1   **Biomorphogenic feedbacks and the spatial organisation of a dominant grass steer dune**
2   **development**

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Abstract

21 Nature-based solutions to mitigate the impact of future climate change depend on restoring biological
22 diversity and natural processes. Coastal foredunes represent the most important natural flood barriers
23 along coastlines worldwide, but their area has been squeezed dramatically because of a continuing
24 urbanisation of coastlines, especially in Europe. Dune development is steered by the development of
25 vegetation in interaction with sand fluxes from the beach. Marram grass (*Calamagrostis arenaria*,
26 formerly *Ammophila arenaria*) is the main dune building species along most European coasts, but also
27 in other continents where the species was introduced. Engineering of coastal dunes, for instance by
28 building dunes in front of dikes, needs to be based on a solid understanding of the species' interactions
29 with the environment. Only quantitative approaches enable the further development of mechanistic
30 models and coastal management strategies that encapsulate these biomorphogenic interactions. We
31 here provide a quantitative review of the main biotic and physical interactions that affect marram grass
32 performance, their interactions with sand fluxes and how they eventually shape dune development.
33 Our review highlights that the species' spatial organisation is central to dune development. We further
34 demonstrate this importance by means of remote sensing and a mechanistic model and provide an
35 outlook for further research on the use of coastal dunes as a nature-based solution for coastal
36 protection.

37 Keywords: Nature-based solution, dune, coastal safety, ecological feedbacks, cover, spatial configuration,
38 synthesis, model, remote sensing

I.   Introduction

As climate change induces sea level rise and possibly heavier storms, coastal protection is in a transition phase from hard structural engineering towards soft measures that can adapt dynamically to a changing environment (Borsje et al., 2011; IPCC, 2014, 2018; Vousdoukas et al., 2018). Ecosystem-based approaches complementing engineering with functional parts of the natural system provide such an alternative to conventional coastal defense ('hard engineering'). Indeed, estuarine and coastal soft sediment systems are dynamic by nature and their inherent ecological processes may be exploited to enhance resilience (Temmerman et al., 2013). Coastal foredunes represent the most important natural flood barrier for much of the European coastline and 30% of all shorelines worldwide (Martinez and Psuty, 2004; Reijers et al., 2019). In contrast to urban and other infrastructure, coastal dunes have the capacity to grow with rising sea level due to interactions between plant growth (Duarte et al., 2013) and aeolian sediment supply (de Vries et al., 2012; Strypsteen et al., 2019a). Therefore, they are currently considered as an important nature-based solution for coastal protection (Borsje et al., 2011; Duarte et al., 2013; Temmerman et al., 2013).

The use of foredunes as an engineering tool cannot be achieved without a deep understanding of the organizational properties of the natural dune system. Coastal dunes develop in first instance by sand accretion at the upper beach. In regions with predominant onshore winds, the magnitude of aeolian sand flux can primarily be described as a function of wind speed and grain size, but it also depends on soil moisture content, fetch length, beach and dune morphology (Delgado-Fernandez 2010, de Vries et al. 2012, Strypsteen et al. 2019). These aeolian fluxes impact the performance of a keystone species in foredunes from the European Atlantic coast : marram grass (*Calamagrostis arenaria (L.) Roth*, formerly *Ammophila arenaria;* Huiskes 1977). The species is the dominant species from white dunes, as protected within the directive 92/43 EEC [Shifting dunes along the shoreline with *Ammophila arenaria*, code 2120] (Perrino et al. 2014, European Commission 2007).

Biomorphogenesis refers to the process where biota like plants but also animals induce changes in the form of the environment they live in. Marram grass is such as an engineering species (Bakker, 1976; Puijenbroek et al., 2017) as its growth and performance depends on, and in turn influences, aeolian sand fluxes and hence, dune development (Hesp, 2002; Zarnetske et al., 2015; Strypsteen et al., 2019). Phenomena where the value of one state variable directly or indirectly affects the sign, direction and rate at which that variable changes, is defined as a feedback (Maxwell et al., 2017). These feedbacks can be positive (self-amplifying) or negative (self-dampening). As soon as sand dynamics cease, marram grass starts to lose its vigour and declines in abundance, making way for the development of grey dunes [called "Fixed coastal dunes with herbaceous vegetation (grey dunes)" code 2130* (European Commission 2007)] the next stage in the vegetation succession, dominated by drought tolerant mosses (Fig. 1). The degeneration of marram grass by sand stabilization was already noted by Marshall (1965), who called this phenomenon "The *Ammophila* problem" (not to be confused with the "Ammophila problem" referring to the invasion of the species outside its natural range as mentioned by e.g., Wiedemann & Pickart (1996).

