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Green beach vegetation dynamics explained by embryo dune development

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Abstract

Sandy coastlines are dynamic environments with potential for biodiverse habitats, such as green beaches. Green beach vegetation can develop on nutrient-poor beaches landward from embryo dunes. It is characterised by low-dynamic coastal wetland habitat such as salt marshes and dune slacks. It has been hypothesised that the establishment of green beach vegetation is facilitated by the shelter provided by embryo dunes, however evidence is lacking.

We explored the importance of geomorphology and soil conditions on the species richness and turnover of green beach vegetation over a time period of 10 years. We recorded 107 plots along 11 transects over a gradient from beach to dune on the island of Schiermonnikoog, the Netherlands. We characterised transect geomorphology at transect level and soil conditions and vegetation at plot level in 2006 and 2016.

We found that the green beach vegetation was highly dynamic, total plant cover increased by 62% within 10 years. In 2006 beach width was an important factor in explaining species richness, with the highest number of species occurring on narrow beaches with a large volume of embryo dunes. In 2016, species richness was positively associated with the build-up of organic matter. Overall species richness declined relative to 2006 and was accompanied by an increase in elevation due to sand burial and the expansion of embryo dune volume.

Our data suggests that geomorphology influenced the vegetation indirectly by affecting sand burial rate. Plant species richness declined less at sheltered conditions where sand burial was limited, allowing the build-up of organic matter. This indicates a time-dependent relationship between the development of embryo dunes and plant species richness: embryo dunes can be a source of shelter, thus increasing species richness, but can compete for space over time, lowering species richness again. Our results are relevant for engineering and management of biodiverse sandy shores.

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Introduction

Sandy coastlines are dynamic environments with potential for rich biodiverse pioneer habitats, such as green beaches. Green beaches form a transitional habitat between the beach, the dune system including dune slacks and salt marshes, containing a varying mix of species from all three habitats. Besides having a high floral diversity they are also important for wintering granivorous birds (Dierschke, 2002). Green beaches thus support more biodiversity than other coastal habitats (Speybroeck et al., 2008) and represent a high conservation value (Acosta, Carranza, & Izzi, 2009; de Groot, Janssen, et al., 2017; European Commission, 2007). Sandy coastlines are also increasingly under pressure from recreation and measures aimed at improving flood safety. Safeguarding green beach habitats in the face of these competing demands requires in-depth knowledge about the spatial-temporal dynamics and environmental drivers necessary for their development and maintenance.

Species occurrence in coastal ecosystems is mainly determined by gradients in salinity, sand burial, moisture and soil development, which in turn are related to beach and dune geomorphology (Maun, 2009; Packham & Willis, 1997; Rozema, van Manen, Vugts, & Leusink, 1983). Green beaches develop between the storm drift line and foredune (McLachlan & Defeo, 2018) with the formation of microbial mats on moist and nutrient-poor sandy soil with a low content of organic matter. Green beaches develop at locations that are slightly protected from the erosive force of the sea and high rates of sand burial (Gares & Nordstrom, 1988; Hesp, 2002). Historically, they have been recorded from wide beaches or beaches sheltered behind intertidal bars (Bakker, Veeneklaas, Jansen, & Samwel, 2005; Edmondson, Traynor, & McKinnell, 2001; Kers & Koppejan, 2005; van Tooren & Krol, 2005). Although wide beaches are often associated with high rates of sand transport (Wright & Short, 1984) they may also provide shelter against sea erosion by attenuating waves better than narrow beaches (Ruggiero, Komar, McDougal, Marra, & Beach, 2001) or by facilitating development of embryo dunes (van Puijenbroek et al., 2017). In addition wide beaches may act in concert with the larger secondary dune complexes to increase the availability of fresh seepage water on the beach (de Groot, Oost, et al., 2017; Röper, Greskowiak, Freund, & Massmann, 2013; Stuyfzand, 2016), enabling the coexistence of salt-sensitive dune slack species and salt-tolerant salt-marsh species (Grootjans, Geelen, Jansen, & Lammerts, 2002; Lammerts & Grootjans, 1998).

Once plants have established, plant growth will result in the development of an organic layer. With the increase in organic matter, nutrient availability may increase, eventually enabling more competitive species to become dominant (Berendse, Lammerts, Olff, & Ecology, 1998), until succession is reset again by erosive or sedimentary processes (Feagin, Sherman, & Grant, 2005; M. A. Maun, 1998; Silva, Martínez, Odériz, Mendoza, & Feagin, 2016). Erosive and sedimentary processes may not only fully set back succession but also shift the direction of succession away from green beach formation by locally altering the abiotic conditions (Bitton & Hesp, 2013; M. a. Maun & Perumal, 1999). The green beach landscape may thus be spatially dynamic as a result of accumulation or erosion of substrate by wind and water. To what extent changes in beach geomorphology affect development and succession of green beaches has not yet been investigated.

In this study we explored how geomorphology and abiotic soil conditions relate to species richness and species turnover of green beach vegetation. We addressed the following questions: 1) how does beach geomorphology affect the abiotic soil conditions in the rooting zone, and can this relationship change over time? 2) Which abiotic soil conditions drive species composition and turn-over of biodiverse pioneer vegetation along a beach-dune gradient? We hypothesised that green beach vegetation would be positively associated with the presence and development of embryo dunes. As embryo dunes potentially provide shelter against storm erosion and sand burial in the overall dynamic beach environment (Bakker et al. 2005). To test our hypothesis, we assessed the geomorphological setting (elevation, beach width, volume of embryo dunes and volume of secondary dunes), abiotic soil conditions (soil salinity and organic layer thickness) and vegetation (species composition, species richness, Shannon index) in 107 plots along 11 transects from beach to dune on the Dutch barrier island of Schiermonnikoog in 2006 and 2016.

