) and the  
324 season (qualitative data) treatments and their interactions on species composition. For the  
325 position treatment, we used the shoreline distance as a continuous variable with also a quadratic  
326 expression to detect concave or convex shapes.

327 Finally, in order to detect if differences in geomorphology among blocks may have  
328 affected our results and in particular sand deposition, we assessed geomorphological block  
329 effects, the EN treatments and their interaction on the sand deposits surfaces and volumes  
330 observed behind the established foredune with a two-way ANOVA. We also search for  
331 relationships between the sand deposits surface and the volume and the dune morphological  
332 parameters (i.e., oceanward foredune slope, foredune elevation, foredune width, transition dune  
333 elevation and difference between foredune and transition dune elevation) at the level of each  
334 transect by independent linear regressions. Finally, we assessed the geomorphological block  
335 effects and the EN treatments and their interaction on the foredune oceanward slope and the  
336 established foredune width with a two-way ANOVA. All statistical analyses were performed  
337 using the software R (version 1.2.5033).

338

## 339 **Results**

### 340 *Mixed models and PCA*

341 PCA axis 1 was primarily correlated to litter decomposition rates and transect positions and  
342 secondarily to elevation variation, wind intensity and the EN treatment (Fig. 2). The fastest rate  
343 of decomposition for the two species (with *Elymus farctus* litter decomposing almost twice  
344 faster than *Helichrysum stoechas* one, as shown by the highly significant species effect in Table  
345 1 and see App. 2) occurred at positions 9 (and then 7 and 11) of the East EN treatment (positive



346 side of axis 1 in Fig. 2 and highly significant position and marginally significant treatment  
347 effects in Table 2). The highest elevation increase due to sand deposition and highest wind  
348 intensity were also observed at these positions (Table 1 and see results of LSD and sample t-  
349 tests in Fig. 3 for elevation and App. 4 for wind). Axis 2 was explained by shoreline distance  
350 and grain size, the latter decreasing with increasing distance to the shoreline (Fig. 2 and Tables  
351 1 & 2 and see LSD test for the position effect in App. 3). Wind intensity contributed to the two  
352 axes with the highest values in the established foredune and for the East EN treatment (Table 1  
353 and see LSD test for the position treatment in App. 4). All together, these results highlight that  
354 the most important variation in environmental conditions affecting decomposition rates  
355 occurred during our experiment at the crest and behind the established foredune, and in  
356 particular for the East EN treatment.

357

#### 358 *Large-scale dune geomorphology*

359 Sand deposition sheets mainly occurred at three transects in block 2 and four in block 3 (App.  
360 5), and extended from the established foredune crest up to a hundred meters within the transition  
361 dune. They reached a surface and volume of 130 354 m<sup>2</sup> and 1827 m<sup>3</sup> for block 2 and 130 821  
362 m<sup>2</sup> and 1878 m<sup>3</sup> for block 3. The surface and volume of these sand deposition sheets were not  
363 significantly different between blocks nor EN treatments (Table 3.a). However, there were  
364 highly significant correlations between these sand deposition sheets parameters and both the  
365 oceanward slope and width of the foredune (Table 3.b). Finally, only the oceanward foredune  
366 slope was significantly different among blocks with a mean slope of 0.24, 0.17, 0.15 and 0.23  
367 for the blocks 1 to 4, respectively (Table 3.c).

368

#### 369 *Vegetation*

370 There was a strong arc effect on CA 1-2 diagram showing that one main factor was driving  
371 differences in species composition along the two axes (Fig. 4.a). Indeed, the quadratic distance  
372 (to the shoreline) was highly significantly correlated to both axes in the ANCOVA on plot  
373 scores, with the incipient foredune community at the extreme upper left of the cloud and the  
374 transition dune community at its extreme upper right (App. 6). However, two other treatments  
375 also significantly explained the CA axes, the EN treatment for axis 1 and the season for axis 2.  
376 Additionally, there was a highly significant block effect on both axes, as well as interactions  
377 between block and distance and between block and quadratic distance on both axes. Thus, CA  
378 axis 1 appeared to be primarily correlated to species tolerance to disturbance by sand deposition  
379 (see also Fig. 4.b) and CA axis 2 to species phenology. The effect of EN treatment on axis 1  
380 can be easily understood with the results displayed in Fig. 4.b, with lower scores on axis 1 for  
381 the East EN treatment than for the two other EN treatments, highlighting that EN dug in the  
382 established foredune induced an increase disturbance by sand deposition, in particular behind  
383 the foredune crest at the ecotone with the transition dune. Additionally, the interaction between  
384 the block, EN treatment and distance to the shoreline on axis 1 can be understood in App. 7,  
385 with the scores on axis 1 of the East EN treatment decreasing faster than those of the West and  
386 Control EN treatments with increasing distance to the shoreline, in particular for blocks 3 and  
387 2. Overall, blocks 1 and 4 appeared to be less disturbed, which is consistent with the results of  
388 App. 5 showing that the sand deposition sheets occurred preferentially in blocks 2 and 3.

389

## 390 **Discussion**

391 In response to our first question, we found that only the EN positioned close to the foredune  
392 crest (East EN), simulating wind-driven blowouts, induced an increase in litter decomposition  
393 at the ecotone between the established foredune and the transition dune, where sand deposition  
394 was also the highest. Additionally, across the four km of our study site, we found, in response

395 to our second question, strong spatial variation in sand deposition, correlated to dune  
396 geomorphology and contributing to explain changes in vegetation in interaction with our  
397 treatments. Our results suggest that physical disturbance is likely to increase ecosystem  
398 functioning in stressed coastal sand dunes as documented in conditions of low stress, but only  
399 in particular conditions of sediment deposition, which are highly variable across time and space.

400 Our knowledge of the effects of disturbance on nutrient cycling and productivity in  
401 stressful environments is limited. Additionally, previous studies that have shown positive  
402 effects of disturbance on ecosystem functioning in stressful systems such as coastal dunes and  
403 salt marshes were conducted along complex environmental gradients. Variation in disturbance  
404 were likely to be confounded by variation in stress because both environmental constraints  
405 varied in opposite directions along a gradient of distance to the ocean or of inundation (e.g.,  
406 Forey et al., 2008, 2010; Proença et al., 2019).

407 In our study, we controlled stress variation by applying EN at two positions along the  
408 complex disturbance/stress gradient and comparing community and ecosystem responses to  
409 controls. We showed that only the East EN, positioned in the foredune crest and simulating  
410 natural blowouts with a wind origin, induced a positive effect on litter decomposition and, thus,  
411 ecosystem functioning. The West EN positioned in a less stressful position along the gradient,  
412 closer to the ocean spray in the incipient foredune and simulating natural blowouts with a  
413 marine origin, had no effect on both vegetation composition, maybe because the pioneer species  
414 in incipient foredune are already highly adapted to disturbance. These differences were not  
415 likely to be explained by different positions along the stress gradient, but rather by patterns of  
416 sand deposition. Indeed, the PCA results showed that there was along the first axis a highly  
417 significant correlation between litter decomposition, flag abrasion by wind and changes in  
418 elevation due to sand accretion. Additionally, variation in these direct variables were highly  
419 explained by both the position along the transect and the East EN. Finally, changes in vegetation

420 composition along the first CA axis were also significantly explained by the position along the  
421 gradient and the East EN treatment, with more disturbed vegetation behind the East  
422 experimental blowout.