The extraordinary sand fixing capacity of marram grass has been recognized in northwestern Europe for many centuries. *C. arenaria* was introduced for dune fixation in different parts of the world such as North America (Buell et al. 1995), Chile (Castro 1988), South Africa (Hertling & Lubke 1999), New Zealand (Hilton et al. 2004) and Australia (Webb et al. 2000). We here review the current state of the art with respect to the species' biotic and abiotic drivers of performance (Part II). We subsequently review the quantitative evidence of feedbacks with sand dynamics and demonstrate by both a new model and remote sensing how marram grass spatial configuration affects dune development (Part III). We end this review by an outlook towards further research.
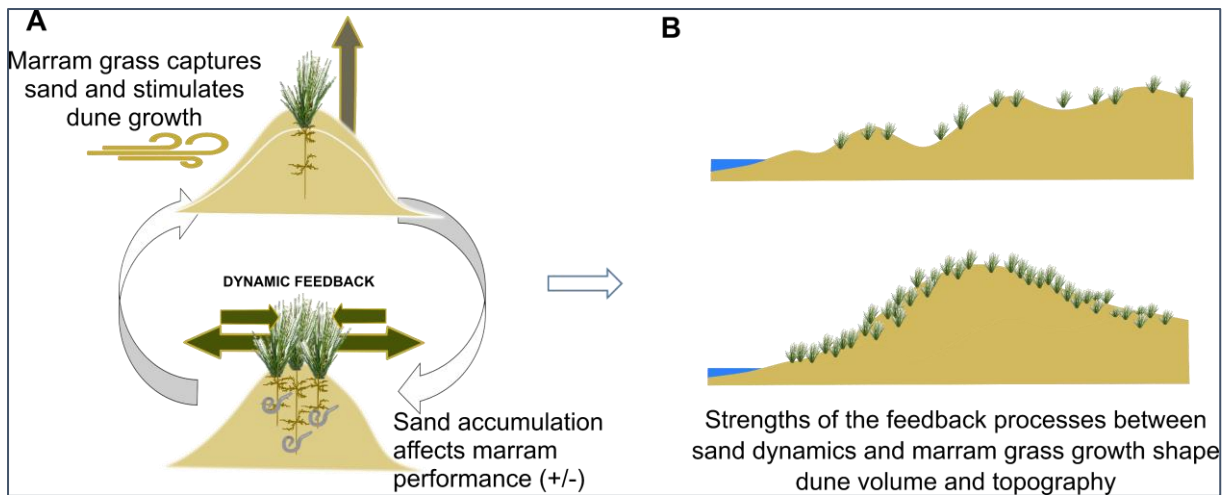
Figure 1. Conceptual figure on the role of marram grass as an engineer in foredune formation. A. Once established, the species' sand capture ability shapes local sand accumulation, leading to an increase in dune volume. This sand accumulation will promote the species' growth, unless burial is too severe. If sand accumulation ceases, either due to decreased input from the sea, or to sheltering effects from surrounding vegetation, the plant performance will decrease due to pathogen accumulation in the roots, after which marram grass will degenerate. B. These dynamic feedbacks depend on the species' spatial configuration and external environmental conditions and will eventually shape the development of its volume and form, and, hence, its stability and resilience against storm surges under climate change.

II. Abiotic and biotic drivers of marram grass performance

II.1 Abiotic drivers of marram grass performance

II.1.1. marram establishment

Marram grass establishes through seed germination or shooting of rhizome fragments detached from tussocks by coastal erosion. Konlecher & Hilton (2009) showed the potential for marine dispersal of such rhizome fragments over hundreds of kilometres, depending on regional sea currents. Seeds are mainly dispersed by wind, although the species only shows week morphological adaptations to wind dispersal (Huiskes 1979). Dispersal experiments by Pope (2006) and McLachlan (2014) suggest that a large majority of the seeds end up within a distance of less than 1 meter from the parent plant and wind dispersal abilities are probably restricted to several tens of meters. The potential for seed establishment of *Calamagrostis arenaria* is very high. First, this is due to a substantial seed production. Salisbury (1952) estimated over 20 000 caryopses are formed yearly per plant tussock. Second, marram grass has a long-lived seedbank. Viable seeds of up to 21 years old were recovered (Hilton et al. 2019). Third, the germination potential is high. Experiments under optimal laboratory conditions yielded germination percentages between 82 and 94% (Huiskes et al. 1979; Van Der Putten 1990, Bendimered et al. 2007, Lim 2011). In the field however, the establishment success of *C. arenaria* from seed is reputed to be very low on average (Huiskes 1977), although locally frequent germination (has been)/was observed in coastal dunes in The Netherlands (Van Der Putten 1990), New Zealand (Esler 1974) and North-America (Wiedemann 1987). Frequent establishment of marram is observed in embryonic foredunes and damp dune slacks (authors' personal observations). Seed germination strongly decreases with sand burial (Van der Putten 1990, Lim 2011, McLachlan 2014). Seedling emergence decreases linearly with burial depth, with a 3 cm burial already resulting in a germination reduction of 60% and no more seedlings emerge when seeds are buried under 9cm of sand; Fig. 2). The results we obtained from a burial experiment (See Supplementary material 1) are very similar to the findings of Lim (2011).

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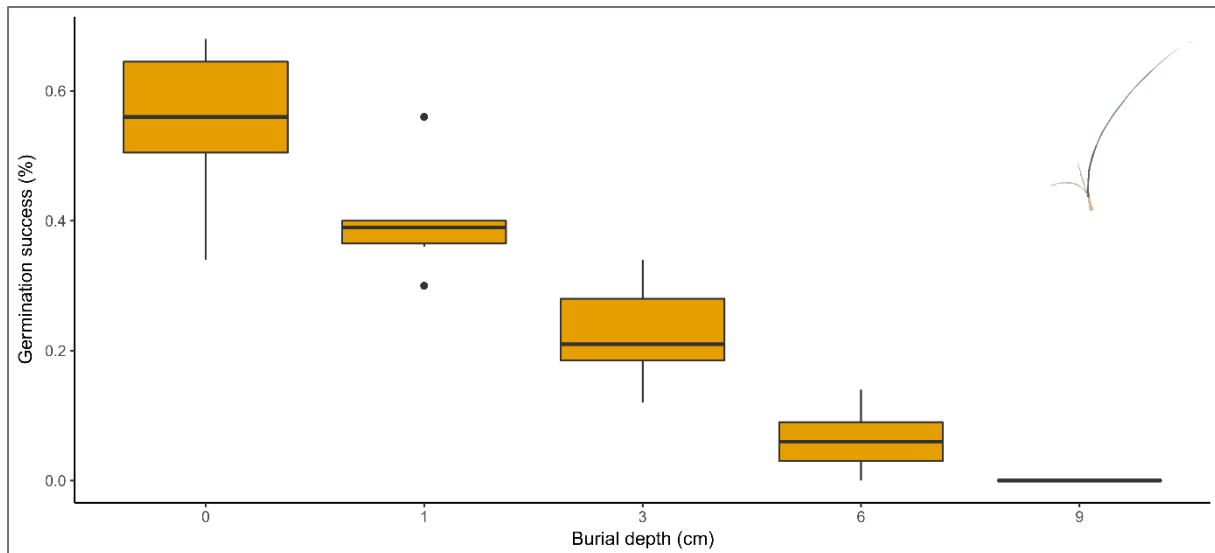
Figure 2. Seedling emergence in relation to sand burial (see supplement1)