Materials and methods

Study site and plot selection

The West-Frisian barrier island of Schiermonnikoog, the Netherlands, has wide dissipative sandy beaches with a high degree of hydrodynamic reworking of the sand, which results in a high aeolian transport potential and a concomitantly high potential rate of sand burial. The westward facing beaches on Schiermonnikoog are facing the tidal inlet between the islands of Ameland and Schiermonnikoog (Fig. 1). The northward facing beaches are facing the North Sea. The beaches on Schiermonnikoog have been accreting since the period 1980 − 1995, resulting in relatively wide beaches compared to the Dutch mainland coast. Especially the westward facing beaches are very wide (up to 2545 m in 2016). The northward facing beaches were narrower, but still had a beach width between 375 m and 815 m, wide

Fig. 1. Aerial photograph of our study area Schiermonnikoog in 2016 (Clyclomedia, 2016). The grey part of the lines indicates the position and orientation of the transects, and the red part of the lines the plot locations. The texts indicate the transect number and the beach width of the transect. Transects I-III are westward-facing, transects IV-XI are northward-facing.

enough to support large embryo dune complexes (van Puijenbroek et al., 2017). At all beaches a foredune was present, most beaches also had secondary dunes landward from the foredunes, except for the most eastern part of the island: at these beaches only an artificial sand-drift dike was present. We established 11 transects from foredune to beach (Fig. 1) representative for the variation in beach geomorphology on Schiermonnikoog. The upper sand layer for different transects had similar grain size distribution: grain size mostly ranged between 125 μm and 250 μm. A large fresh water body is present underneath the island, with a maximum depth of 85 m, and a maximum elevation of 3.2 m (Beukeboom, 1976; Grootjans, Sival, & Stuyfzand, 1996). The isohypse lines indicate that groundwater can exfiltrate onto the beach. Hence, transects I – VIII can be affected by freshwater seepage from the large dune system. Transects IX – XI, north of the artificial sand-drift dike, are beyond the influence of the regional fresh water body (Beukeboom, 1976). They may be affected by local freshwater bodies from small dunes or the sand-drift dike. Storm intensity between 1996 – 2005 was mild with only a few low intensity storms, which most likely contributed to the establishment of green beach vegetation around the year 2000 (Bakker et al., 2005), which began with the development of microbial mats (Bolhuis, Fillinger, & Stal, 2013; Stal, Severin, & Bolhuis, 2010).

In 2006 we established 116 plots in 11 transects along fixed beach poles. In 2006 the transects started at the toe of the foredune. From this point onwards and every 20 m along the transect in the direction of the sea a plot of 2 m x 2 m was established, with the last plot established at the edge of the vegetation limit on the beach. In 2016, we revisited all plots, starting again at the toe of the foredune and continuing until we reached the vegetation limit on the beach. For both years, the fieldwork took place for three weeks in August. Although the toe of the foredune had not changed in position, the vegetation limit on the beach in 2016 was closer to the dunes than in 2006. For 6 out of 11 transects this difference in the end of the transect resulted in fewer plots in 2016 compared to 2006. We only included plots that were measured in both years in our analyses, resulting in 107 plots, with 8 – 14 plots per transect.

Transect geomorphology

Beach width (m) and embryo dune volume (m^3/m) were derived for each transect by using cross-shore elevation profiles for 2006 and 2015 derived from the JarKus database (Rijkswaterstaat, 2014b). The cross-shore profiles correspond precisely with the position of the transects. The

JarKus database contains annual elevation measurements covering foredune, beach, and foreshore, and has been used in several studies addressing coastline dynamics from an annual to a decadal scale (Burgh et al., 2011; de Vries, Southgate, Kanning, & Ranasinghe, 2012; Keijsers, De Groot, & Riksen, 2015; Keijsers, Poortinga, Riksen, & Maroulis, 2014; van Puijenbroek et al., 2017). The distance between elevation measurements along each JarKus profile is 5 m. Profile elevation was measured using laser altimetry, which resulted in an accuracy of 0.1 m (De Graaf, Oude Elberink, Bollweg, Brügelmann, & Richardson, 2003; Sallenger et al., 2003).

We calculated beach width and embryo dune volume from the profiles for each transect. To calculate beach width, we defined the beach area as the expanse between the shoreline and the foredune, i.e. between 0 m and +6 m NAP (NAP refers to Amsterdam Ordnance Datum, the mean high tide (MHT) is +1.05 m NAP). We defined embryo dune volume as the area (m^3/m) under the curve of the beach area between +2 m and +6 m NAP, as well as the change in embryo dune volume between 2006 and 2015.

Volume of secondary dunes for each transect was calculated by creating a profile extending 500 m from each transect landward, including the foredune. To create the profile we extracted the elevation at 5 m interval from a digital elevation model of 2014 (Rijkswaterstaat, 2014a). We only used the digital elevation model of 2014, since we did not expect any significant changes in the volume of secondary dunes within a decade (Arens, Mulder, Slings, Geelen, & Damsma, 2013). The volume of secondary dunes was calculated as the area under the curve (m^3/m) for each profile.

Plot-level changes in elevation between 2006 and 2016 were calculated from laser altimetry data of the coast from 2006 and 2016 (Rijkswaterstaat, 2006; Rijkswaterstaat 2015). We used the GPS-coordinates (Garmin eTrex GPS Basic, 4 m − 5 m accuracy) for the middle of each plot to extract the approximate coordinates.

