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Foredune initiation and early development through biophysical interactions

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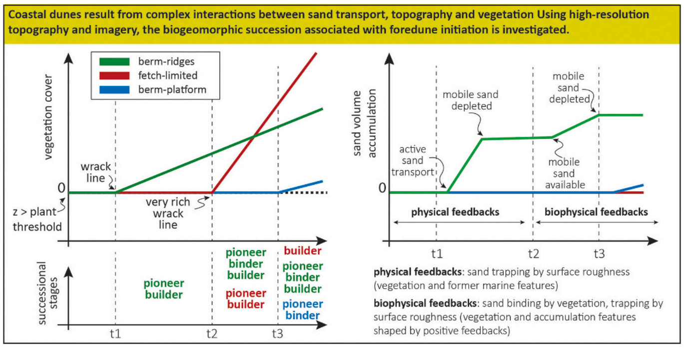
HIGHLIGHTS

- Natural foredune initiation documented by high-resolution topographic and plant surveys
- Marine processes provide the conditions for foredune initiation.
- Two morphological types (ridge and terrace) linked to plant colonisation strategies
- Sand accumulation is controlled by physical factors during dune initiation.
- Biophysical feedbacks control sand accumulation during early development stages.

GRAPHICAL ABSTRACT


Coastal dunes result from complex interactions between sand transport, topography and vegetation Using high-resolution topography and imagery, the biogeomorphic succession associated with foredune initiation is investigated.

physical feedbacks: sand trapping by surface roughness (vegetation and former marine features)

biophysical feedbacks: sand binding by vegetation, trapping by surface roughness (vegetation and accumulation features shaped by positive feedbacks)

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ABSTRACT

Coastal dunes result from complex interactions between sand transport, topography and vegetation. However, uncertainty still persists due to limited quantitative analyses, integrating plant distribution and morphologic changes. This study aims to assess the initiation and maintenance of feedback processes by analysing the early development stages of incipient foredunes, combining data on the evolution of the plant cover and communities and dune morphology. Over three years, the monitoring of a newly formed dune (1 ha plot) reveals the progressive plant colonisation and the episodic accumulation of sand around vegetated areas controlled by sediment availability. Distinct colonisation rates were observed, influenced by inherited marine conditions, namely topography and presence of beach wrack. Berm-ridges provided elevations above the critical threshold for plant colonisation and surface roughness, aiding sediment accumulation. Beach wrack above this threshold led to rapid expansion and higher plant concentration. In the initial stages, vegetation cover significantly influenced sediment accumulation patterns, with higher accumulation around areas with high plant cover and low slopes or around areas with sparse vegetation but milder slopes. As the dune system matured and complexity grew, the link between vegetation cover and accumulation became nonlinear. Mid to low coverages (5–30 %) retained most of the observed accumulation, especially when coupled with steep slopes, resulting from positive feedbacks between vegetation, topography and sand transport. As foredune developed, vegetation cover and diversity

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increased while inherited morphologies grew vertically, explaining the emergence of dune ridge morphological types. Flat surfaces lacking wrack materials experienced a three-year delay in colonisation and sand accumulation, leading to the formation of terrace-type incipient foredunes. These observations underline feedback processes during the early stages of dune formation, with physical feedbacks primarily driving initiation and biophysical feedbacks prevailing in subsequent colonisation stages.

1. Introduction

Coastal dunes are dynamic and heterogeneous ecosystems with significant conservation value due to their rich ecological diversity, serving as habitats for endangered, endemic or highly specialized flora and fauna species (Martínez and Psuty, 2004). In addition, coastal dunes offer an array of important ecosystem services that are sustained by coastal geomorphic processes and location-specific conditions, providing direct and indirect economic benefits to humans (e.g., Barbier et al., 2011; Richardson and Nicholls, 2021). They are also critical for nutrient cycling and groundwater recharge zones, and they offer vital protection and defense against coastal erosion, flooding, and sea-level rise (e.g., Acosta et al., 2009; Biel et al., 2017; Mendoza-González et al., 2012; Richardson and Nicholls, 2021). These multiple values and benefits explain the interest in understanding and preserving these dynamic but fragile habitats threated by the intense human occupation of the coast and climate change.