125 Huiskes (1977) and Van Der Putten (1990) showed that the highest germination rates are obtained
126 with a fluctuating (day/night) temperature regime and a day temperature exceeding about 20°C. These
127 results are enhanced by stratification (cold pre-treatment). Optimal germination was obtained with a
128 20/30°C night/day temperature, with germination inhibited at lower temperatures of 10/20°C
129 night/day. These germination requirements retrieved in the lab correspond well with observations of
130 seeds germination in spring, when the temperature has risen sufficiently. Germination occurs only
131 under moist conditions (Huiskes 1979) and is inhibited when salinity exceeds 9 g/l (Chergui et al. 2013).
132

133 II.1.2. Marram growth and survival
134 Once established, marram grass growth and survival depends largely on the exposure of its local
135 environment for the physical forces of wind and water, that can directly dislodge plants or indirectly
136 affect growth and survival by transporting sediment. Partial burial of seedlings resulted in a 50-60%
137 increase of shoots length and root dry mass, but this vertical growth increases at the expense of lateral
138 growth and overall shoot biomass (number of tillers, which was maximal at 0-40% burial of the shoot
139 height) (Ievinsh and Andersone-Ozola, 2020). *C. arenaria* biomass increase showed a parabolic
140 response to burial with optimal growing performance at burial rates of 31 cm of sand per growing
141 season. (Nolet et al. 2018). The tolerance for burying was estimated to 78 to 96 cm burial/year. Reijers
142 et al. (2021) found more mature tussocks (clonal fragments containing ± 8 shoots) to perform equally
143 well under 0 or 2 cm burial every two weeks, but high mortality when burial reached 4 cm. Sediment
144 burial also indirectly influence marram grass growth by protecting the plants against the detrimental
145 effects of coastal flooding. Higher and larger embryo dunes are less susceptible to erosion during the
146 winter storm season, which positively influences marram grass growth during summer (Van
147 Puyenbroek et al. 2017).

148 Besides exposure to physical forces, soil nutrient levels can have a large influence on marram grass
149 performance as well. In general, sandy coastal systems are nutrient-limited and *C. arenaria* can cope
150 with these nutrient-poor conditions through symbiosis with arbuscular mycorrhizal fungi and by
151 recycling its own plant material through slow decomposition (Kowalchuk et al. 2002, Reijers et al.
152 2020).

153 Despite its occurrence in nutrient-limited conditions, *C. arenaria* requires substantial
154 levels of nitrogen, phosphorus and potassium for good growth (Willis 1965). A higher availability of N
155 and P in lime- and iron-poor dunes, due to atmospheric deposition, has been proposed as a mechanism
156 of the species' local expansion in coastal dunes (Kooijman et al., 1998; Kooijman and Besse, 2002).

157 Increases in temperature, nutrients and precipitation stimulate vegetation growth and lead to a global
158 greening of coastal dunes (Jackson et al., 2019). This global greening affects the natural sediment-
159 sharing capacity of coastal dunes, by hampering sediment transport to the hinterland (Gao et al. 2020).
160 Reduced sediment mobility and dune stabilization are thought to threaten several ecological functions,
161 while it can increase the protective function of coastal dunes by lowering erosion susceptibility
162 (Delgado-Fernandez et al. 2019, Gao et al. 2020, Pye & Blott 2020).

163

164 *II.2 Biotic constraints on marram grass performance*
165 II.2.1. Negative plant-soil feedback
166 Marram grass was found to perform worse in its own rhizosphere soil than in either sand from the sea
167 floor or in sterilized soil from its own rhizosphere (van der Putten et al. 1988, 1993), demonstrating
168 that a biotic factor in the soil causes a decline in marram grass performance. The exact cause of this
169 biotic control is to date unclear. The first studies attempting to pinpoint the soil organisms causing the
170 decline of marram grass implicated root-feeding nematodes as well as pathogenic fungi (Van der
171 Putten et al. 1990, De Rooij and van der Goes 1995, van der Putten and van der Stoel 1998, van der
172 Stoel and van der Putten 2002). However, the exact species causing a performance reduction could
173 not be identified across these studies. Competitive and facilitating interactions among these co-
174 infecting belowground parasites (Brinkman 2005&a,b,c) but also more complex trophic interactions,
175 including those with microbes within the rhizosphere (Piśkiewicz et al. 2008, 2009; Costa et al. 2012)
176 were found to be mediators of marram performance under experimental conditions. Furthermore, it
177 has been shown that the negative effect of certain nematode species can be mitigated by the positive
178 effect of mycorrhizal and endophytic fungi (Little and Maun 1996, de la Peña et al. 2006, Hol et al.
179 2007). Overall, the net effect on marram grass performance of all naturally occurring members of the
180 soil community is generally negative. Although the exact mechanism is difficult to identify, evidence
181 for the "escape hypothesis" remains strong, i.e., marram grass needs regular burial by wind-blown
182 sand free of soil organisms so that it can grow new roots into an –at least temporarily– enemy-free
183 space. Plant-soil feedbacks caused by other plant species also play a role. Conditioning of soils by
184 *Carpobrotus edulis* (L.) N.E.Br., a species originating from South Africa and one of the most invasive
185 plant species in the Mediterranean, suppresses marram grass biomass and in some cases survival rate
186 (de la Peña et al. 2010). The increase of *Carpobrotus* in the dunes of central Italy (Sperandii et al. 2018)
187 has therefore been linked to large-scale decreases in marram grass. Marram grass also shows a
188 reduced germination on soil invaded by *Acacia longifolia* (Andrews) Willd., yet it performed better on
189 invaded than native soil after 12 weeks of growth (Morais et al. 2019).

190

191 II.2.2. Aboveground biotic interactions
192 The aboveground organisms associated with marram grass are in general well known (i.e., Huiskes
193 1979, Heie 1982, 1986, Holman 2009, Vandegehuchte et al. 2010a), but very little is known about their
194 effects on plant performance. The associated herbivore species have the potential to induce serious
195 reductions in aboveground performance in a controlled environment (Balachowsky and Mesnil 1935,
196 Nye 1958, Heie 1986, Vandegehuchte et al. 2010a), but so far no experiments were conducted in
197 nature. Marram grass does not seem to be controlled to any significant extent by mammalian grazers
198 either (Badhresa 1977, Huiskes 1979), except for some feeding on young shoots (Rowan 1913). Seed
199 predation has been observed (Huiskes 1979) but its magnitude and/or impact on marram grass
200 demography is unknown.