423         Results of flag surface degradation measurements allowed to indirectly highlighting the  
424 wind speed profiles from the beach to the transition dune (Rutter, 1965). The presence of coastal  
425 dunes generates a wind flow acceleration, promoting sand transport on the upwind dune side,  
426 then deceleration, promoting sand deposition on the leeward dune side, respectively by  
427 streamlines compressing and decompressing (Walker and Hesp, 2013). This flag surface  
428 degradation was even more marked in the East EN, in particular at the dune crest position  
429 (position 9). Indeed, the EN was set up slightly West of this position and the blowouts are  
430 known to be depressions causing wind flow acceleration with a greater sand transport (Hesp,  
431 2002). This interaction between the EN treatment and wind intensity may explain the greater  
432 sand deposition observed behind the crest dune in the East treatment.

433         Concerning sand erosion and accretion, Truc Vert beach is subject to the impact of  
434 winter storms (Castelle et al., 2015), which caused significant beach erosion with the formation  
435 of localized erosion cliffs on the incipient foredune during winter 2017-2018 (Laporte-Fauret  
436 et al., 2019 and Fig. 2). In contrast, significant accretion rates were monitored from the  
437 established foredune crest to the transition dune, with a significantly higher deposition for the  
438 East EN (Fig. 3). This gradient of elevation variation on the Truc Vert beach system during our  
439 study contrasts with the study conducted by Forey et al. (2008) along the whole Aquitaine coast,  
440 which showed that the maximum sand deposition occurred in the incipient foredune with a  
441 regular decrease towards the transition dune. This divergence can be explained by likely both  
442 the higher precision of measurements of sand deposition in our study than in that of Forey et al.  
443 (2008) and the absence of major storm events favoring sand erosion and deposition during their  
444 study (Dodet et al., 2019). This latter difference might also explain why the West EN had no

445 effect in our study. It is very likely that the dominance of erosion downstream the West EN,  
446 due to a year with important storm events, impeded sand deposition and any increase in litter  
447 decomposition. The sand deposition occurred more easily downstream East EN, because of its  
448 close proximity to the foredune crest and, thus, to the strong wind flow deceleration occurring  
449 after the dune crest on its leeward side.

450         The highest decomposition rates were measured in the upper established foredune  
451 positions for both species, positions where sand deposition was also the highest. Forey et al.  
452 (2008) also found that the highest decomposition occurred at the position where sand deposition  
453 was the highest. However, in her study both sand deposition and litter decomposition were the  
454 highest in the incipient foredune, likely due to a year with lower storm event. In our study,  
455 although the West EN treatment was positioned closer to the wind spray than the East EN,  
456 decomposition was lower in the former, which strongly suggests that sand deposition rather  
457 than ocean spray controlled litter decomposition. Increased disturbance increases soil fertility  
458 and litter decomposition through plant tissues rejuvenation and reduced nutrient uptake (Grime,  
459 1974; Wardle et al., 2004; Davis et al., 2000). However, our results and the study of Forey et  
460 al. (2008) suggest that decomposition rates might not increase when disturbance is too high,  
461 with dominant sand erosion. Disturbance might increase ecosystem functioning in stressful  
462 environments only when soils or sediments accumulate but not when soil erosion dominates  
463 due to excessive disturbance. This might explain also why productivity decreases in alpine and  
464 dry systems on convex topographic positions when disturbance remove soils (Michalet, 2006),  
465 whereas productivity increases with disturbance in floodplains, salt marshes, coastal dunes and  
466 avalanche slopes in wet mountains where soils or sediments accumulate (Forey et al., 2008;  
467 Proença et al., 2019). When disturbance is too high in those latter systems like in our West EN  
468 treatment, erosion dominates over sediment accretion and ecosystem functioning decreases,  
469 through plant and soil removal, and eventually collapses (Kéfi et al., 2007; Bowd et al., 2019).

470           The surface and volume of the important sand deposition sheets that we observed from  
471 the foredune to the transition dune (Laporte-Fauret et al., 2019) were correlated to dune  
472 geomorphology, and in particular the oceanward slope and width of the foredune. Sand  
473 deposition sheets were only present at transects where the oceanward foredune slope was less  
474 than 20°. Indeed, gentle dune slopes act as a springboard and facilitate the transport of sand  
475 beyond the crest, whereas steeper dune slopes render sand transport beyond the crest more  
476 difficult (Iversen and Rasmussen, 1999). We also found that the oceanward foredune slope  
477 varied significantly across blocks. Indeed, each block measured 500 m alongshore and there  
478 were significant morphological differences at this spatial scale, as shown by the DSM in Fig.  
479 1.a. We must be aware that these morphologic parameters alone cannot explain the location and  
480 surface of these sand deposition sheets. Other parameters should be taken into account, such as  
481 the beach width, which directly defines the sand stock available for transport, the surface  
482 moisture (Nickling and Davidson-Arnott, 1990), the wind intensity and direction affecting the  
483 fetch surface (Walker and Hesp, 2013) and the feed-back effect of vegetation cover (Hesp,  
484 2002).

485           Thus, geomorphological variations on the beach dune system affected sand transport  
486 and deposition through the system alongshore, as much as did our EN treatment and the West-  
487 East position along transects. Ultimately, these three complex factors affected vegetation  
488 composition, as shown by the occurrence of a significant interaction between the block, EN  
489 treatment and distance to the shoreline on CA axis 1 (see also App. 7).

490

## 491 **Conclusion**

492 We found that physical disturbance increased litter decomposition in the stressful  
493 environmental conditions of the coastal sand dunes. However, this positive effect for ecosystem  
494 functioning occurred and affected vegetation composition only when associated with sand

495 deposition at the ecotone between the established foredune and the transition dune, as observed  
496 in our East EN transects or even in control transects in specific conditions of dune  
497 geomorphology. When disturbance was too high and sand erosion dominated there was no  
498 effect for ecosystem functioning, like in the West EN treatment. This suggests that the  
499 relationship between disturbance and ecosystem functioning in stressful conditions is unimodal  
500 and highly stochastic across time and space. Our results provide important new knowledge for  
501 understanding and predicting responses of stressful systems to increased disturbances in a  
502 changing environment. They suggest that coastal dunes may keep an important resilience to  
503 increasing probability of storm events and sea-level rise in a changing climate, only in case of  
504 intermediate disturbances. Indeed, increasing sand deposition after storm events may trigger  
505 ecosystem functioning, vegetation growth and dune stabilization. In contrast, extremely high  
506 disturbances inducing intense sand erosion may induce a collapse of the whole system as  
507 observed for example at the emblematic Dune du Pilat, the highest European sand dune with  
508 almost no plant allowing a stabilization of the system. This stresses the importance, in dry  
509 stressful systems, to maintaining the soft control of sand movements in a climate change  
510 context.

511

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688 **Tables**

689

690 **Table 1.** Results of the ANOVAs on the effects of the EN (Experimental Notch), position (P),  
 691 species (Sp, only for litter decomposition rate) treatments and their interactions on  
 692 environmental variables. Since interactions with the species treatment were not significant, they  
 693 are not represented in the table. Significant results are indicated in bold and marginally  
 694 significant in italics.