Coastal dunes result from the accumulation of wind-blown sand, transferred inland from the beach and trapped by physical barriers such as vegetation, which plays a central role in the process of dune growth by promoting accumulation and fixation of sediment in place (Davidson-Arnott et al., 2012; Hesp, 2002). In addition, vegetation has been shown to have an active role in dune growth through feedbacks with the dune topography and air flow (Hesp et al., 2015; Kombiadou et al., 2023; Walker et al., 2022). Dune vegetation is responsible not only for trapping sand and promoting dune growth, but also for preventing its erosion (Kombiadou et al., 2023; Woodhouse, 1978), functions that are largely determined by plant functional morphologies (Hacker et al., 2019; Walker and Zinnert, 2022). These capabilities allow plants to promote the formation of shadow dunes (Charbonneau et al., 2021; Hesp, 1989) and reinforce these morphologies, growing concurrently with sand accumulation (Bonte et al., 2021; Brown and Zinnert, 2018). The latter is possible because of the ability of some plant species to grow in pace with sand accumulation, which functions in turn as an active source of nutrients to these plants also known as dune builders (Maun, 2009, 1998; Yuan et al., 1993). In addition, vegetation plays a role at the landform scale, through the spatial distribution of plants (i.e., plant spacing, cover) and dominant plant species (e.g., Hesp et al., 2019). Plant spatial distribution has been recognised to impact sediment accumulation, with greater rates of sand deposition associated with more irregular plant spacings (Hacker et al., 2019, 2012; Reijers et al., 2019). Plant growth strategies appear to control dune growth patterns (i.e., horizontal or vertical), with plants characterised by rapid horizontal growth promoting wider dune development (Jay et al., 2022; Zarnetske et al., 2015). Plant morphology (e.g., tall, erect plants vs short prostrate plants) also affects aeolian sand accretion and foredune development (Hesp, 2002, 1989). In fact, differences in functional morphologies and growth strategies among dune builder plant species explained different dune shapes at decadal timescales (Ruggiero et al., 2018; Zarnetske et al., 2015), supporting the relevance of these traits to morphological change also at a landscape scale. However, the intricacies of these relationships remain elusive due to the limited availability of quantitative data regarding the growth and sand-capture capabilities of coastal dune vegetation (McGuirk et al., 2022). Uncertainties persist surrounding the underlying causes of observed topographic heterogeneity, which are linked to varying plant species and densities (Charbonneau et al., 2021). It is essential to acknowledge that coastal dune formation arises from complex biophysical interactions, involving a myriad of factors including climate and rainfall (Hesp et al., 2021). This complexity renders the identification of primary drivers and causal triggers exceedingly challenging.

Research has demonstrated that dune morphology and volume can be partly explained by physical factors, such as sediment budgets (Davidson-Arnott et al., 2018; Herrero et al., 2020; Psuty, 2004), pre-existing morphologies (Houser et al., 2008; Hovenga et al., 2023), surfzone-beach types (Moulton et al., 2021; Short and Hesp, 1982), and shoreline change rates (Biel et al., 2019; Costas et al., 2023). In addition, physical factors appear to regulate the role of vegetation within the plant-sand feedback, ultimately promoting or inhibiting vegetation effects on dune topography (Costas et al., 2023). Plant distribution and community composition appear to be largely controlled by erosion/sedimentation patterns (Bitton and Hesp, 2013; Maun and Perumal, 1999; Tsoar et al., 2009), marine-generated disturbances (Costa et al., 1996; Hesp and Martínez, 2007; Miller, 2015), elevation (Galiforni Silva et al., 2019; Moreno-Casasola, 1986) and factors such as salinity, nutrient availability, and sand abrasion (Maun, 2009). In addition, physical factors also determine how plant seeds are first delivered to the backshore, which can happen in an organised or random way. For example, where the high spring tide swash aligns seeds in a narrow line or zone along the backshore, or where seeds are randomly blown and spread across the backshore (Hesp, 1989).

Even though dune and vegetation patterns have been well documented in a variety of coastal systems (Bitton and Hesp, 2013; Konlechner et al., 2019), the necessary information to fully understand biophysical interactions controlling dune evolution is often missing. Few studies have simultaneously studied both dunes and vegetation through time in order to quantify the dynamic relationship between geomorphology and vegetation (Miller, 2015). Biophysical interactions seem to arise as early as a foredune is initiated, determining the type of incipient dune formed (Hesp, 1989). The latter has been associated with both the mode of beach colonisation (including colonising plant species, their cover and distribution) and the availability of sand, whose combinations give rise to ramp, terrace or ridge morphologies (Hesp, 1989). Plant initiation at the backshore through seed germination or plant fragment growth (McGuirk et al., 2022) is facilitated by the presence of swash-aligned drift material (Hesp, 1989; Hilton and Konlechner, 2011). Despite the relevance of biophysical interactions during the early stages of coastal dunes to the natural or artificial evolution of the system, very few examples that quantitatively characterise dune initiation and subsequent early stages exist (van Puijenbroek et al., 2017b). To fill this gap, field and wind tunnel experiments have been carried out to establish relationships between plant characteristics (i.e., morphology, cover and distribution) and generated topography, using artificial and natural plants (e.g., Bauer et al., 2022; Charbonneau et al., 2021; Hesp et al., 2019; Li et al., 2022; Miri et al., 2019; Rotnicka et al., 2023). While these studies offer valuable insights for designing foredune planting strategies and management practices, they may not capture landscape-scale biogeomorphic succession. This limitation arises from their limitation to fully replicate the dynamic interplay between vegetation and sediment transport over time.