201

202 II.2.3. Control of above- and belowground communities by marram grass intraspecific variation
203 Intraspecific variation among marram grass populations can have strong effects on the abundance and
204 community composition of both above- and belowground invertebrate species (Vandegehuchte et al.
205 2011). This variation is linked to genetic variation in plant growth, which likely explains higher

206 abundances of aboveground invertebrates on local than on non-local marram grass populations.
207 Contrasting effects were found for root herbivores as their abundance and species richness negatively
208 covaried with the aboveground ones (Vandegehuchte et al. 2011, 2012). Additionally, it has to be
209 noted that a full soil biota community can have stronger effects on marram grass performance than
210 local abiotic soil properties (Vandegehuchte et al. 2010c), although performance can differ significantly
211 among soils differing substantially in abiotic properties. The relationships between marram grass and
212 its aboveground invertebrates can therefore not be understood independently of its belowground
213 invertebrates and the abiotic conditions of the soil.
214
215

216 II.2.4. Learning from elsewhere: marram grass as invasive species
217 Explanations for success of marram grass in its novel range have been sought in the popular "enemy
218 release hypothesis" (Keane and Crawley, 2002), mainly focusing on belowground enemies. Growth of
219 marram grass was significantly less reduced on soils from South African sites than on soils from the
220 Netherlands, indicating a weakened negative plant-soil feedback and thus potential role for enemy
221 release in South African soils (Knevel et al. 2004). However, this contrasts with findings from coastal
222 dunes of California, where soil sterilization experiments have shown that the performance of marram
223 grass is reduced to similar extents as in Europe when grown on non-sterilized soil (Beckstead and
224 Parker 2003), suggesting there is no enemy release. Furthermore, soil biota from three native South
225 African plant species did not suppress marram grass growth, but biota from soils beneath the tropical
226 cosmopolitan dropseed *Sporobolus virginicus* (L.) Kunth did, suggesting that this plant species may
227 confer biotic resistance against invasion by marram grass (Knevel et al. 2004). A large sampling
228 campaign of soil and roots from Tasmania, New Zealand, South Africa and the west coast of the USA
229 revealed that marram grass did not have fewer root-feeding nematode taxa in these regions than in
230 its native range. However, native plants in the novel range had more specialist root-feeding nematode
231 taxa than marram grass, while specialists such as cyst and root-knot nematodes, which are common in
232 the native range of marram grass, were not found in the southern hemisphere (van der Putten et al.
233 2005). Invasiveness of marram grass thus seems correlated with an escape from specialized root-
234 feeding nematodes.

235

236 *II.3. Dynamic feedbacks between aeolian fluxes and vegetation development*
237 The capture rates of sand by vegetation and its effect on dune topography have been intensely studied
238 (e.g., Hesse & Simpson 2006). There is also abundant literature on how obstacles that represent
239 vegetation obstruct or facilitate sand fluxes, with strong analogies to research on fluid dynamics.
240 Typically, multiple configuration of height and density of the obstacles are used (e.g., reed stems (Arens
241 et al., 2001); see (Mayaud and Webb, 2017) for a comprehensive review on aeolian sand transport in
242 drylands). These studies quantify how much of the total force of the wind by drag is reduced by the
243 vegetation, also referred to as shear stress partitioning and expressed as drag coefficients (Raupach,
244 1992). All studies show this drag coefficient to be positively related to the roughness induced by the
245 density and impermeability of the set of obstacles, and their height (Hesp et al., 2019). Since these
246 experiments use marram-grass surrogates like artificial cylinders, stem bundles or even dead plant
247 material, they do not represent the realised morphology of dune vegetation, which precludes further
248 progress in understanding the feedbacks between sediment capture and plant growth. Clusters of
249 tillers enhance sand deposition by lowering wind speed and associated shear stress within the
250 vegetation canopy (Charbonneau & Casper 2018). Larger tussocks are able to capture more sand,
251 thereby imposing a positive feedback on their own development and vigour. The plants react to burial
252 by rapid production of elongated stem internodes, but the exact extent of this growth response is
253 unknown except for young plants under lab conditions (Levinsh and Andersone-Ozola 2020). As sand
254 burial induces the production of high-density vertical tillers and horizontally expanding rhizomes
255 (Reijers et al., 2021), marram grass steers dune morphology (van der Putten et al. 2005, Hart et al.

256 2012, Darke et al. 2016). *C. arenaria* is, because of this growth strategy, associated with the
257 development of higher and steeper dunes compared to those formed by its North-American sister
258 species *C. breviligulata*, making dunes build by the former potentially more resistant to erosion
259 (Zarnetske et al., 2012; Seabloom et al., 2013; Charbonneau et al., 2016).

260 Both vertical and horizontal growth responses influence the size and shape of *C. arenaria* tussocks, but
261 also directly determine remaining sand drift at the rear side of these vegetated patches (Reijers et al.,
262 2021). With increasing densities and cover, *C. arenaria* subsequently stabilizes the mobile sand
263 (Huiskens 1979). At least in European coastal dunes, the ceasing sand fluxes mediated by the species'
264 increasing densities, and the resulting increases in dune height and slope, then induce on longer time
265 frames a negative feedback on the species' vigour in the long run, causing the species to slowly die off
266 (e.g., Van der Putten 1994, De Rooij and Van der Goes 1995, van der Putten and van der Stoel 1998,
267 van der Stoel and van der Putten 2002) as the resource (fresh sand) becomes limiting. The spatial
268 configuration and morphology of the vegetation is therefore dynamically coupled to shear stress. Sand
269 capture directly alters potential density, growth and lateral expansion of the vegetation, which
270 feedbacks to patterns in flow parameters (velocity, turbulence, intermittency) because of sheltering
271 effects by vegetation and dune topography. The qualitative importance of these feedbacks for the
272 large-scale geomorphology of coastal dunes is well-appreciated (Durán and Herrmann, 2006; Hesse
273 and Simpson, 2006; Durán et al., 2009; Durán and Moore, 2013), but very few data on the feedbacks
274 between sand fluxes and vigour of the foredune vegetation are available. So far, different vegetation
275 states rather than vegetation dynamics have been linked to dune height potential and subsequent risks
276 of overtopping events and flooding (Seabloom et al., 2013).