<i>Factors</i>	<i>Elevation variation</i>			<i>Litter decomposition</i>			<i>Wind abrasion</i>			<i>Median grain size</i>		
	Df	F	P	Df	F	P	Df	F	P	Df	F	P
EN	2	0.82	ns	2	2.08	<i>0.06</i>	2	1.83	ns	2	0.87	ns
P	12	6.22	<b>&lt;0.001</b>	4	5.64	<b>&lt;0.001</b>	4	6.32	<b>&lt;0.001</b>	4	5.95	<b>&lt;0.001</b>
EN x P	24	0.16	ns	7	0.41	ns	8	2.58	<b>0.02</b>	8	1.79	ns
Sp				1	840	<b>&lt;0.001</b>						

695

696 **Table 2.** Results of the ANOVAs on the effects of the EN (Experimental Notch), position (P)  
 697 treatments and their interactions on PCA axes 1 and 2. Significant results are indicated in bold  
 698 and marginally significant in italics.

<i>Factors</i>	<i>PCA Axis 1</i>			<i>PCA Axis 2</i>		
	Df	F	P	Df	F	P
EN	2	2.46	<i>0.09</i>	2	1.50	ns
P	4	38.2	<b>&lt;0.001</b>	4	44.4	<b>&lt;0.001</b>
EN x P	8	0.50	ns	8	1.70	ns
Residuals	65			65		

699



700 **Table 3.** (a) Results of the two-way ANOVAs on the effects of the block (B), EN (Experimental  
701 Notch) treatments and their interactions on sand field surface and volume, (b) Results of linear  
702 regressions between dune morphological parameters and sand field surface and volume and (c)  
703 Results of two-way ANOVAs on the effects of the geomorphological block (B), EN  
704 (Experimental Notch) treatments and their interactions on foredune elevation, oceanward slope,  
705 width, transition dune elevation and elevation difference between foredune and transition dune.  
706 Significant results are indicated in bold and marginally significant in italics.

**a.**

<i>Factors</i>	<i>Sand deposition sheet surface</i>			<i>Sand deposition sheet volume</i>		
	Df	F	P	Df	F	P
B	3	3.11	ns	3	3.24	ns
EN	2	0.61	ns	2	0.57	ns
B x EN	6	0.37	ns	6	0.40	ns
Residuals	4			4		

**b.**

	F	P	R	F	P	R
Foredune elevation	0.11	ns	-0.08	0.05	ns	-0.06
Oceanward foredune slope	25.95	<b>&lt;0.001</b>	-0.81	26.13	<b>&lt;0.001</b>	-0.81
Transition dune elevation	0.67	ns	0.21	0.70	ns	0.22
Foredune width	9.02	<b>0.009</b>	0.63	10.42	<b>0.006</b>	0.65
Dz grey dune and foredune	0.85	ns	0.24	0.72	ns	0.22

**c.**

	<i>Oceanward foredune slope</i>			<i>Foredune width</i>		
	Df	F	P	Df	F	P
B	3	48.25	<b>0.01</b>	3	3.63	ns
EN	2	0.93	ns	2	0.25	ns

B x EN	6	2.27	ns	6	0.11	ns
Residuals	4			4		

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711 **Figure legends**

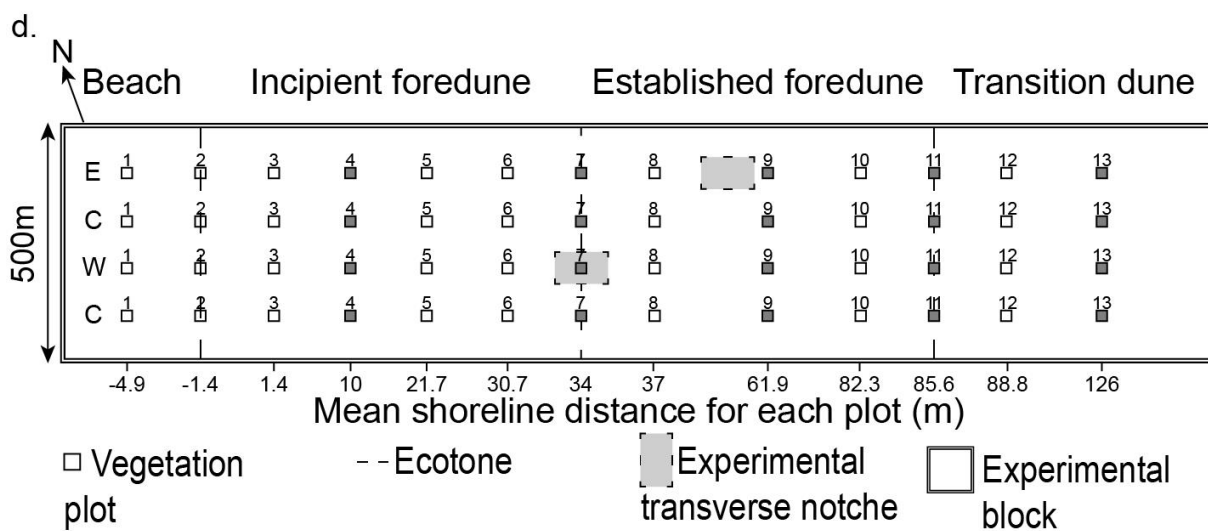
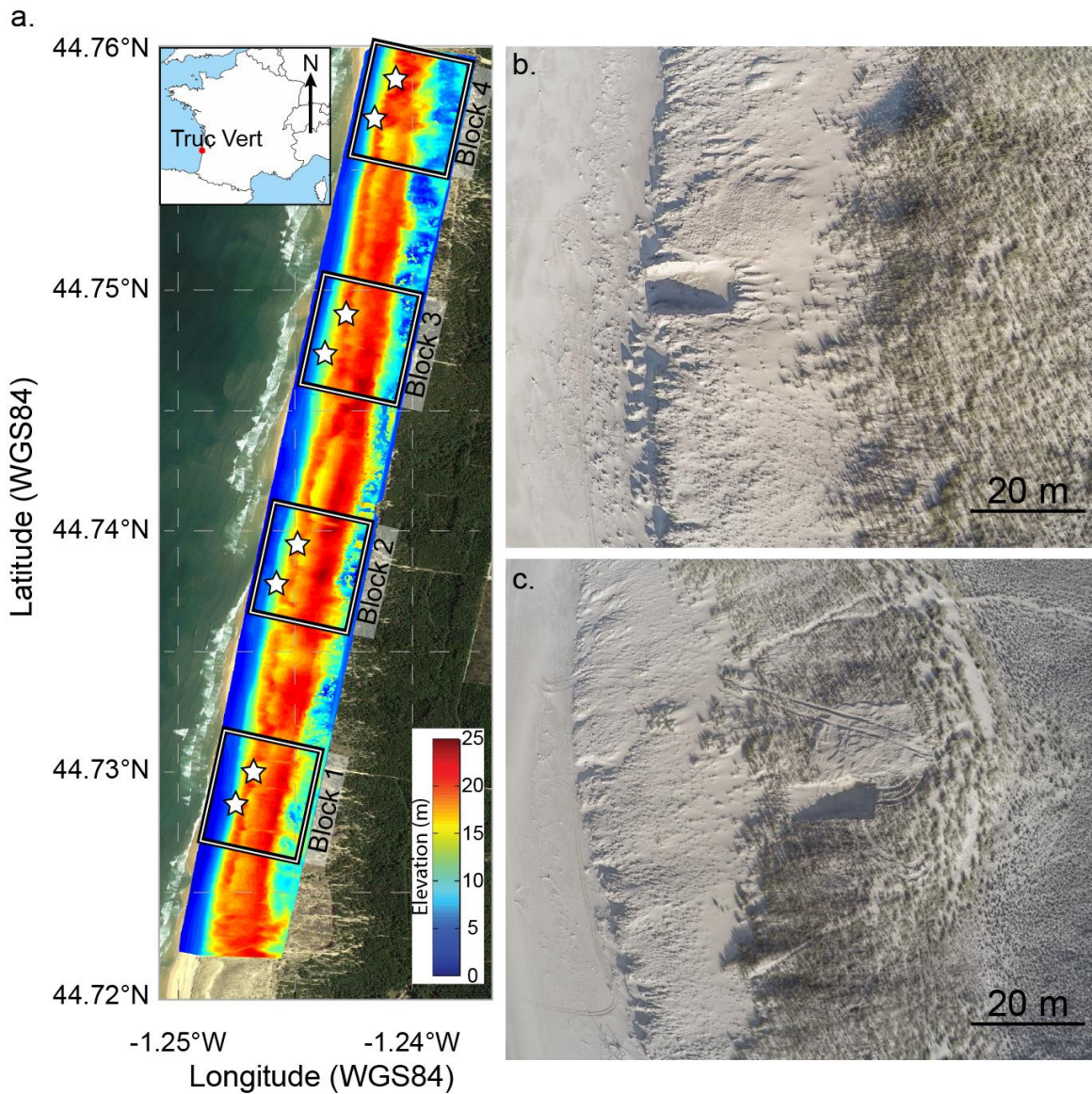
712 **Fig. 1.** (a) Truc Vert beach location map with a digital surface model showing the elevation.  
713 The solid rectangles represent the experimented blocks with the ENs (represented by white  
714 stars), (b) Aerial photography of EN in the incipient foredune of block 3 and (c) in the  
715 established foredune of block 2 and (d) Location of the quadrats (squares with numbers) though  
716 the four cross-shore transects with ENs (grey rectangles) in each block. The grey plots indicate  
717 the environmental measurement locations. The letter C, E and W correspond to the control, East  
718 EN and West EN treatments, respectively.