This work seeks to assess how certain biophysical feedback processes are initiated and maintained in temperate coastal dunes, by analysing the early development stages of a foredune, combining data on the evolution of its biotic (plant cover and plant communities) and abiotic (morphology) components. In this study, we investigate the formation and early-stage development of a coastal dune facilitated by the generation of new accommodation space after the elongation of a sandy peninsula. Our analysis, conducted over a plot of 105 m × 95 m, between 2019 and 2022, employed high-resolution images and photogrammetry data obtained from Unmanned Aerial Vehicle (UAV) surveys. Information from biotic (plant cover and community composition) and abiotic (topography, slope, distance to shoreline, sand accumulation/erosion) factors is integrated in order to understand the relative contributions to dune initiation and growth and the relevance of their interaction to the evolution of the overall system. Namely, patterns of vegetation distribution are compared to local physical parameters, such as elevation, distance to shoreline and sand accumulation/erosion in order to identify spatial plant colonisation and expansion preferences and their impact on the accumulation of sand.

2. Study site

The study area is located at the eastern end of the Ancão Peninsula, within the western flank of the Ria Formosa barrier island system at the southern coast of Portugal (Fig. 1). Sediments within the dune-beach system of Ancão have been classified as very well sorted medium to coarse quartz sands, with mean grain sizes varying from 0.35 mm to 0.80 mm at the beach (Costas et al., 2018) and around 0.50 mm at the dune (Costas et al., 2020). Ancão Peninsula is separated from the adjacent barrier island (Barreta Island) by Ancão inlet, a small, migrating, mixed-energy tidal inlet, driven by the combined action of tides and waves (Morris et al., 2001). The inlet migrates eastward until a maximum distance or limiting position is reached, after which it loses hydraulic efficiency (Vila-Concejo et al., 2002) and eventually enters a new migrating cycle through breaching of a new opening at a westward position. Breaching can be natural (∼1945 and 1996) or artificial (1997