277

III Towards an integrated model of the plant-sand feedbacks

III.1 The integration of vegetation-dune feedbacks in existing process-based models

280 The importance of the vegetation-dune feedbacks is still not well understood, let alone quantified and
281 incorporated into predictive models for coastal dune dynamics (Puijenbroek et al., 2017). Current
282 state-of-the-art 3D models for coastal dune development (e.g., DUBEVEG (Keijsers et al., 2015), CDM
283 (Durán and Moore, 2013), AeoLIS (Hoonhout and de Vries, 2016)) are able to simulate topographic
284 development of coastal dunes and sediment transport at spatial scales relevant for coastal managers
285 as a function of sediment supply, probabilities of vegetation development, descriptions of flow field,
286 and dune erosion by waves. These (coupled) 3D coastal dune models are a product of the basic physical
287 principles and sediment transport models, and they are essential for the prediction of dune
288 development. Furthermore, they need validation from field experiments containing high-quality
289 datasets relevant for dune development. With exception of the DUBEVEG model (De Groot et al.,
290 2011), which has coarse vegetation dynamics incorporated, recent coastal functioning models have
291 ignored ecological interactions across scales (e.g., Duran and Moore 2013, Van Westen et al. 2019). As
292 important engineer species from coastal dunes differ in physical features and life history, they
293 differently affect dune development, with for instance sand couch grass (*Elymus farctus* (Viv.)
294 Runemark ex Melderis) giving rise to 'lower broader dunes', and marram grass enabling dunes to
295 develop into a 'higher, hummocky peaked topography' (Hesp, 2002; Puijenbroek et al., 2017; Reijers
296 et al., 2019; Schwarz et al., 2019).

297 All existing dune erosion models treat the processes at the dune face in a simplified way. No process-
298 based description is implemented to describe the formation of vertical cliffs at the dune foot
299 undermining the dune slope with subsequent geotechnical failures of the dune slope that results in
300 slumps of sand on the beach that can be taken away by the waves. For this marshes, Bendoni et al.
301 (2019) implemented a hydro-morphodynamic interaction model in XBeach (Roelvink et al., 2009) to
302 evaluate erosion of marsh boundaries due to wave impact. Although this study is limited to the
303 cohesive sediments' environment, soil reinforcement due to roots has been modelled, which might be
304 extended to other environments in the future. Physical scale model experiments, with dunes,

305 vegetation and disturbances scaled towards lab conditions, have demonstrated that roots, which
306 geotechnically strengthen a sand volume, significantly reduce the dune erosion compared to bare sand
307 (Feagin et al. 2019, Bryant et al. 2019). Presently, only indirect implementations are possible namely
308 by tuning calibration parameters influencing the morphodynamics.

309

310 *III.2. Insights from a new simulation model*
311 III.2.1. The geography of marram spatial configuration
312 From II.3, it is clear that feedbacks between the environment and the spatial distribution of marram
313 grass impact dune development. We mapped marram cover and spatial contingency in 20x20 m² grid
314 cells along the coastlines of northern France, Belgium, Netherlands and South-England (see
315 supplement S2), to identify realistic ranges in nature. Marram grass is –as predicted from the species'
316 biology- predominantly showing a clustered distribution with JC (join-count; an established method
317 that quantitatively determines the degree of clustering or dispersion, see S2) values between 20 and
318 80, so ranging from random (values close to zero) to highly clustered patterns (Figure 3). A mean
319 clustering pattern with JC values around 50 is stable over the four studies regions. No underdispersed
320 (so regular) patterns were observed. Interestingly, marram grass spatial cover at these spatial scales is
321 strongly country-specific with UK and France being represented by well-vegetated dunes. Dunes in
322 Belgium and the Netherlands appear to be in more dynamics states with quite a substantial presence
323 of areas with a low cover (see IV).

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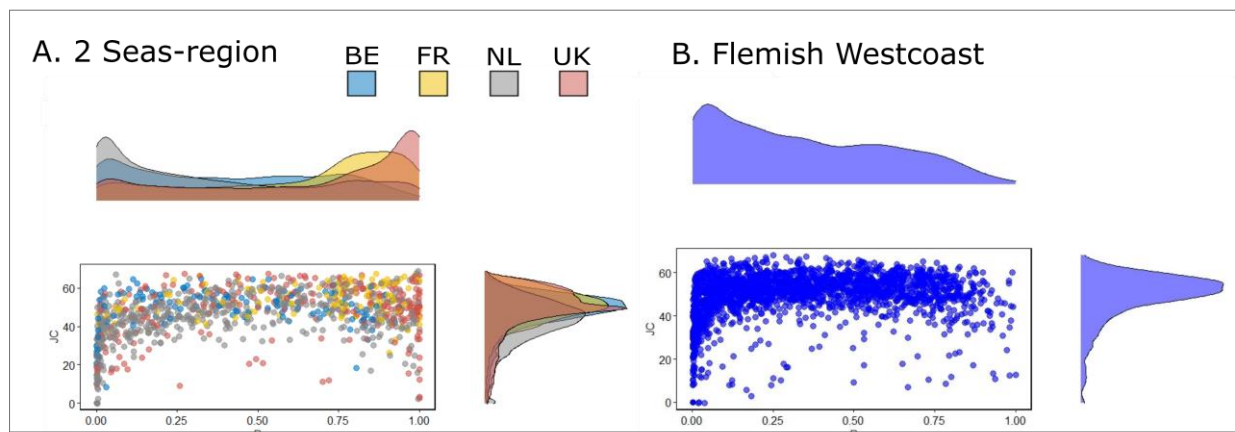
326 **Figure 3. Density distribution plots of observed cover (P) and spatial correlation (JC) of marram grass in 20x20 m² grid cells**
327 **in dunes from the Isles of Scilly to Norfolk in England (UK) and from Somme (Fr) to Texel (NL) on the continental side along**
328 **the North Sea and the Flemish West coast (B) (right panel). Note that for visualisation, a subsampling of 1000 points (2%)**
329 **was performed for (A).**