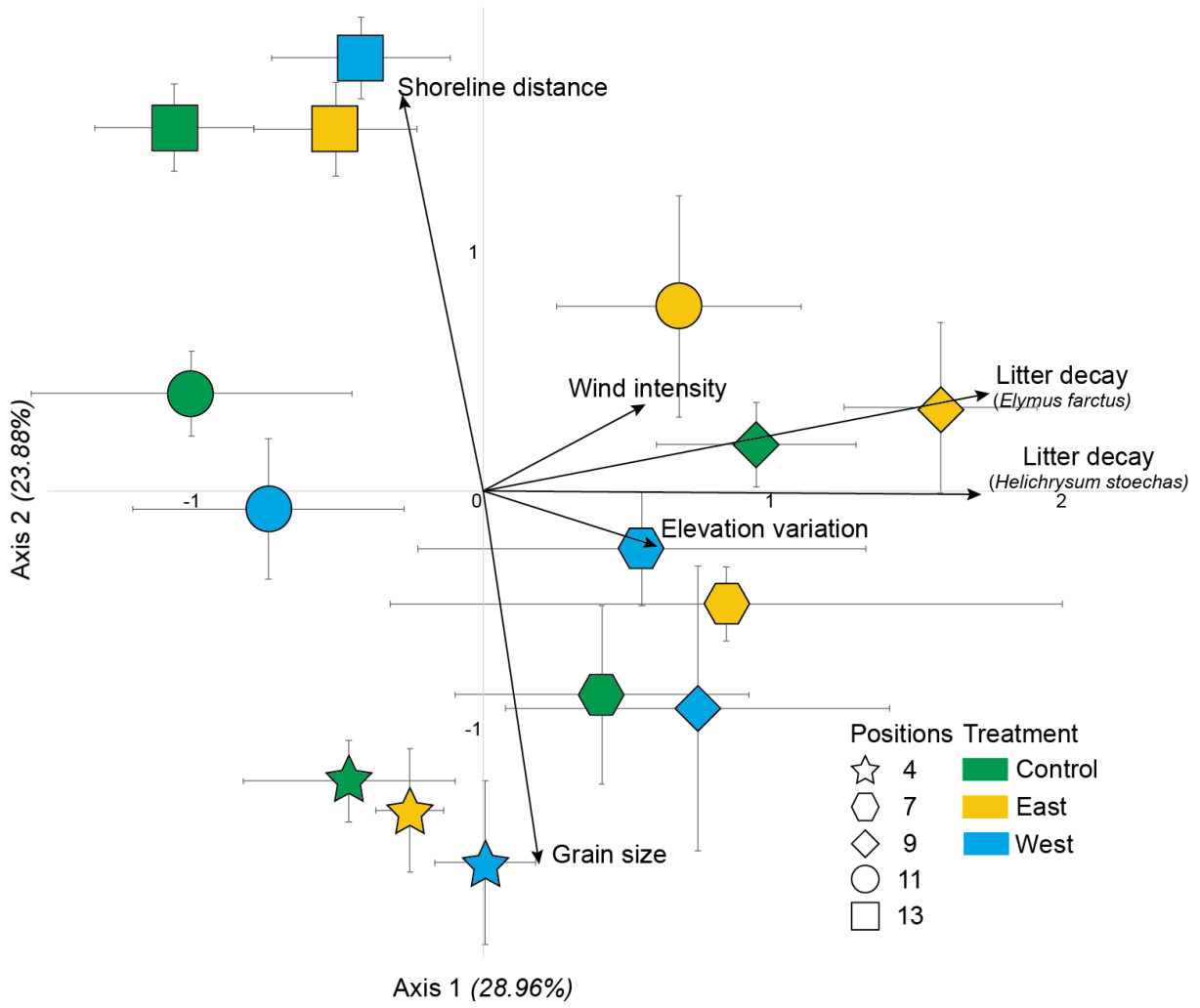
719  
720 **Fig. 2.** PCA results with mean quadrats scores ( $\pm$  SE, N = 8 for Control and 4 for East and West  
721 positions) on axis 1 and 2 for each treatment. Arrows represent correlations with environmental  
722 variables.

723  
724 **Fig. 3.** Mean elevation variation ( $\pm$  SE, N = 8 for Control and 4 for East and West positions)  
725 between December 2017 and May 2018 at each transect position of the three treatments. LSD  
726 test results of the position treatments are represented by capital letters. Sample t-test ( $p < 0.1$ ;  
727 \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ).