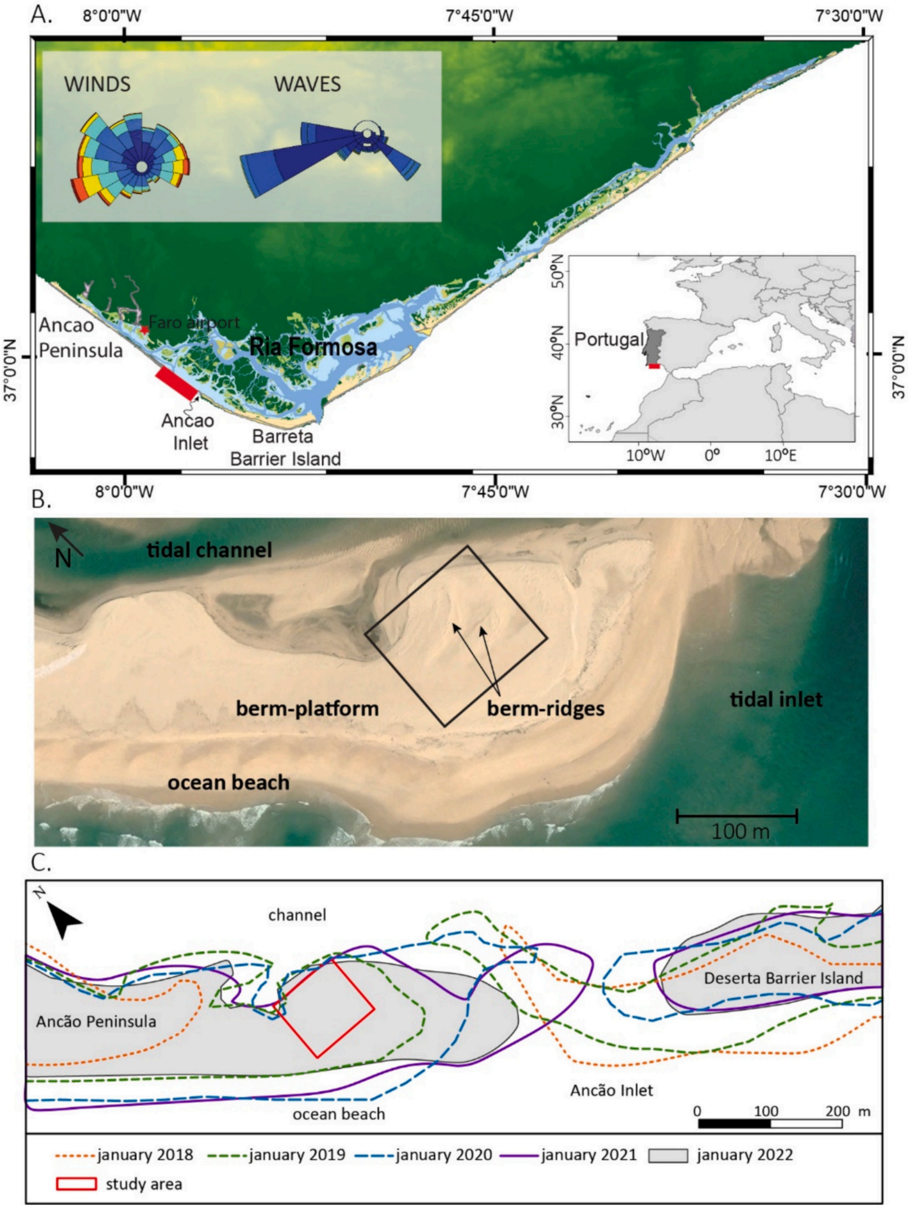

Fig. 1. Location of the study area. A. Panel showing the location of the site within the Ria Formosa barrier island system, including characteristic wave and wind roses. B. Panel showing the detail of the study area, located at the downdrift end of the Ancão Peninsula and highlighted with a square. The image used is from December 2019 and was retrieved from Google Earth. The terminology used for the progradational features was adopted from Hine (1979). C. Panel showing the evolution of the shoreline (mapped from Sentinel-2 imagery) between January 2018 and January 2022, illustrating the elongation of the sandy peninsula to the east.

and 2015). After its last relocation in 2015, the inlet moved westward, eroding part of the updrift peninsula. The maximum westward excursion was forced by the impact of a high-energy storm in February/March 2018 (Costas et al., 2023). The subsequent recovery promoted the elongation of the peninsula towards the east, with the growth of a recurved spit, forming a new relatively flat area through berm-ridge progradation (Fig. 1). Elongation resulted in the extension of the peninsula by around 400 m eastwards and the migration of Ancão inlet until January 2022 (Fig. 1). This created new accommodation space, allowing for new habitats and services and providing the opportunity to study the initiation and early stages of a coastal dune located in a temperate zone and the possible interaction between the emerging dune and the associated vegetation cover.

2.1. *Environmental conditions*

Oceanic conditions exhibit a moderate wave climate, with average annual offshore significant wave heights of around 1.0 m and peak periods of 8.2 s, with waves approaching from W-SW (70.6 % occurrence) and E-SE (26.7 % occurrence) (Costa et al., 2001). Tides are characterised by a mesotidal regime with a mean tide range of 2.2 m that reaches 3.5 m during spring tides. Net longshore drift is considered the main sand supplier of this coastal system and is directed eastwards (Andrade, 1990). Estimates of longshore sediment supply vary from author to author, with the most recent one suggesting values on the order of 110,000 m^3/year (Santos et al., 2014).

Local winds during the monitoring of the study area were characterised using forecasted wind velocities and directions retrieved from the THREDDS (Thematic Realtime Environmental Distributed Data Service) server operated by MeteoGalicia and simulated by a Weather Research and Forecasting (WRF) model. Forecasted data correspond to the model domain of 12 km resolution (www.meteogalicia.gal). Wind data suggest that winds were not very strong and did not show a clear temporal distribution. An apparent increase in the magnitude of the winds seems to occur during winter months (December to March), while lower intensity winds appear to prevail during the rest of the year (Fig. 2A). Regarding wind directions, dominant winds approach the area from the north-west sector, negative quadrants (i.e., north-westerly winds), while winds from positive quadrants (i.e., easterly winds) are less frequent (Fig. 2).