Environmental conditions

Soil conditions

After vegetation assessment, three soil cores (5cm diameter, 50 cm deep) were taken from each plot in 2006 and 2016. For each core the A horizon was measured, and the thickness of the organic layer was measured. Organic layer thickness was averaged over the three cores before statistical analysis. In 2006 none of the plots had an A horizon.

In 2016 electrical conductivity was measured in a water extract of the soil. To this end rhizosphere soil (10 − 40 cm depth) from the three soil cores per plot was mixed and a compound sample taken. Samples were weighed, dried at 105°C for 18 hours, and weighed again to determine the gravimetric soil moisture content. Dried samples were diluted on a 1:5 mass basis with distilled water and shaken for 2 hours, after which the EC was measured with an EC meter (Eurotech instruments, EcoScan, COND 6+). Values were multiplied with a factor 17 to derive the EC at saturated conditions (ECe) (Shaw, 1994). As soil sampling was spread over three weeks in August, we cannot exclude that weather variations contribute to the variation in electrical conductivity, even though we standardised for soil moisture.

Vegetation

Vegetation assessments of each plot were made using the extended Braun-Blanquet scale for the estimation of the cover of individual species (van der Maarel, 1979). Nomenclature of plant species followed van der Meijden et al. (Meijden, 2005). Nomenclature of plant communities was according to Weeda et al. (Weeda, Schaminée, & Duuren, 2003). For performing statistical analyses, ordinal scale measurements were later transformed to interval type cover percentages (van der Maarel, 2007).

We calculated the species richness and the Shannon diversity index for 2006 and 2016; these indices provide information on vegetation composition and species diversity and are commonly used in vegetation science (Mulder et al., 2004; Shannon, 1948). We calculated the indices for all species and for a subset of species with an affinity for green beaches, namely, young dune slacks (EUNIS habitat classification: B1.8) and salt-marsh species (EUNIS habitat classification: A2.5) (Agency European Environment, 2019). For young dune slacks we considered the following plant community associations to be characteristic: *Parnassio-Juncetum articapilli, Junco baltici-Schoenetum nigricantis*, and *Cicendietum filiformis*. For the salt marshes we used the plant community associations within the orders *Thero-Salicornietalia* and *Glauco-Puccinellietalia* (de Groot, Janssen, et al., 2017; Petersen, Kers, & Stock, 2014). From these plant community associations we selected species that had a 10% faithfulness for that particular association (see Appendix A: table 1, for an overview of all species), using the software package SynBioSys (Hennekens, Smits, & Schaminée, 2010). Out of the total of 126 recorded species, 42 species were considered characteristic of green beaches. Of these 42 species 15 species are associated with dune slack vegetation whereas 30 are associated with salt marsh vegetation. Three species, *Odontites vernus* subsp. *serotinus, Parapholis strigosa*, and *Carex distans*, are associated with both salt-marsh and dune slack vegetation. Together we refer to these species as green beach wetland species. The dune slack species mainly encompassed stress-tolerant short herbs and grasses, of nutrient-poor and moist soils with low salinity (Ellenberg et al., 1991). Ten of these 15 species are endangered and highly protected in the Netherlands, such as *Liparis loeselii*, which is an EU habitat-directive species, *Schoenus nigricans*, and *Sagina nodosa*. The salt-marsh species mainly encompassed short grasses and herbs of moist, saline and basic soils (*Artemisia maritima, Limonium* *vulgare*, and *Puccinellia maritima*) of moist, saline and basic soils, but also included taller and competitive grasses (*Elytrigia atherica, Juncus maritimus, Festuca rubra)*, and shrubs (*Salix pentandra*) (Ellenberg et al., 1991).

We calculated the change in species richness (t1 − t0) and the Shannon diversity index (t1 − t0) between 2006 and 2016 for all species and green beach wetland species. Furthermore, as a proxy for species turnover we calculated the fraction of stable species in each plot, which is the number of species that occurred in the same plot in 2006 and 2016 divided by the total number of species in 2006.

Statistical analyses

For the statistical analysis we explored how the abiotic factors were correlated with beach geomorphology. The electrical conductivity, moisture content, and organic layer thickness were analysed by linear regression models with elevation, beach width, and embryo dune volume as explanatory variables, for organic layer thickness the change in elevation was added as explanatory variable. For these models we used the data from 2016. For the linear regression models with either electrical conductivity or moisture content as response variable we also included the volume of the secondary dunes and organic layer thickness as explanatory variables. The change in elevation between 2006 − 2016 was analysed with the 2006 values for elevation, beach width, and embryo dune volume as explanatory variables.

Species richness, diversity and composition were analysed with three separate methods. First, we explored the factors that influenced the richness and diversity of the vegetation of 2006. The species richness of all species and green beach wetland species was analysed with a generalised linear mixed model with Poisson distribution and transect as a random intercept (Bolker et al., 2009; (Pinheiro et al., 2009)). We also analysed the Shannon diversity of all species and green beach wetland species, with a general linear mixed model with transect as a random intercept (Pinheiro et al., 2009). The explanatory variables for the models for plant species richness and diversity index in 2006 were elevation, beach width, embryo dune volume and the volume of secondary dunes. We did not include soil moisture content in our statistical model, because it was highly correlated with elevation (Pearson correlation: - 0.75, t-value105 = -11.54, p<0.001).