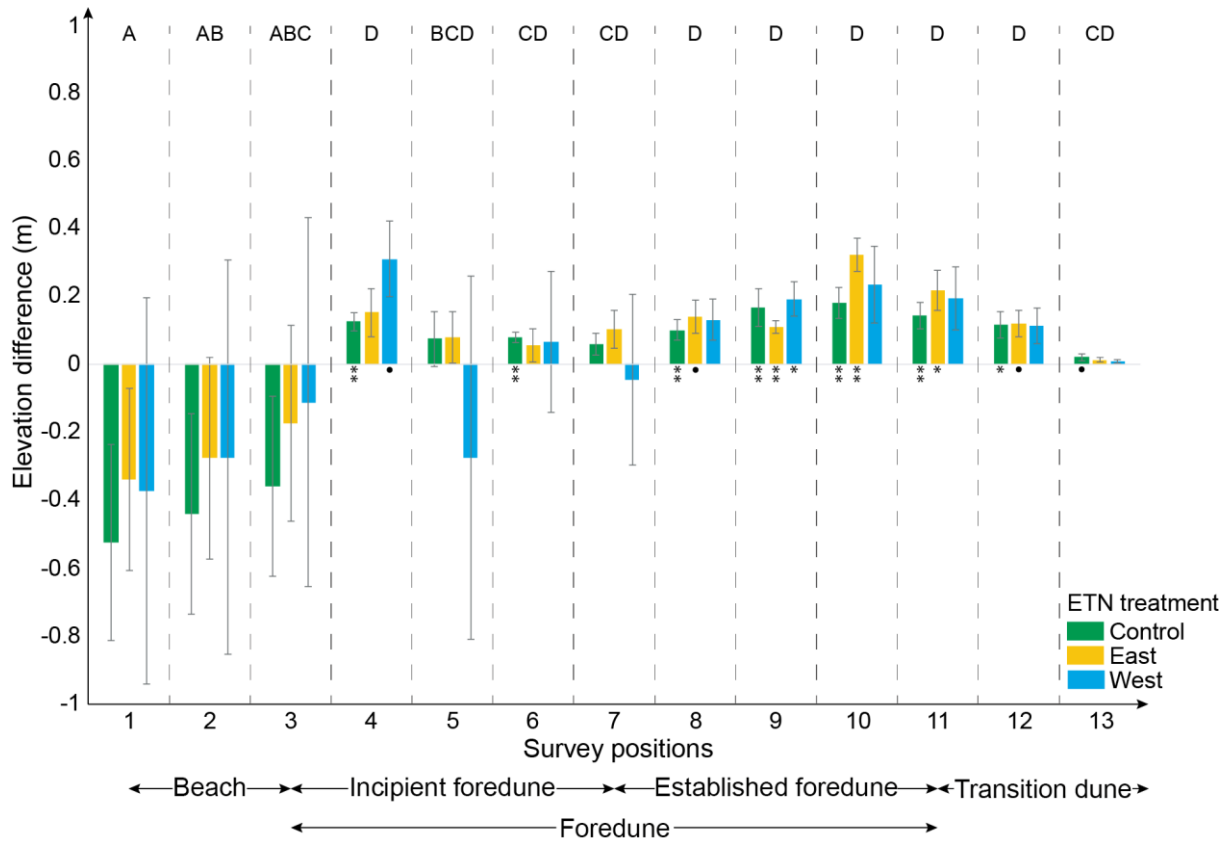
728  
729 **Fig. 4.** (a) CA 1-2 diagram for vegetation quadrats, (b) Mean CA axis 1 quadrat scores with  
730 their second-degree tendency curve in function of the shoreline distance.

731

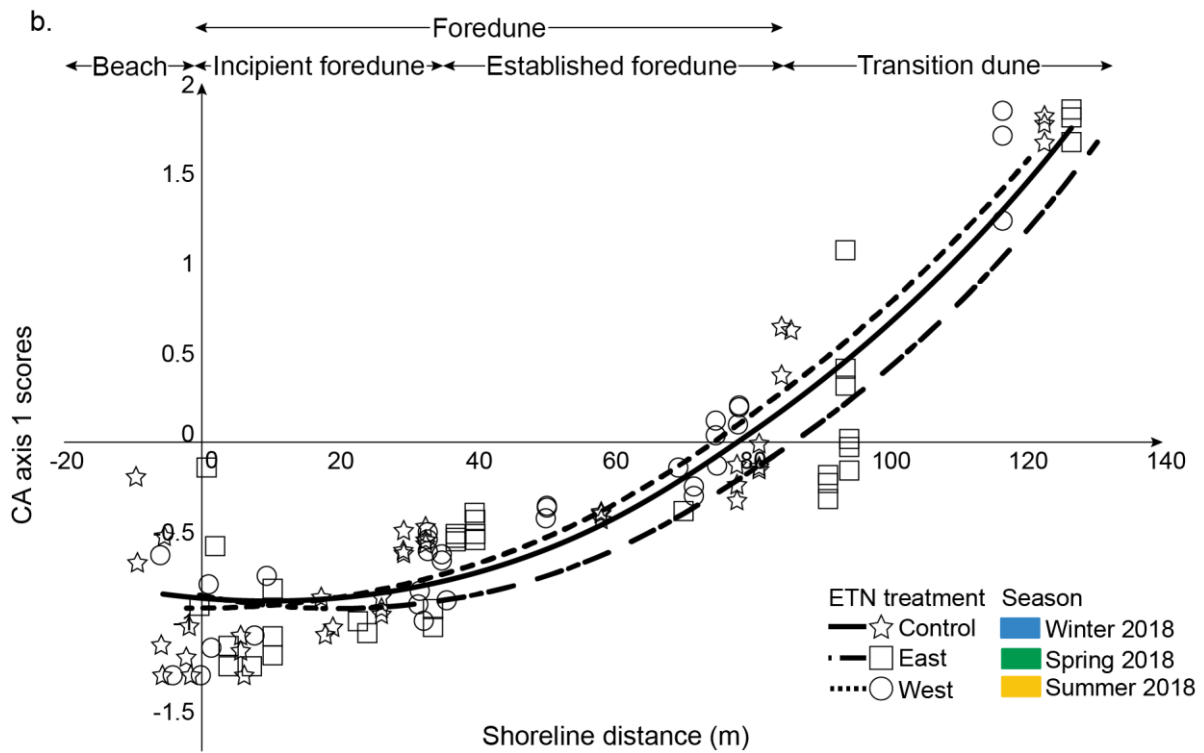
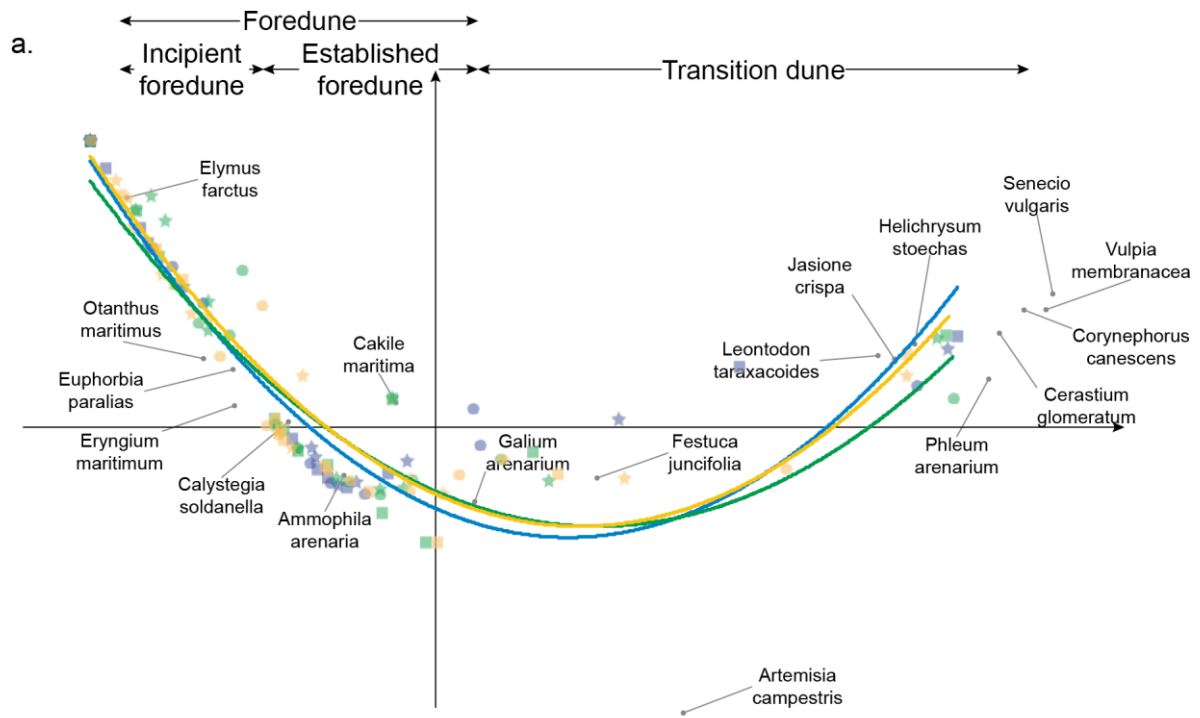