Wind events capable of inducing sand transport in the area (threshold ~8 m/s) were more frequent during the period between October 2020 and May 2021 and during the period between October 2021 and May 2022 (Fig. 3). In relation to wind directions, the quadrant that concentrates most of the strong winds is again the fourth one (northwesterlies), which recorded the stronger winds through most of the period of analysis. The second most important was the second quadrant (south-easterlies), while the first quadrant (north-easterlies) showed lower frequencies. Variable wind directions and intensities explain different potential sediment transport directions through the period of analysis, which, given the low elevation and high exposure of the study site, could promote the vertical growth of incipient dunes under favourable conditions.

3. Data and methods

3.1. *High spatial resolution imagery and topography*

The area of interest was periodically (autumn and spring seasons) surveyed between September 2019 and May 2022, namely in: September 2019, May 2020, October 2020, May 2021, October 2021, and May 2022. Two UAVs were used to obtain images for vegetation mapping and topographic reconstruction. In both cases, flying elevations were around 30 m because of imposed limitations at the study area related to its proximity to an airport (Fig. 1). For vegetation mapping, a Phantom 4 Multispectral (PM4) drone was used. This platform collects images with a RGB camera and a multispectral camera array with 5 sensors (RGB, RedEdge, and NIR), all at 2 MP with global shutter. The near infrared (NIR) and red bands were used to obtain the Normalized Difference Vegetation Index (NDVI), to assist with the vegetation mapping. Topographic changes were detected using a Mavic 2 Pro UAV from DJI, equipped with a Hasselblad L1D-20c Camera, and applying UAV Structure-from-Motion (SfM) techniques to obtain high-resolution digital surface models (DSMs). In both cases, UAV flights were designed to ensure frontal and side overlaps of 80 % and 75 %, respectively. Surveys were performed flying parallel and cross-shore to the shoreline and were later combined to improve the quality of the products (Bon de Sousa et al., 2022), namely of the orthophotomosaics and the DSMs.

The position of ground control points (GCP) and check points were taken using a RTK-DGPS. GCPs were collected to assist image rectification and check points were used to assess product accuracy. Ground sampling distances ranged between 0.52 and 0.69 cm. Products were obtained using the Agisoft Metashape software. The assessment of the quality of the products was carried out by estimating horizontal and vertical mean squared error (MSE) by comparing the data extracted from the products and the check points. Obtained accuracies ranged between 3 and 11 cm.

3.2. *Topographic changes*

Topographic changes were obtained from the comparison and subtraction of consecutive surveys to obtain the DSMs of Difference (DoDs). In order to account for the vertical error of the DSMs, the accumulated error was estimated for each DoD. Given the high spatial variability in vertical error within a single survey, the highest error was selected as representative of the overall error as a conservative approach, to minimise uncertainty in derived topographic changes. This prevented errors induced for example by surface reflectance variability, which were

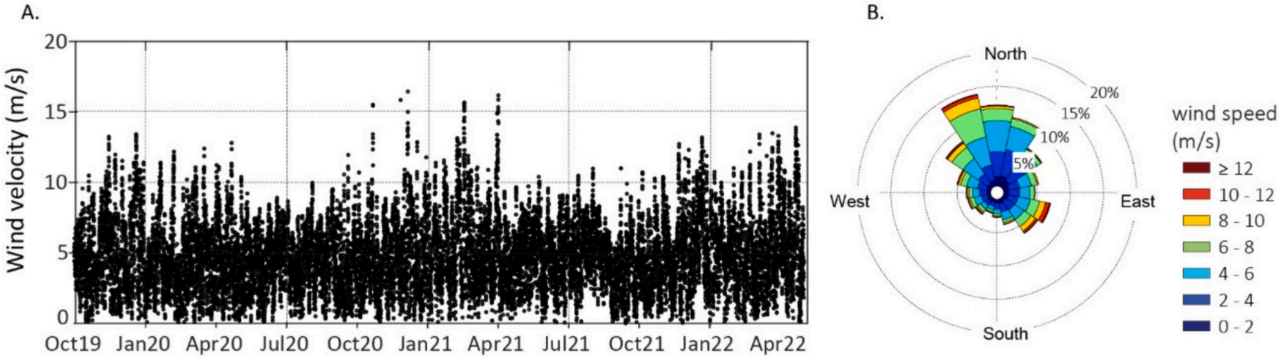

Fig. 2. Wind velocities during the monitoring period. Forecasting winds were retrieved from the THREDDS server operated by MeteoGalicia and simulated by a WRF model domain at a 12 km resolution (www.meteogalicia.gal).