330

331 III.2.2. Simulating dune growth in relation to marram grass spatial configuration
332 We developed a grid-based dune simulation model that computes aeolian transport processes and
333 changes in vegetation growth and dune morphology based on their dynamic feedbacks and marram
334 spatial organisation. The landscape is grid-based with cells having dimensions of 0.20x0.20 m². The
335 100x100 cell matrix therefore corresponds with a dune area of 20x20m². We refer to supplementary
336 material S2 for a detailed process overview, references to the code. We simulated changes in aeolian
337 processes and wind dynamics at a day-resolution. We used averages over 7 years (2010-2017) received
338 from the Royal Meteorological Institute at Koksijde, and scaled them to the four main different wind
339 directions as used in the model by (Nolet et al. 2018b), each corresponding to a side of the landscape.
340 Wind speed and direction is drawn daily from a normal distribution, based on monthly average wind
341 speed and its standard deviation. *Sand input*, the material blown into the system from the beach (N-
342 direction here), is expressed as a relative percentage of the maximum sand saturation flux, i.e. the

343   maximal amount of sand that can be carried by the wind. Lateral winds (E and W-directions in the grid)
344   have an influx which corresponds with the most recent outflux of a lateral wind (thus, we represent
345   the landscape as tube to avoid edge artefacts). This amount is constantly updated during a simulation.

346   *Sand deposition* is directly dependent on shear velocity which is a function of wind velocity Hoonhout
347   and de Vries 2016; Durán et al., 2010), vegetation density (Durán et al. 2010) and its roughness (Durán
348   and Moore 2013). Increases in shear stress due to funnel effects are included, as are gravity and shelter
349   effects. Maximum angles of repose are set to 34° (Durán et al., 2010)when vegetation is absent (Durán
350   et al., 2010). These angles increase with vegetation density. As such, avalanches are less prevalent
351   when plant density is high. Moreover, erosion is inhibited in locations sheltered by lee slopes at an
352   angle of maximal 14° (Kroy et al., 2002). *Marram grass* dynamics are seasonal (only growth in spring
353   and summer), with local growth modelled as outlined in this review. Vertical as well as lateral growth
354   during the growing season is modelled as a logistic function up to maximal heights, and directly
355   depending on sand deposition (Nolet et al., 2018), leading to positive growth under intermediate sand
356   accretion and complete burial leading to marram grass die-off. Lateral growth follows Lévy-patterns as
357   determined by (Reijers et al., 2019), and are here modelled by simplified neighbour expansion
358   processes. No growth occurs during autumn and winter but sand accumulation continuous. The net
359   height after winter burial determines the starting conditions for vertical growth in the next season. No
360   germination events were modelled as these are to date not (or only rarely) witnessed in foredunes the
361   last decade.

362   To validate the model predictions, we compared outcomes from the model with those from a statistical
363   model linking changes in topography over five years as derived from LIDAR in relation to the initial
364   marram spatial configuration as determined from aerial photographs in 2015 in Belgium (Fig. 4;
365   detailed methods in supplementary material S3 and S4). Our model simulations (Fig 5, upper panels)
366   were run for initial marram cover in the range 0.1-0.9 (as without marram cover, only erosion of the
367   initialised sand volume is occurring without establishment) and join counts between 20 and 70).
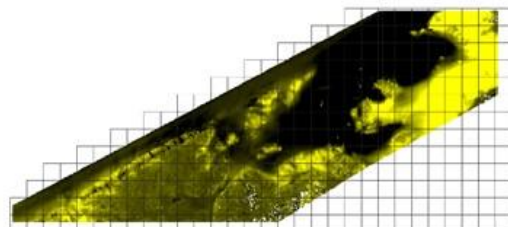
**A. The RGB, NIR and DTM data are retrieved for the sites under study**

**B. All input data are used to generate vegetation maps (marram cover, 20x20 cm²)**
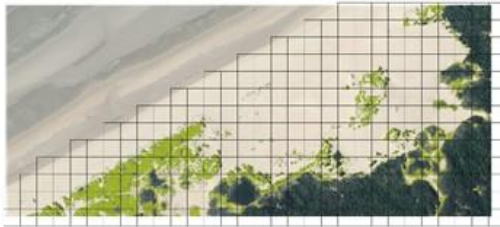
C. Differential DTM's of changes in dune height over 5 years are produced (20x20 cm²)

D. Marram spatial distribution statistics are calulated at grids of 20x20 m² (darker colours are higher values)

Cover (P)

Spatial correlation (JC)
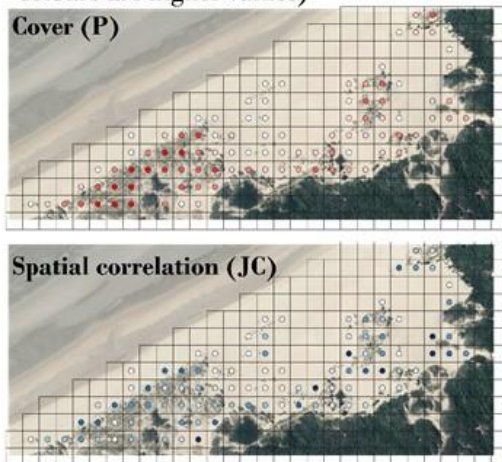
**E. Differential heights are integrated into grids of 20x20 m² (red: erosion; blue: accretion)**

368
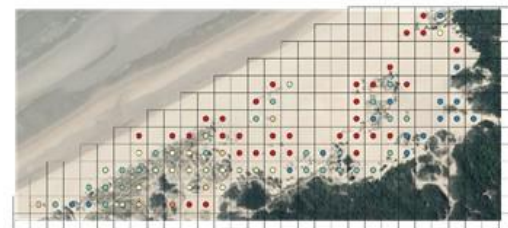
Figure 4. Workflow for connecting observed differences in dune height over a period of 5 years to marram spatial configuration in coastal foredunes (case presented: Schipgatduinen, Koksijde, Belgium)