733



734



735



736 **Appendix legends**

737 **Appendix 1.** (a) Aerial photography of Truc Vert beach dune system performed by drone  
738 showing the different dune communities, (b) 4 km alongshore averaged beach dune profile at  
739 Truc Vert with (1) the oceanward foredune slope, (2) the foredune elevation, (3) the foredune  
740 width, (4) the transition dune elevation and (5) the elevation difference between the foredune  
741 and the transition foredune.

742

743 **Appendix 2.** Mean litter decomposition rate ( $\pm$  SE, N = 8 for Control and 4 for East and West  
744 treatments) for (a) *Elymus farctus* and (b) *Helichrysum stoechas* at the five specific transect  
745 positions in the three EN treatments. LSD test results for the position treatment are represented  
746 by capital letters. The litter bags in position 4 for control were all removed by the marine erosion  
747 during the violent winter storms.

748

749 **Appendix 3.** Mean median grain size ( $\pm$  SE, N = 8 for Control and 4 for East and West  
750 positions) at the five specific transect positions in the three EN treatments. LSD test results for  
751 the position treatment are represented by capital letters.

752

753 **Appendix 4.** Mean flag surface degradation ( $\pm$  SE, N = 8 for Control and 4 for East and West  
754 positions) at the five specific transect positions in the three EN treatments. LSD test results of  
755 the position treatment and the position X EN treatment interaction are represented by capital  
756 and lower case letters, respectively.

757

758 **Appendix 5.** (a) Orthophoto of the entire 4-km study area of Truc Vert beach dune system on  
759 13 March, 2018. The black dotted lines represent the cross short transects. The three black  
760 squares show locations of the most important sand deposition sheets which are zoomed in 3D

761 textured Digital Surface Model (performed by UAV photogrammetry processes) for (b) the  
762 block 3, (c) the block 2 and (d) south to the block 1.

763

764 **Appendix 6.** Results of the ANCOVA on the effects of the block (B), EN (Experimental  
765 Notch), distance (D), quadratic distance ( $D^2$ ), season (S) and their interaction on CA axes 1 and  
766 2 scores. Significant results are indicated in bold and marginally significant in italics.