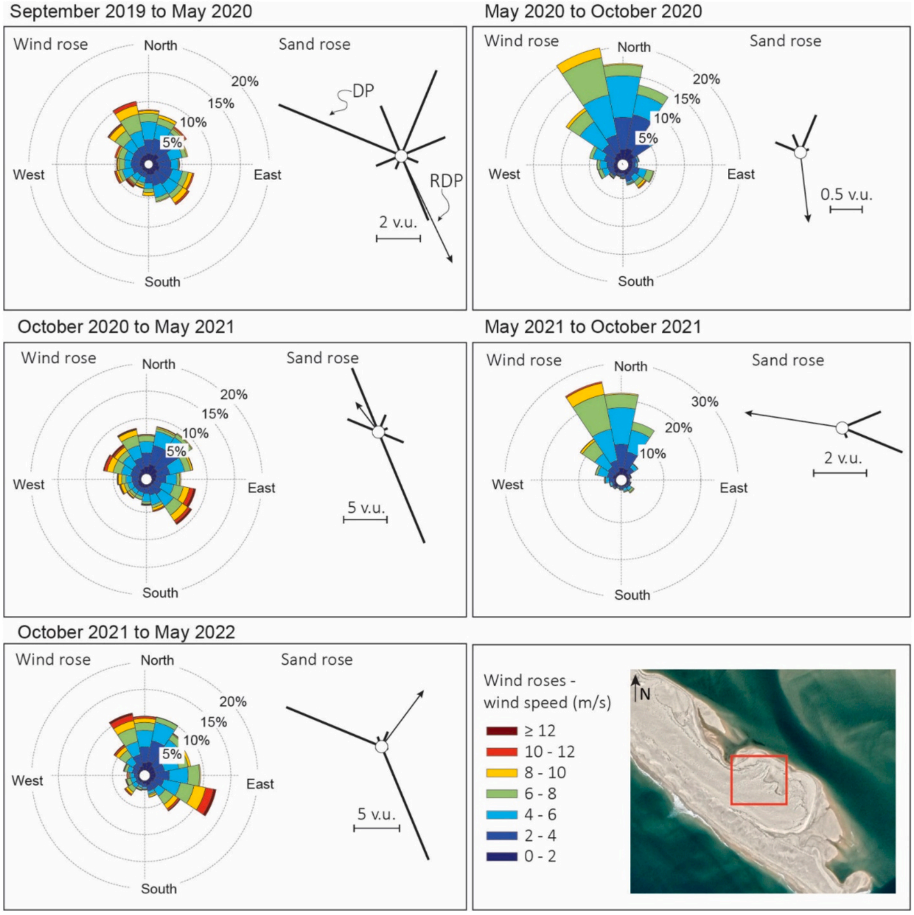

Fig. 3. Representation of wind and sand roses for each interval of time between the field surveys carried out in September 2019, May 2020, October 2020, May 2021, October 2021, and May 2022. Sand roses represent the drift potentials (DP) for each wind direction and the resultant drift potential (RDP), represented with an arrow.

particularly frequent around flat bare-sand areas. The selected value was 0.13 m, which appeared suitable for all DoDs, and was used as a cut-off value, so that measured elevation changes within the error range (−0.13 to +0.13 m) were discarded from the analysis. A careful examination of the obtained DSMs suggested additional sources of error related to the occurrence of highly reflective surfaces and to the overlap of marine and aeolian processes around the boundaries of the area of interest. To rectify this issue, images were clipped to the area subject to aeolian processes, avoiding significant impact of marine processes and additional sources of error. In order to make this data more easily comparable with the data from the vegetation surveys, topographic data was downscaled, calculating vertical elevation changes and DSM slopes over a grid with resolution of 1 m × 1 m.

3.3. Vegetation cover evolution

The changes in the vegetation cover across the area of interest were documented by mapping the plants on the orthophotomosaics obtained from the PM4. The mapping included several steps to extract the vegetation from the NDVI image and transfer the data to the grid used for topographic changes. Initially, plants were isolated from the sand, applying a threshold value of 0.07 to the NDVI mosaics. The validity of the NDVI threshold applied, was verified against the higher spatial resolution imagery from the Mavic, which allowed visual recognition of plants. A careful assessment of the quality of the results was carried out by visually inspecting and manually cleaning other elements (e.g., wrack or other debris materials) mapped as plants. Once vegetation was extracted as polygons, plant cover was calculated over the same (1 m × 1 m) grid created to aggregate the information about the topographical changes.