Secondly, detrended correspondence analysis (DCA) was used to extract the dominant patterns of variation in the vegetation composition. DCA is an indirect gradient analysis which ordinates only the species data and does not include environmental factors (Braak et al., 1995). We used a DCA method because the data showed unimodal response (Oksanen et al., 2010). We plotted the plots of 2006 and 2016 on the first and second axes of the DCA. In order to relate the changes in plant species composition between the years and abiotic conditions directly, the abiotic factors were fitted onto the species ordination. We included the following abiotic variables: elevation, embryo dune volume, secondary dune volume, and beach width.

Thirdly, we analysed the change in species richness, of all species and green beach wetland species between 2006 and 2016 and the fraction of stable species, with a general linear mixed model with transect as random intercept. As explanatory variables we used the change in elevation, beach width, embryo dune volume, organic matter layer thickness between 2006 and 2016, and the volume of secondary dunes.

Since we were mainly interested in the relative importance of the explanatory variables, we calculated the standardized estimates for all models. For all mixed models we calculated the marginal and conditional R^2 (Nakagawa, Johnson, & Schielzeth, 2017). The marginal R^2 is the variance explained by the explanatory variables and the conditional R^2 is the variance explained by the entire model (including the random variables). For the models with abiotic soil conditions and the change in species richness as response variable the R^2 for the fixed factors was calculated with the r2glmm package in R (Jaeger, 2017). This method could not be used for the species richness of 2006, because of the use of a generalised linear mixed model. To calculate the individual R^2 for the fixed factors we used a stepwise regression. The sum of the individual R^2 of the fixed factors can be higher than the model R^2, because the factors are correlated. The normality and homogeneity of variance of the data was visually checked. The electrical conductivity in 2016 was transformed with a ln transformation. Organic layer thickness was transformed with a square root transformation. All statistical analyses were done in the statistical program R (R Core team, 2016).

Results

Changes in beach and dune geomorphology

Between 2006 and 2016 most beaches eroded, becoming shorter by -84.2±12.7 m (mean±SE) (Appendix A: fig. 1.). The changes in beach morphology did not hamper embryo dune development, as embryo dune volume increased by 40.2±3.6 m^3/m between 2006 and 2016. The position of the embryo dunes did shift landward however, reducing the space between embryo dunes and foredunes (Appendix A: fig. 1).

Abiotic soil conditions in the rooting zone

The abiotic soil conditions were clearly affected by beach and dune geomorphology. We found that soil salinity, moisture content and organic layer thickness were negatively correlated with elevation (Table 1). Wider beaches had overall higher soil salinity and moisture content than narrow beaches (Appendix A: fig. 2 A,C,E), because wider beaches had an overall lower elevation and gradual slope. Taken over all transects, soil salinity and moisture content were not related to the volume of

Table 1. Statistical models for the Electrical conductivity, moisture content, organic layer thickness in 2016 and change in elevation between 2006 - 2016. For Electrical conductivity, moisture content, organic layer thickness the explanatory data was from 2016, for the change in elevation the explanatory data was from 2006. The standardized estimates and level of significance are shown for the models.

Abiotic variables	Response variables							
	Electrical conductivity		Moisture content		Organic layer thickness		Δ Elevation	
	Est.	R^2	Est.	R^2	Est.	R^2	Est.	R^2
Intercept	1.20***		14.31***		1.52***		0.23***	
Elevation	-0.32***	0.21	-4.37***	0.37	-0.22***	0.17	-0.24***	0.23
Beach width	0.18**	0.11	1.13*	0.05	-0.10*	0.05	-0.27***	0.19
Volume embryo dunes	-0.02	0.00	-0.67	0.02	0.14**	0.10	0.18**	0.09
Volume secondary dunes	0.10	0.04	0.84	0.03	-		-	
Organic layer thickness	0.15*	0.06	3.86***	0.34	-		-	
Δ Elevation	-		-		-0.10*	0.04	-	
R^2	0.48		0.71		0.28		0.34	
Adjusted R^2	0.46		0.70		0.26		0.32	
Observations	107		107		107		107	
Residual Std. Error	0.50		4.65		0.41		0.44	
F Statistic	18.8***		49.93***		10.22***		17.33***	

Note: *p<0.05; **p<0.01; ***p<0.001.

secondary dunes (Appendix A: Fig. 2G). The volume of embryo dunes on the beach had a weak, albeit significant, positive effect on the organic matter layer thickness of the green beach (Table 1; Appendix A: Fig. 2D).

Vegetation in 2006

In 2006 the vegetation had a sparse cover (27.8±2.2%) and mainly consisted of short herbs and grasses with a small contribution of woody shrubs (0.3±0.1%, Supplementary data S4 Table 1). The vegetation was dominated by green beach wetland species and species characteristic of dunes, with green beach wetland species accounting for 61.2± 3.1% of the total vegetation cover. Most of the green beach wetland species were salt-tolerant species characteristic of salt marshes (14.2±1.5% cover), with only a few freshwater or brackish species characteristics of young dune slacks (2.9±0.7% cover). Abiotic soil conditions or beach geomorphology explained only a small part of the variation in species composition and species richness per plot (Table 2). The species richness of all species was negatively related to beach width, with the highest richness occurring on the narrower northward-facing beaches (Table 2; Fig. 2A). Overall richness and green beach wetland species richness were positively correlated to embryo dune volume (Table 2). The Shannon diversity index was positively related to beach elevation (Appendix A: table 2 and 3).