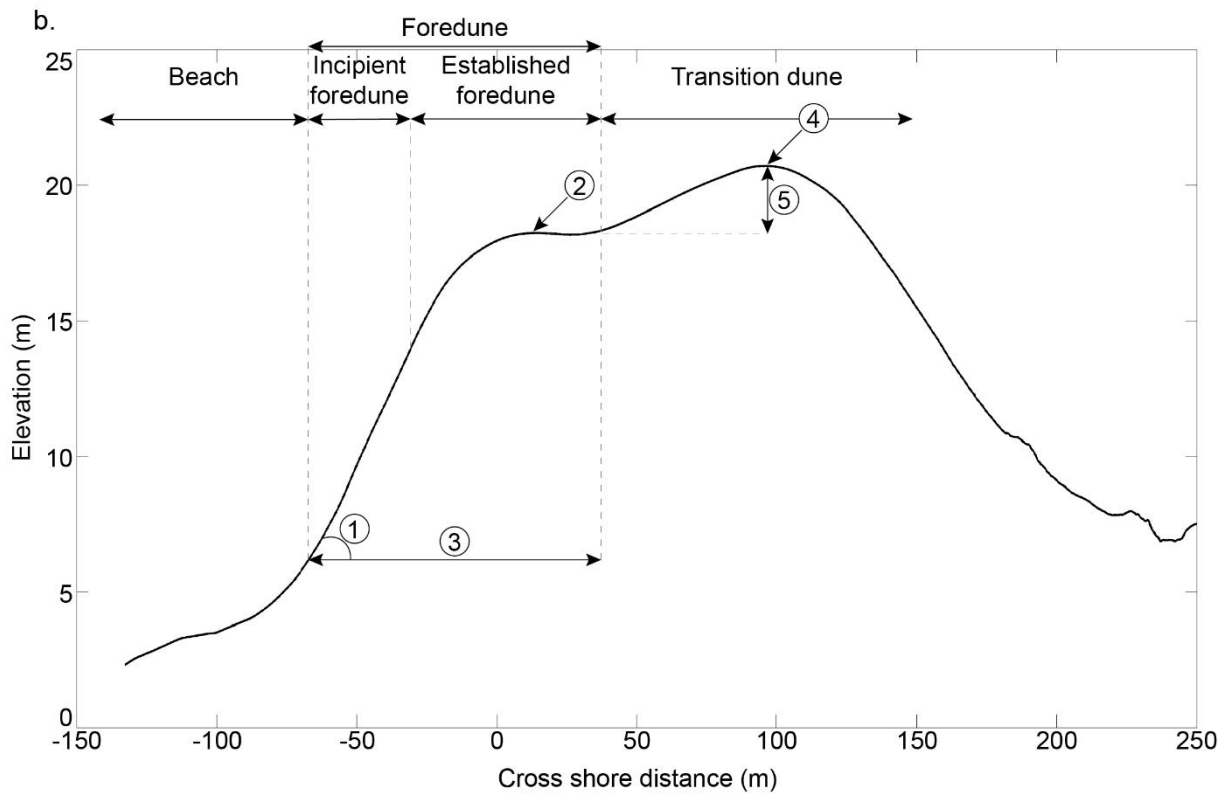
767

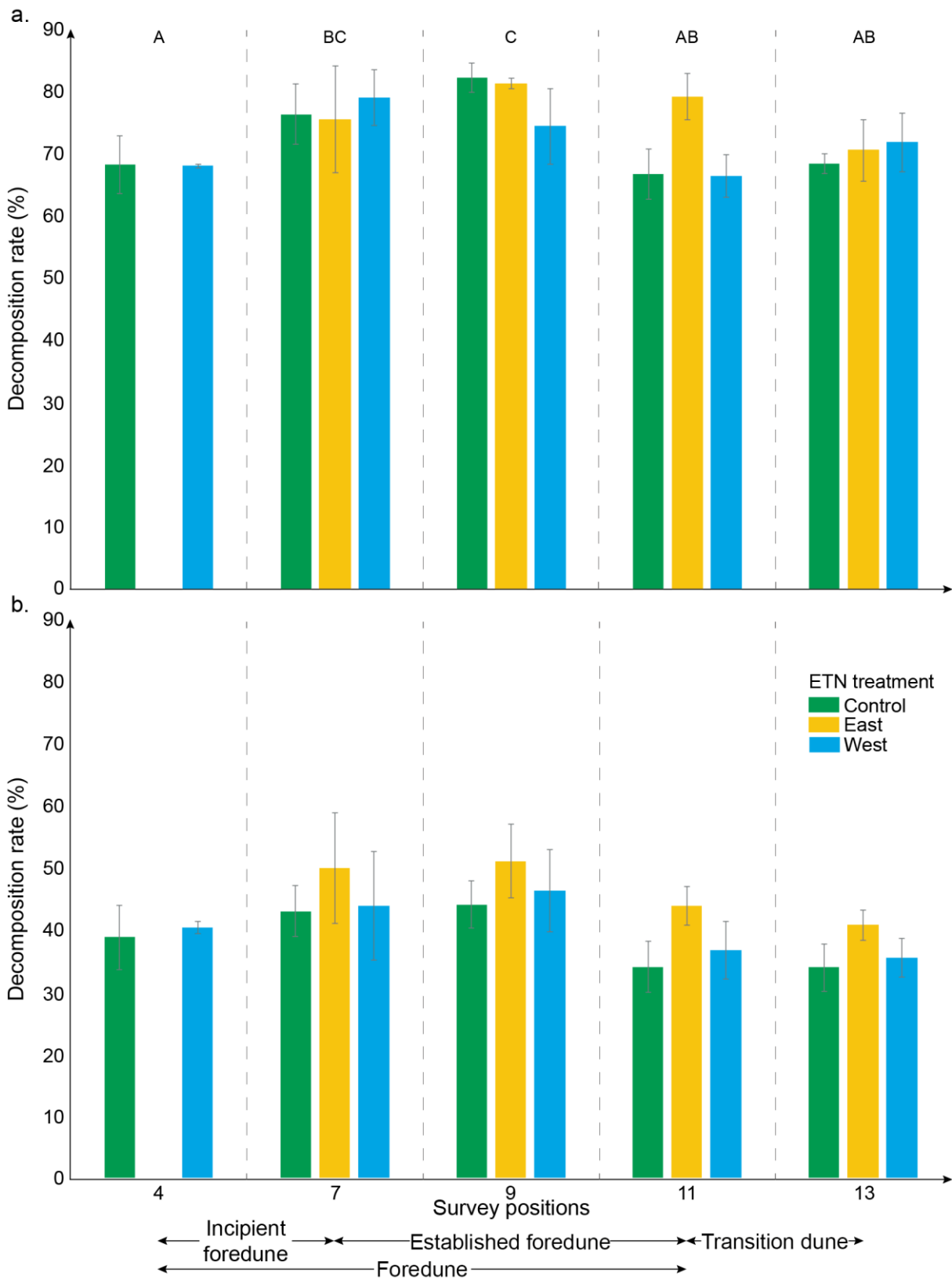
768 **Appendix 7.** CA axis 1 quadrat scores as a function of the shoreline distance for the three EN  
769 treatments in the four blocks.

a.

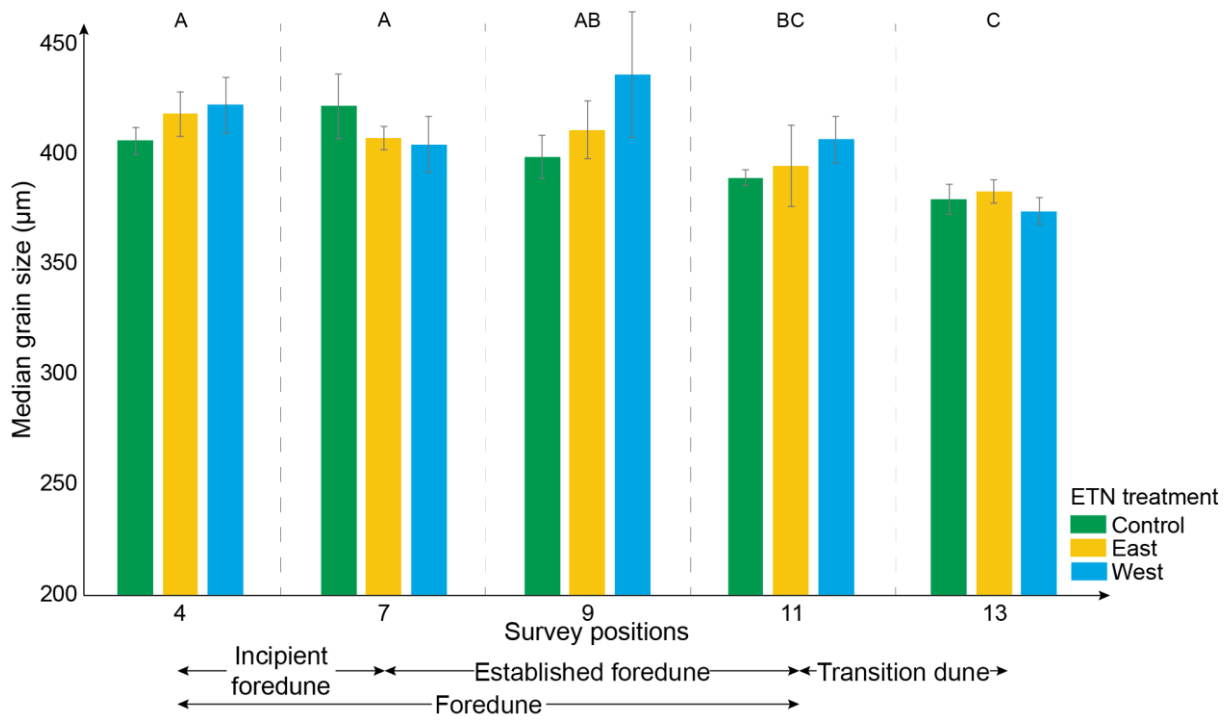


b.