High-resolution orthophotomosaics were used to identify individual plant species (see Supplementary Fig. 1) and showed that some zones were dominated by one or two plant species, allowing to using these dominant species to classify and group the plant polygons extracted from the NDVI. The name of the dominant species was given to the group. In cases where multiple species dominated, they were listed based on their apparent abundance, prioritizing the most prevalent ones. The plant groups and sandy surface were also classified in terms of successional stages into four stages, increasing the complexity/maturity level: bare-sand, pioneer plants, dune builder and sand-binder plants. This classification was adapted from Feagin et al. (2005), including the discrimination between typical pioneer colonisers (e.g., *Cakile maritima*) and typical dune builder species (e.g., *Ammophila arenaria*). The former group refers to the typical first colonisers of the beach bare-sand (Martins et al., 2013) while the latter group includes plants that tolerate and benefit from high burial rates, promoting vertical dune growth (Pickart, 2021). Sand-binders are known to still tolerate sand burial (e.g., *Otanthus maritimus*) and prevent erosion by binding sediments (Feagin et al., 2015). This approach was considered due to the limited spectral resolution provided by the PM4 that prevented the direct classification of plant species as shown by previous works applying hyperspectral cameras (Laporte-Fauret et al., 2020). The classified plant maps were used to count the number of isolated plants within each group and to assess major compositional changes through time. Each isolated plant was assigned information regarding its elevation relative to the mean sea level (MSL) and the distance to the nearest shoreline. The first was obtained by intersecting the output of the plant mapping with the corresponding DSM. While the second consisted on measuring the minimum distance between the isolated plants and the shoreline mapped from the orthophotomosaics. One-way ANOVA (“analysis of variance”) was performed on the data, to identify potential preferences of plant group/species (independent variable) in terms of elevation and distance to the shoreline (dependent variables). When ANOVA showed significant differences ($p < 0.05$), pairwise comparisons, applying a Tukey’s Honest Significant Difference (HSD) test, were done to explore significant differences between all pairs of independent variables. The relative size of the effect (Eta-squared value) was also determined to support the ANOVA output.

Finally, identified wrack zones were analysed to evaluate the impact of the presence of these nutrient and seed rich zones to the distribution of plants. Beach wrack in the study area was dominated by fragments of seagrasses (mainly *Zostera noltii*), reeds and other plants. Individual wrack zones identified in September 2019 were mapped and were used to obtain values of mean elevation, vegetation cover and sediment accumulation within the zones through time. Variance between the various wrack zones was analysed through One-Way ANOVA, as described above.

4. Results

4.1. Morphological characterisation and evolution

The study area is located on a hook spit that was formed recently, comprising distinct morphological regions. Two berm-ridges (ridge-1 and ridge-2) with elevations between 1.9 and 2.2 m (Fig. 4A) can be easily identified and defined using the DSMs obtained during the