Change in vegetation

Between 2006 and 2016 vegetation cover increased by 62.1% percent (cover 2016: 89.9±5.6%) and composition changed from low herbs to shrubs (cover 13.3±3.9%) and highly productive grass species of later successional salt-marsh and dune habitats (Appendix A: table 2). The increase in tall grasses and shrubs, was accompanied by a decrease in cover of low productivity short grasses and herbs, such as green beach wetland species. The green beach wetland species still accounted for half (50.7±3.0%) of the total vegetation cover in 2016, which was slightly less than in 2006 (10.5% decrease). Similar to 2006, most green beach wetland species where species characteristic of salt marshes, with only a few dune slack species with low cover. Overall, fewer species per plot were found in 2016 than in 2006 (2006: 11.9±0.6, 2016: 10.1±0.6,

Table 2. Statistical models for the species richness in 2006 of all plant species and the green beach wetland species. The standardised estimates and level of significance are shown for the models.

Plant species richness 2006	Response variables			
	All species		Green beach wetland species	
	Est.	R^2	Est.	R^2
Intercept	2.40***		1.90	
Elevation	0.13***	0.06	-0.02	0.00
Beach width	-0.41***	0.29	-0.29**	0.02
Volume embryo dunes	0.20	0.00	-0.33**	0.08
Volume secondary dunes	-0.01	0.04	0.09	0.00
Marginal R^2	0.48		0.26	
Conditional R^2	0.70		0.49	
Observations	107		107	
Akaike Inf. Crit.	655.68		609.34	
Bayesian Inf. Crit.	671.72		625.31	

Note: *p<0.05; **p<0.01; ***p<0.001.

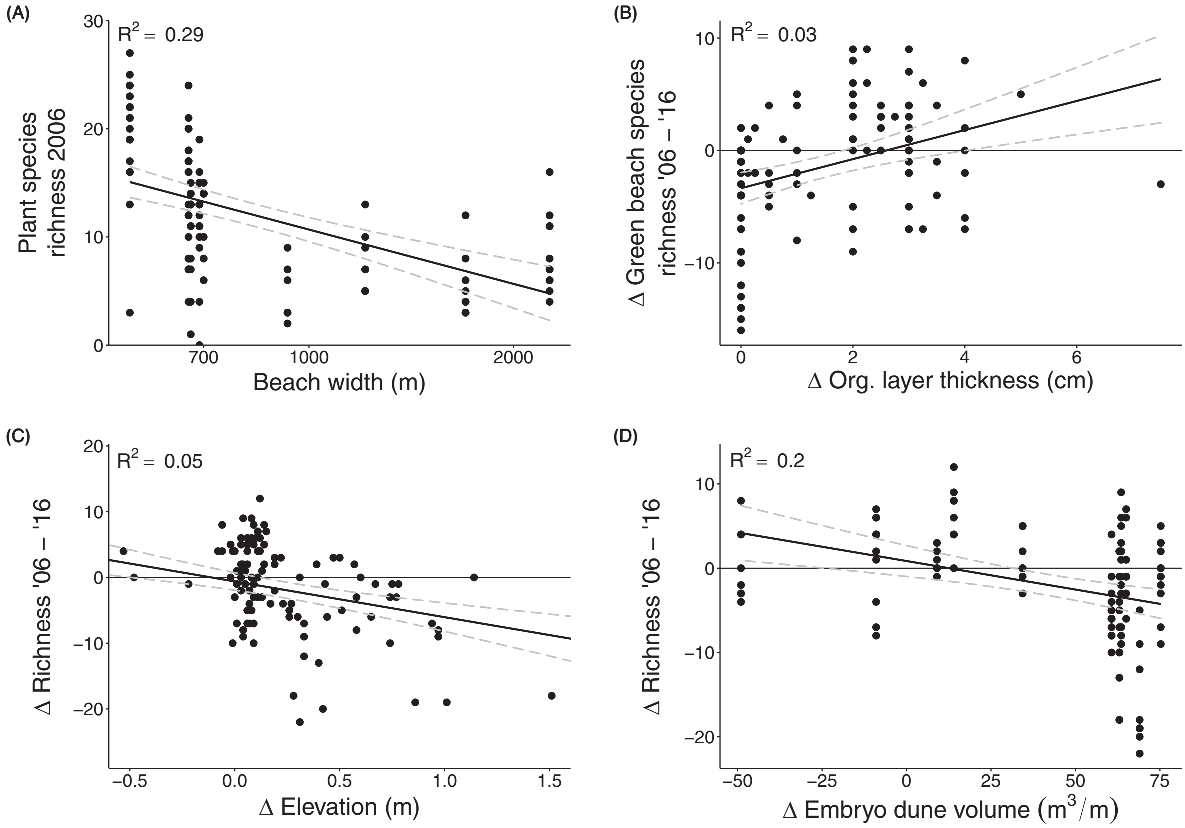

Fig. 2. The relationship between (A) beach width and the species richness of all plant species in 2006, beach width is on a log scale; (B) change in organic layer thickness and change in species richness of green beach wetland species between 2006 and 2016. (C) change in elevation and change in species richness of all plant species between 2006 and 2016, 3 outliers have been removed; (D) Change in embryo dune volume and change in species richness of all plant species between 2006 and 2016; The solid lines indicate the fit of linear regression models and the dashed lines the confidence intervals of the mean. The R^2 from the statistical models (A: Table 2, B-D: Table 3) are added.

t-value$_{211}$ = -2.24, p = 0.026). Also, the green beach wetland species richness was significantly lower in 2016, compared to 2006 (2006: 5.8±0.4, 2016: 4.6±0.3, t-value$_{211}$ = 2.29, p = 0.023).