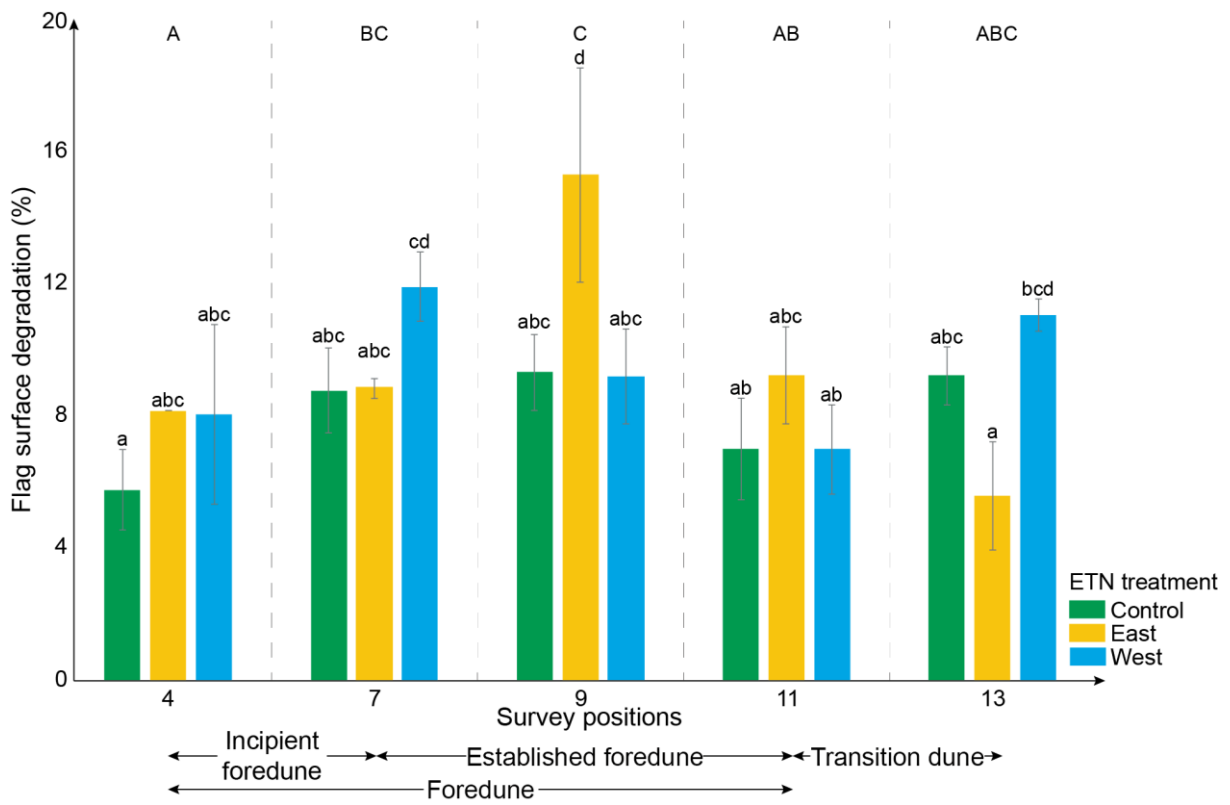


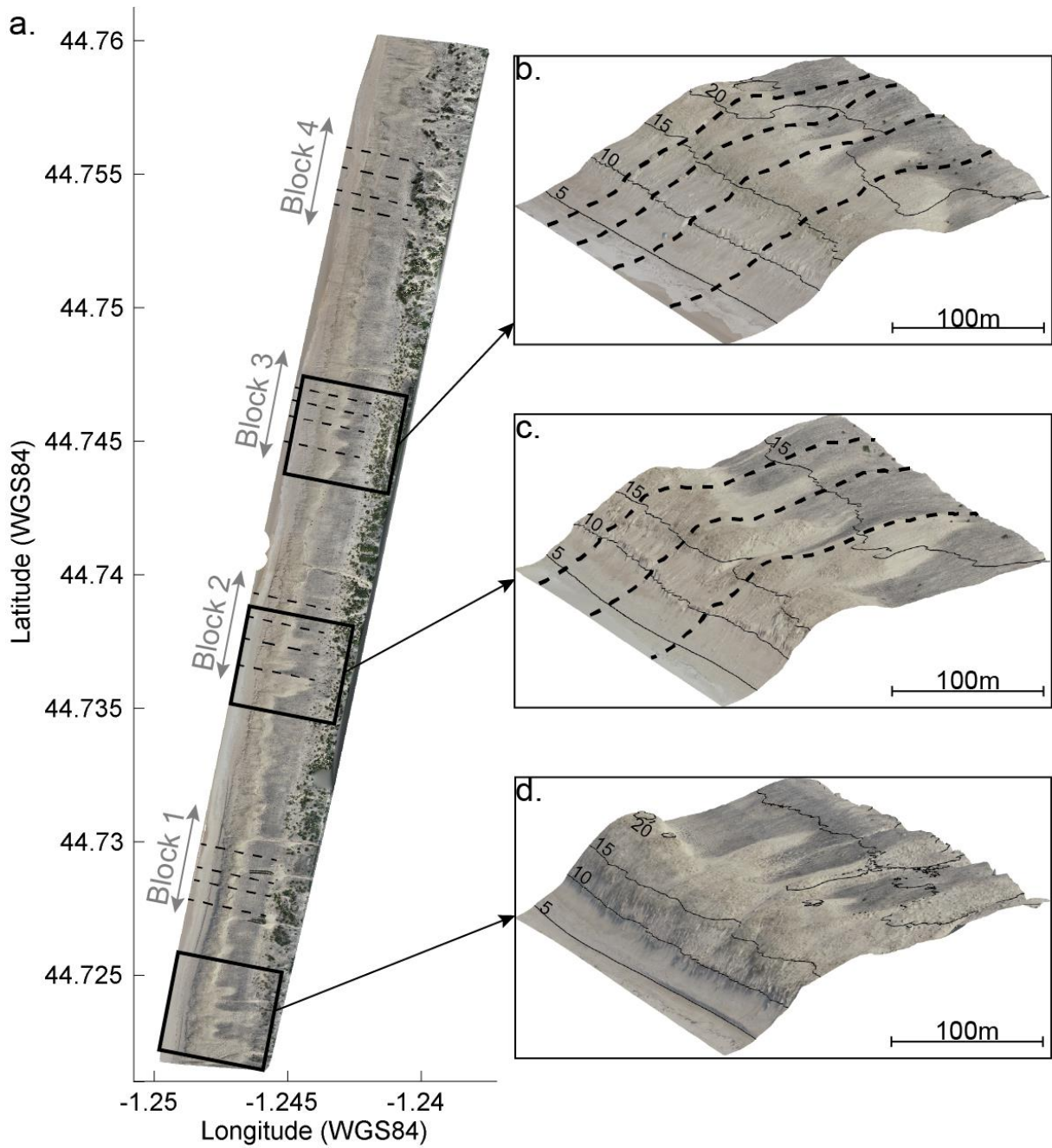


774 Appendix 3.



775





<i>Factors</i>	<i>CA Axis 1</i>			<i>CA Axis 2</i>		
	Df	F	P	Df	F	P
B	3	50.15	< <b>0.001</b>	3	10.98	< <b>0.001</b>
EN	2	8.79	< <b>0.001</b>	2	0.73	ns
D	1	1.77	ns	1	458.21	< <b>0.001</b>
D <sup>2</sup>	1	173.14	< <b>0.001</b>	1	317.83	< <b>0.001</b>
S	2	0.03	ns	2	4.95	<b>0.007</b>
B x EN	6	5.95	< <b>0.001</b>	6	1.23	ns
B x D	3	7.70	< <b>0.001</b>	3	2.98	<b>0.031</b>
B x D <sup>2</sup>	3	5.27	<b>0.001</b>	3	4.39	<b>0.005</b>
B x S	6	0.43	ns	6	0.06	ns
EN x D	2	2.27	ns	2	2.96	<i>0.053</i>
EN x D <sup>2</sup>	2	0.58	ns	2	2.75	<i>0.065</i>
EN x S	4	0.24	ns	4	0.57	ns
D x S	2	1.44	ns	2	0.94	ns
D <sup>2</sup> x S	2	1.38	ns	2	0.79	ns
B x EN x D	6	2.24	<b>0.039</b>	6	1.81	<i>0.097</i>
B x EN x D <sup>2</sup>	6	2.07	<i>0.056</i>	6	1.54	ns
B x D x S	6	0.72	ns	6	0.49	ns
B x D <sup>2</sup> x S	6	0.58	ns	6	0.22	ns
B x EN x S	12	0.16	ns	12	0.35	ns
EN x D x S	4	0.74	ns	4	0.71	ns
EN x D <sup>2</sup> x S	4	0.97	ns	4	0.76	ns
B x EN x D x S	12	0.89	ns	12	1.25	ns
B x EN x D <sup>2</sup> x S	12	0.73	ns	12	0.98	ns
Residuals	349			349		