371

372   The modelled height changes agree in general terms with those observed. The observed larger effects
373   in the field therefore suggest slightly larger sand input, either due to sand availability or changes in
374   wind strengths, from the beach as sand input initiated in the model based on rough estimates from
375   the Belgian coast (unpub. data Rauwoens & Strypsteen). Alternatively, the small scale of the
376   mechanistic model may underestimate wind saturation and therefore sand displacements (see IV.
377   outlook). Dune height increases at intermediate cover of marram grass, so *P~0.5*. However, the
378   simulation model predicts increases to be maximal under low cover and more random (i.e., less
379   clustered) distributions of the marram grass tussocks (low *P* and low *JC*). According to the simulation
380   model, local changes in dune topography, estimated as the coefficient of variation (CV) of grid cell-
381   level differences in height, show most changes occurring in dunes with clustered marram patches or
382   patches with a low amount of vegetation, but more random patterns. Predicted changes from LIDAR
383   follow the same pattern as the ones generated by the simulation model. Only under low cover and
384   intermediate clumping, a more homogenous increase of the dune is predicted by the computer model.

385
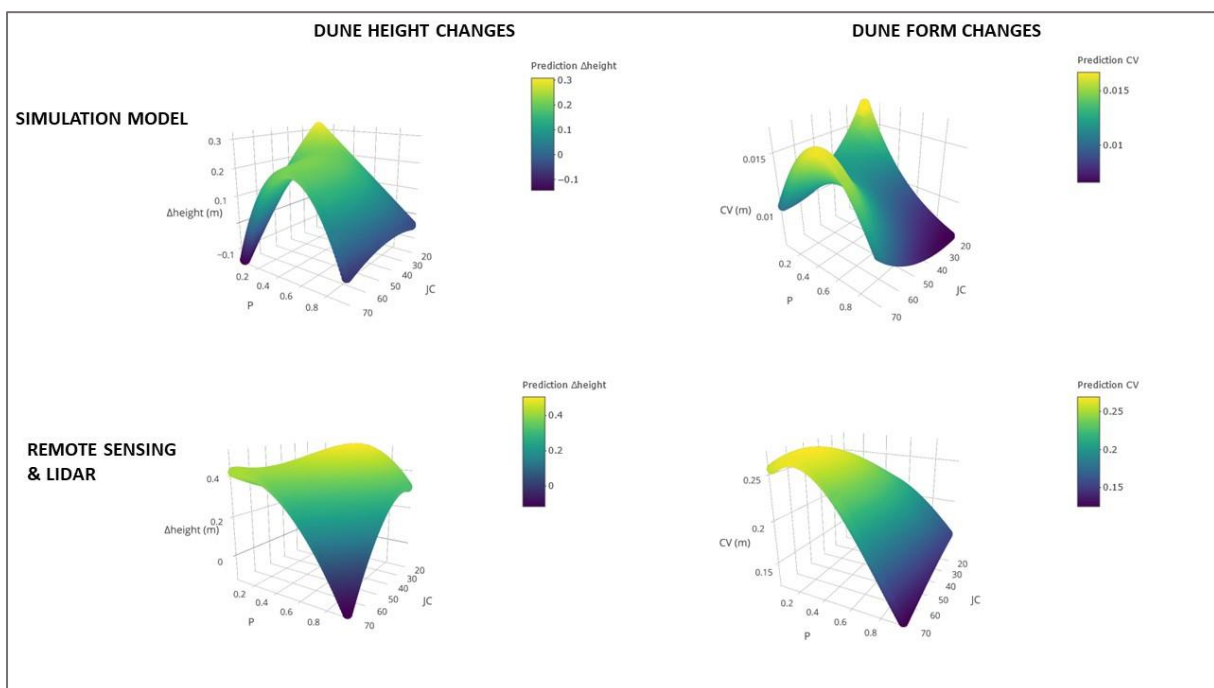
387   **Figure 5. Output of the simulations computing changes in dune height and topography (CV of height changes over all grid**
388   **cells) over a period of 5 years (upper panel), and similar metrics as observed from LiDAR data from coastal dunes along**
389   **the Belgian west coast (lower panels).**

390

391   Analysis of the LIDAR data also showed decreasing dynamics with increasing distance from the sea (see
392   supplement S4). The obtained effect sizes (supplement S4) and accompanying visualisations of the
393   modelled effects (figure 5) indicate that the observed changes in integrated dune height and form
394   differ from those of the simulation in the sign and strength of the cover x spatial clustering (P:JC and
395   the interaction between P² and JC). The most prominent difference lies in the predicted erosion
396   dynamics under low marram cover and a strong clustering. This suggests that the sand accretion
397   capacities of marram grass under these conditions needs to be re-evaluated.

398

IV.   Discussion and outlook

400   A mechanistic understanding of the vegetation-sedimentation feedbacks that steer the natural
401   development of coastal dunes is essential for conserving and restoring the function of coastal dunes

402   as natural flood barriers. Climate change, and its impact on feedbacks between marram grass and sand
403   fluxes, is anticipated to strongly alter dune formation and dune resilience (Pakeman et al., 2015; van
404   Puijenbroek et al., 2017). We here reviewed the state of knowledge on the ecology of marram grass in
405   relation to dune formation, flow attenuation, sediment deposition and plant growth. Our model and
406   LIDAR analysis showed that the joint increase of volume and variability under low cover and less
407   clustered spatial configurations have the highest impact on local sand accretion and dune morphology.
408   Such conditions steer impose a positive feedback on vertical growth. Strong erosion dynamics are
409   conversely anticipated to preclude establishment at further distances from existing tussocks. Scale-
410   dependent feedbacks lead to patterns of self-organisation (Rietkerk & van de Koppel 2008) and need
411   to be quantified and further integrated into mechanistic models to forecast coastal dune formation in
412   relation to climatic conditions. Earlier research showed considerable variation in marram growth
413   (Vandegehuchte et al. 2010a) and expansion strategies (Reijers et al. 2021), and changes here-in can
414   be expected with respect to future climatic conditions. The relevance of this intraspecific variation
415   remains to be understood, also from the perspective of planting actions to actively build resilient dunes
416   in the light of climate change.