Species turnover and changes in species richness between 2006 and 2016 were related to an increase in elevation and the increase in organic layer thickness (Table 3; Fig. 2B and C). The decrease in overall species richness was associated

Table 3. Statistical models for the change in plant species richness of all plant species and the green beach wetland species. Statistical model for the fraction of stable species (species present in 2006 and 2016) compared to all species in 2006. The standardized estimates and level of significance are shown for the models.

Changes in species richness between 2006 − 2016	*Response variable*					
	All species		Green beach wetland species		Fraction stable species	
	Est.	R^2	Est.	R^2	Est.	R^2
Intercept	-1.83		-1.19		0.23***	
Δ Elevation	-1.65**	0.05	-0.83	0.02	-0.05**	0.08
Δ Beach width	-2.70	0.07	-1.24	0.02	-0.09	0.10
Δ Embryo dune volume	-4.14*	0.20	-2.67	0.14	0.01	0.00
Δ Organic layer thickness	0.39	0.00	1.02*	0.03	0.05**	0.07
Marginal R^2	0.29		0.27		0.24	
Conditional R^2	0.61		0.54		0.39	
Observations	107		107		106	
Akaike Inf. Crit.	617.2		618.0		-55.1	
Bayesian Inf. Crit.	638.1		638.9		-34.3	

Note: *p<0.05; **p<0.01; ***p<0.001.

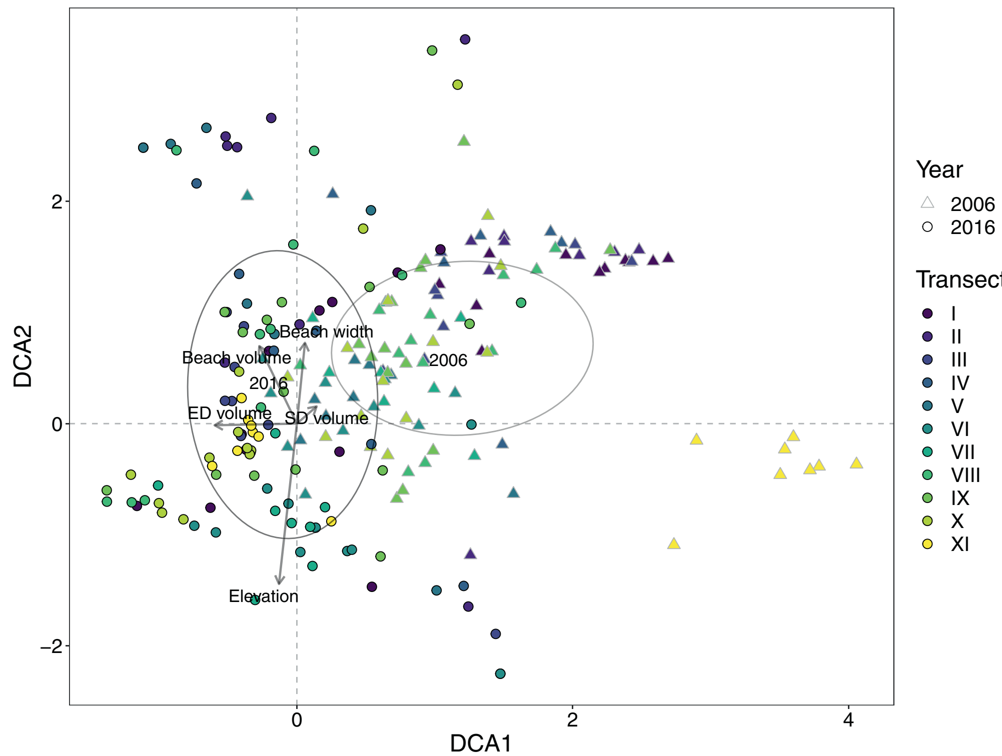

Fig. 3. A detrended correspondence analysis for all the plots and environmental data in 2006 and 2016. The points are the different plots, with different colours indicating the different transects and different shapes and borders indicating the different years. The arrows indicate the factors, beach width, beach volume, volume secondary dunes, embryo dune volume and elevation. The ellipses are the standard error of the weighted centre of the plots for each year. Abbreviations: ED = Embryo dunes, SD = Secondary dunes.

with an increase in elevation (Table 3; Fig. 2C) and an increase in embryo dune volume (Table 3; Fig. 2D). The Shannon index showed similar results as the species richness (Appendix A: table 2 and 3). Green beach wetland species richness was positively correlated with an increase in organic layer thickness. When dune slack species and salt marsh species were analysed separately, the species richness of characteristic dune slack species were negatively affected by the increase in embryo dune volume (Est_{107} = -1.12, $p < 0.05$, R^2 = 0.15). For saltmarsh species only the organic layer thickness had a positive effect on richness (Est_{107} = 0.89, $p < 0.05$, R^2 = 0.067). The fraction of stable species had a positive relationship with organic layer thickness and a negative relationship with a positive change in elevation (Table 3). The DCA analysis illustrates the distinct difference in species composition of the plots in 2006 and 2016. The direction of the change in vegetation composition between 2006 and 2016 was mainly correlated to difference in embryo dune volume between those two years (Fig. 3).