417   A resilient coastal dune system is anticipated to be one where vegetation and bare sand coexist in a
418   stable equilibrium, hence a state to which the system should bounce back after any disturbance, e.g.,
419   by erosion. The permanent loss of sand dynamics by changing sand input, fragmentation or
420   anthropogenic dune stabilization are expected to lead to catastrophic shifts causing dunes to become
421   hyperstatically fixed by plantation and succession (Jackson et al. 2019, Gao et al. 2020). On the other
422   hand, at too low initial densities, the vegetation may be disrupted by strong sand drifts, also following
423   intense trampling by people, leading to a hyperdynamic and unvegetated state. A resilient dune should
424   balance between both extremes (Borsje et al. 2011) and this resilience will thus largely be determined
425   by the current vegetation density and configuration, local conditions of sand supply, connectivity with
426   the beach, and erosion. The state of the marram dune can be expected to impact further inland sand
427   drift. Narrow stretches thereby have the potential to determine dune stability at larger spatial scales
428   by affecting the total dune system volume, and the further vegetation succession dynamics (e.g., Ollf
429   et al. 1993, Fenu et al. 2013). These are less relevant from a coastal protection perspective but of
430   major importance for biodiversity conservation (European Commission on Habitat of Directive 92/43
431   EEC)

432   Coastal dunes along the coast of the North-Sea and Channel show a remarkable convergence in the
433   spatial clustering across the four studied countries, and this clustering seems to be preserved across
434   the range of vegetation cover. This finding suggests an optimal clustering in European dunes, which is
435   anticipated to result from the species' self- organizing capacity. At intermediate cover, this clustering
436   leads to largest changes in dune growth. We anticipate that the availability of sufficient aeolian
437   dynamics at small scales drives this overall increase in dune volume. This review also shows these
438   conditions to facilitate marram grass performance because of the steady supply of fresh sand.
439   Although more research is needed, this finding suggests that such a spatial configuration can optimize
440   both marram grass performance and dune resilience by maximizing growth. Deviations from this state,
441   especially in terms of cover –note that the clustering metric becomes less relevant with increasing
442   cover– are then likely disturbed states resulting from either ceasing sand dynamics or vegetation
443   development. As we only documented patterns in marram grass spatial configuration, we lack insights
444   into the underlying causes. Are they due to sediment transport potential, or correlated to region-
445   specific variables such as tidal amplitude, wave height, or beach width? Alternatively, it is not unlikely
446   that variation in both dune management –especially planting campaigns– and the differences in
447   recreational pressure are at the basis for this variation. Since we showed marram grass' spatial
448   configuration to affect both dune growth and topography and therefore sand fluxes further inland, this
449   variation is anticipated to have strong implications for coastal protection. Pending on the state,
450   recreational pressures may constrain dune stabilisation and keep the system in a dynamic, and
451   presumed optimal state with respect to resilience, or facilitate erosion and the transition to

452 hypermobile states. Clearly, the negative and positive contributions of such recreational pressures
453 need to be assessed case by case, and in direct connection to the local environmental (boundary)
454 conditions (Nunes et al. 2020).

455 Incorporating the available information allowed us to mechanistically build models that support
456 generic predictions of dune volume and topography change at short spatial and temporal scales. The
457 model does, however, still contain gaps in terms of parameterisation and validation (both
458 observational and experimental), especially with regard to very dynamic conditions (low, clustered
459 cover by marram grass). While any prediction in this specific parameter range can be questioned for
460 its relevance ("How natural are these configurations, if we do not observe them?"), we argue that this
461 is of the utmost relevance in the light of dune-building campaigns where marram grass needs to be
462 planted, for instance in front of existing dikes. The presented simulation model also operates at
463 relatively small scales relevant for vegetation dynamics, but potentially underestimating realised wind
464 saturation in barely vegetated dunes. Deviations between the observed and predicted changes in dune
465 volume likely result from such scaling issues. Upscaling of dune-vegetation dynamics can be achieved
466 by linking sand-output conditions from the most seaward-oriented dunes as input conditions for those
467 more inland. Under such conditions, sand-vegetation dynamics need to be extended towards other
468 species occurring along the expected succession gradient. It remains to be studied whether
469 simplifications using vegetation height and biomass (Duran *et al.* 2009), as the mediator of such
470 interactions suffice. A major driver of dune development is the amount of sand input from the beach.
471 While difficult to measure, the joint analysis of vegetation and dune development may be used as a
472 reliable predictor of such sea-land sediment fluxes by means of inverse modelling.

473 More research is needed on potential regional changes in the interactions among vegetation
474 development, dune growth and sand fluxes, for example caused by differences in climatic conditions
475 and marram grass genetic variation. Dune volumes are prime determinants of their functioning in
476 coastal protection, with large bodies of sand providing a larger safe zone against inundation risks from
477 storm surges. Vegetation dynamics are expected to have a strong impact on the healing capacity of
478 foredunes, i.e., how fast they recover to earlier states after erosion by such storm events, or in the
479 longer term resulting from sea level rise. Current models enable us to predict changes in dune volume
480 and form, but it remains unknown how erosion is affected by the vegetated state of the dune. For
481 example, to which degree erosion resistance is determined by the marram grass root network still
482 needs to be elucidated. Ultimately, the addition of such information on the mechanistic underpinnings
483 of the patterns generated by our models would reduce the uncertainty of their predictions to the
484 benefit of all stakeholders involved.

485

489

Contribution to the Field Statement

491 Coastal dunes provide safety against future climate change induced sea-level rises and storm surges.
492 Contrary to hard protections, they have the advantage to grow with the sea-level. Coastal dunes thus
493 provide important safety services, especially in highly urbanised lowland areas. Because these coastal
494 landscapes are formed by the interplay between the dune building marram grass and sand dynamics,
495 a quantitative study of these interactions is necessary to understand and forecast how climate change
496 will impact dune development and its resilience. We here provide a synthesis on the available insights,
497 and complement these insights with new experiments and remote sensing data from coastal dunes
498 along the North Sea. This information is integrated into a mechanistic model to demonstrate the
499 importance of marram grass ecology, and its emerging spatial configuration for dune development.

500   We build on these insights to identify important caveats and future research directions to effectively
501   manage and construct dunes as a solid nature-based solution from the fundamental ecological and
502   geomorphological building blocks.

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