Discussion

The aim of our study was to assess how geomorphology and abiotic soil conditions determine vegetation composition and species turn-over of green beaches. We expected a positive relationship between embryo dunes and richness of green beach vegetation. Although embryo dune volume was positively associated with green beach wetland species richness in 2006, changes in species richness showed an opposite response with the highest species loss occurring on beaches with high embryo dune volume. Furthermore, our results indicate that embryo dune development can take over wetland habitat by sand burial and thereby reduce the occurrence of wetland species, in particular species also known from dune slacks. Consequently, our results suggest a time-dependent relationship between embryo dune volume and plant species richness: embryo dunes can be a source of shelter, thus increasing plant species richness, but can also compete for space, thus lowering plant species richness.

Factors controlling vegetation and species turnover

In 2006, the green beach of Schiermonnikoog was still in an early stage of succession, considering the low vegetation cover and dominance of short herbs and grasses. The highest species richness was at higher elevated areas on more narrow northward-facing beaches. As the beaches on Schiermonnikoog were generally wide compared to the mainland Dutch coast, the positive effect of beach width on species richness, was probably caused by the overall variation in morphology of these northward-facing beaches. These more narrow beaches had consequently a steeper slope and were more sheltered by embryo dunes, which might indicate that a lower, less sheltered highly dynamic beach area was more stressful for vegetation development (Cahoon, 2006; Hesp, 1991). The green beach wetland species in particular may be susceptible to erosion, which is supported by that the greatest species richness is found at beaches with a higher volume of embryo dunes. Embryo dunes not only shelter the dunes against storm erosion and sand burial, but might also provide a source of freshwater on the beach (Röper et al., 2013). The presence of fresh water could be beneficial for dune slack species, however, in our analysis we did not find any significant effects of embryo dune volume or secondary dune volume on electrical conductivity. The absence of this relationship could be because the embryo dune volume and secondary dune volume are not the correct parameters for the presence of fresh seepage water. A better parameter would have been the depth of the fresh water lens at the site of the green beaches (Beukeboom, 1976). Electrical conductivity was negatively related to beach elevation and was highest on wide beaches with gentle slopes.

Between 2006 and 2016 species richness increased in the vegetation plots where no sand burial occurred. Furthermore, the change in green beach wetland species richness and the fraction of stable species was positively correlated to the increase in organic layer thickness. Characteristic green beach wetland species most likely benefitted from the absence of sand burial as indicated by the (thin) organic matter layer in the plots where these species occur. As sand burial by sedimentation could be quite high (0.25 m − 1 m over 10 year), these results indicate the negative effect of sand burial on plant species richness and species turnover. Sand burial is known to cause mortality in a large number of species (Forey et al., 2008; Gilbert, Pammenter, & Ripley, 2008; Maun & Perumal, 1999; Moreno-Casasola, 1986; Sykes & Wilson, 1990). Species that did not seem to suffer by sand burial, and increased their cover since 2006, have often a strong potential for vegetative growth and are therefore well adapted to sand burial (Ecke & Rydin, 2000), for example: *Agrostis stolonifera, Hippophae rhamnoides*, and *Phragmites australis*. Furthermore, sand burial also influences site-specific variables related to elevation, such as moisture and salinity (Maun & Perumal, 1999). Soil moisture levels were mainly determined by elevation in our study, and as such an increase in elevation due to sand burial would lower moisture levels and create a less suitable environment for green beach wetland species, since these had the highest species richness in the lower areas.

The overall species richness and specifically also dune slacks species decreased at transects with a large increase in embryo dune volume. On most transects the embryo dunes were situated closer to the foredune in 2016 compared to 2006, thus squeezing the area suitable for green beach development. The landward migration of the embryo dunes suggests a reduction of suitable habitat for dune slack species by sand burial, resulting in a lower species richness and diversity of dune slack species. In 2016, dune slack species mainly occurred in areas with an organic matter layer, probably due to the absence of sand burial. The diversity and species richness of the characteristic salt-marsh species were less affected by the geomorphological setting of the beach than the overall species richness. This lower sensitivity is probably due to the large variation in plant strategies within this group which includes extremely stress-tolerant species, such as *Salicornia spp*. and *Spartina anglica*, but also less tolerant, more competitive species such as *Elytrigia atherica* and *Juncus maritimus*.

Implications for the diversity of coastal habitats

The future development of the richness of green beach wetland species (dune slack and salt-marsh species) on the green beach on Schiermonnikoog seems to be mainly determined by two processes: sand burial and succession. Sand burial causes plant mortality and changes the vegetation to species that are more resistant to sand burial, but also indirectly lowers characteristic green beach wetland species richness by changing abiotic factors by increasing elevation. Furthermore, due to the build-up of organic matter and further succession towards more competitive species, it is likely that the green beach wetland species richness will decline over the next coming years. Of the green beach wetland species, especially dune slack species are pioneers that over time become replaced by competitive tall grasses and shrubs such as *Hippophae rhamnoides* (Isermann, Diekmann, & Heemann, 2007). To postpone replacement of dune slack species for as long as possible managers could use artificial measures such as mowing or the removal of the organic soil layer (Grootjans et al., 2002). For the development of salt-marsh species, the salinity stress will determine if the pioneer vegetation will be replaced by more competitive salt-marsh species.

The window of opportunity for green beaches to develop likely depends on a combination of storm erosion and wider coastal setting (Fig. 4). Most of the beaches were eroding during our study period, which results in more dune erosion during storms, since narrow beaches can attenuate waves less than wider beaches (Ruggiero, Holman, & Beach, 2004; Short & Hesp, 1982). In the Dutch Wadden Sea in 2012 and 2013 high intensity storms caused dune erosion and sand burial (de Winter, Gongriep, & Ruessink, 2015; van Puijenbroek et al., 2017). The intensity of the storm influenced the landward migration of these embryo dunes, a period with lower intensity storms might have had less landward migration of embryo dunes. If the beaches had still been accreting, as they did between 1980 - 1995, most likely new dunes seaward of the embryo dunes would have developed, reducing storm erosion and sand burial to the area landward of these new embryo dunes. Moreover, on an accreting beach, new embryo dune development seaward of these dunes would ensure that green beach species always

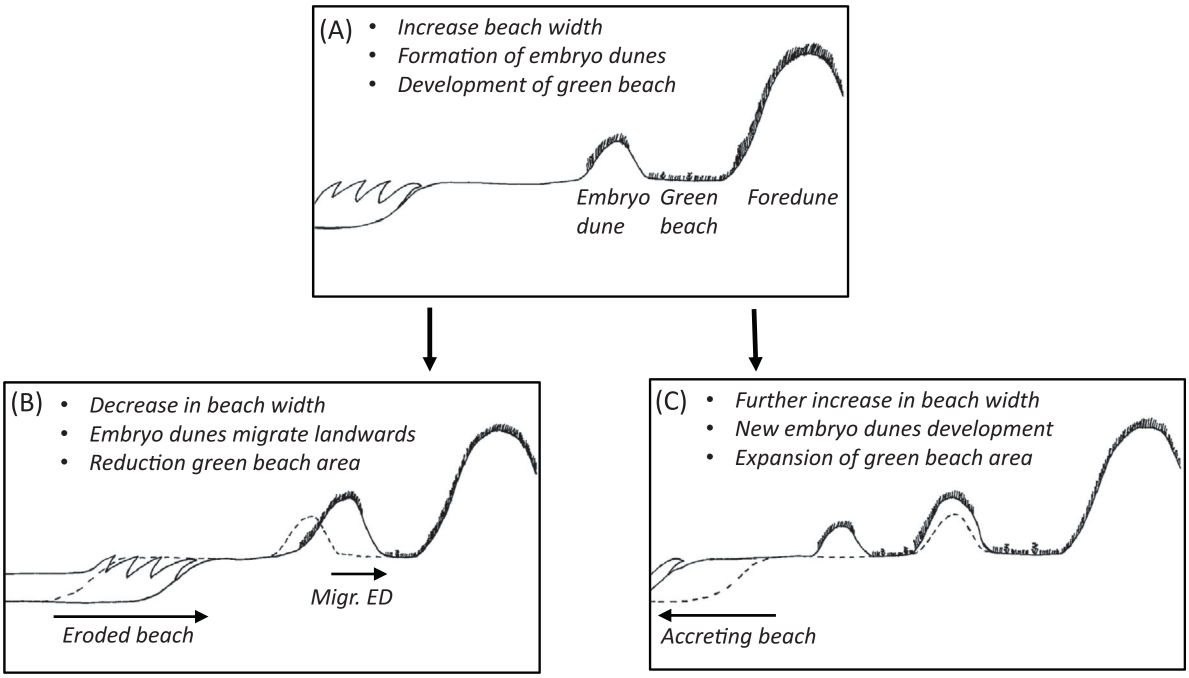

Fig. 4. A conceptual figure of green beach dynamics as consequence of increased (B) and decreased (C) beach width. (A) Beach width increased which gave opportunity for formation of embryo dunes; behind the embryo dunes a green beach vegetation developed. (B) Over time the beach decreased in width, resulting in landwards migration of the embryo dunes. This resulted in a decrease in green beach vegetation area. (C) The beach width further increases, and seaward of the embryo dune a new embryo dune develops. Between the two embryo dunes new green beach vegetation establishes. The dashed line in B and C depicts the original beach morphology of panel A. Abbreviation: ED: embryo dune.

have new habitat for establish. Such a repeating pattern of dune formation on an accreting beach, has been found on other West-Frisian islands such as Texel and Terschelling to have a positive effect on green beach wetland species in general, and dune slack species in particular (Bitton & Hesp, 2013; Grootjans et al., 2002; Kooijman et al., 2016). Hence, managers can predict the potential for development of green beach vegetation by the overall erosion or accretion of the beach. Managers can also make decisions on coastal sand nourishment for coastal protection which would affect the dynamics of green beaches. Sand nourishment can affect the sand budget and result in wider beaches, which could give the possibility for the development of embryo dunes and green beach vegetation. Generally these nourishments are applied to narrow beaches that are eroding, however, on these beaches green beach vegetation is not expected to develop. However, in recent years mega nourishments have been developed along the Dutch coast, on these mega nourishments there could be enough accommodation space for the development of green beach vegetation. For green beach vegetation to develop on such a mega nourishment a low-elevation area with shelter from sand burial should be present.

Conclusion

Our study shows the close interrelationship between beach geomorphology, sedimentation dynamics and green beach vegetation and species turnover. Key findings of this research are: 1) the geomorphological setting of the beach influences plant species richness on the green beach by affecting the amount of sand burial and soil salinity. 2) Plant species richness increased with soil organic layer thickness and decreased with sand burial, illustrating the importance of shelter for plant species on the green beach. 3) Sand burial decreases habitat suitability for green beach wetland (dune slack and salt marsh) species by increasing elevation, which in turn decreases soil moisture and salinity. 4) Green beach wetland species mainly occurred on wide beaches with large embryo dune complexes, while embryo dune development reduced the area suitable for green beach wetland species due to the associated increase in sand burial. This study has important implications for predicting occurrence and succession of dune wetland vegetation, which is relevant for engineering and management of biodiverse sandy shores.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.06.003.

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