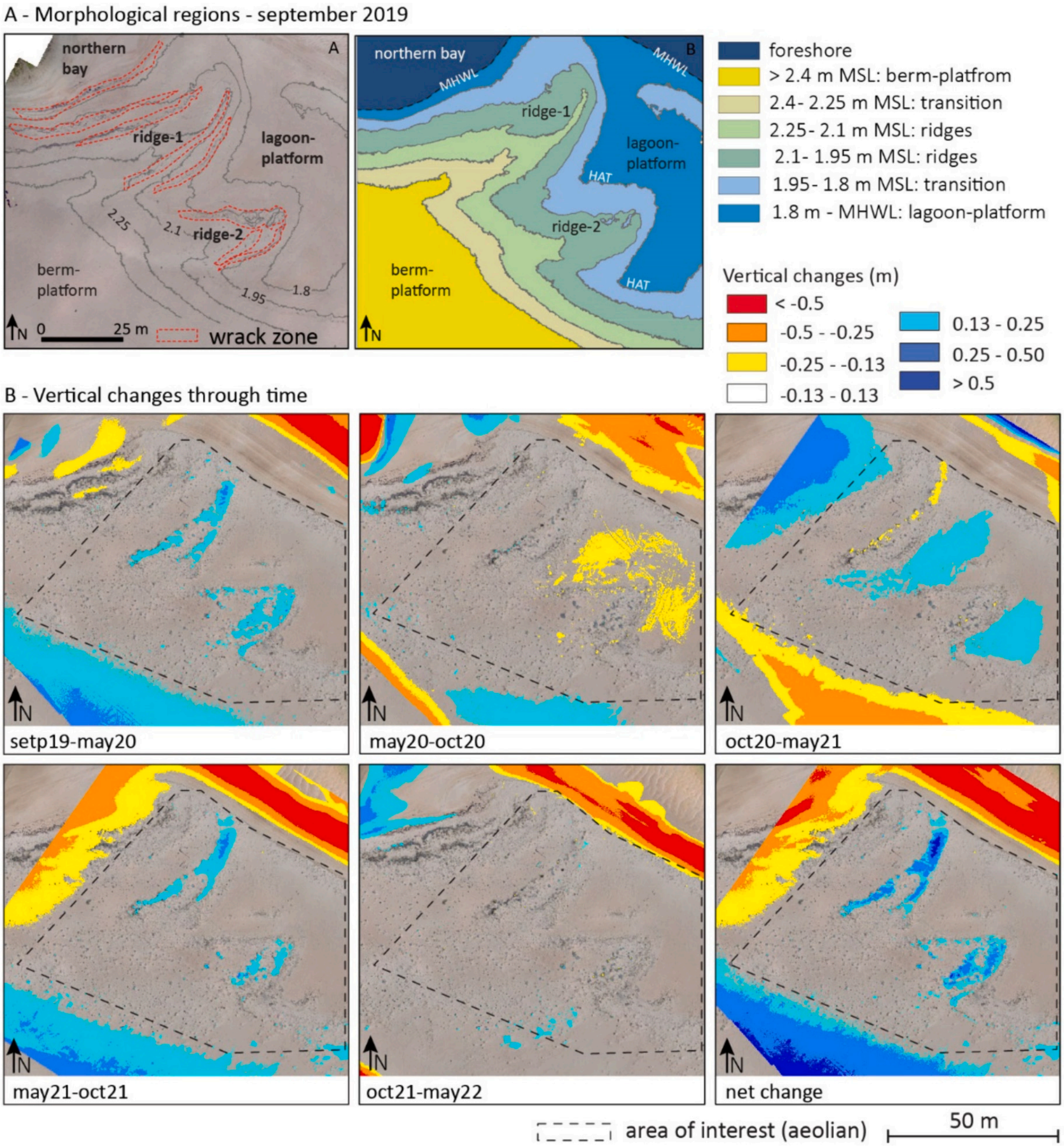

Fig. 4. (A) Image and topography of the study area showing the contour lines (m above MSL), the morphological regions and their typical elevation, as well as the distribution of the main beach wrack zones mapped in September 2019 (dashed red lines). (B) DoDs calculated between each survey and net topographical changes. The image used as the base map is from May 2022. Values between −0.13 and +0.13 m are considered insignificant (i.e., within the estimated vertical error). Dashed line polygon represents the area used for the computation of aeolian sediment accumulation/erosion.

monitoring surveys. These features, formed by the elongation of the spit, were separated by a lower and flat surface located between the mean high-water and the highest astronomical tide levels (1.4–1.8 m), referred to hereafter as lagoon-platform (Fig. 4A). The lagoon-platform was rarely inundated after its establishment and during the initial evolutionary stages (i.e., under high spring tides and/or storm surges). This platform was particularly exposed to easterly winds, functioning as a source of sediment towards the ridges. The study area was protected from the impact of waves by a beach-berm formed above 2.4 m through the seaward progradation of the beach (Fig. 1). The flat surface of this zone will be referred to as berm-platform (Fig. 4A). This region was exposed to westerly winds, providing sediment to the area of interest. Wrack zones (nine in total) accumulated before September 2019 are shown in Fig. 4A, with greater concentration around the northern bay and the edges of the ridges.

After its formation around January 2019, the study site did not show major morphological changes (Fig. 4B). Detectable vertical changes (out of the accepted error range) related to aeolian processes (i.e., excluding interference from marine processes) concentrated at the former berm-ridges during the periods between September 2019 and May 2020 and between May 2021 and October 2021 (Fig. 4B). During these periods the inherited morphology was reinforced with the increase in elevation of the initial ridges of up to 0.55 m, maintaining, the elevation of the platforms. As aforementioned, accretion at the ridges seems to result from the accumulation of blown sand transported from the adjacent bare-sand flat surfaces, but mostly from the adjacent lagoon-platform. Accretion was particularly important at ridge-1, whose related fetch distances over the lagoon-platform were greater (up to 50 m) than the ones surrounding ridge-2 (up to 20 m). Topographical changes during the remaining monitoring intervals were not as significant, suggesting that the system entered periods that can be assumed as quiescent (changes below the detection level of our approach). The occurrence of strong winds throughout the year suggests that transport was most likely controlled by supply limiting conditions (Costas et al., 2020; Delgado-Fernandez and Davidson-Arnott, 2011).

Vertical changes observed across the lagoon-platform appear to be related to aeolian and marine processes due to the occasional inundation of this area. The latter could be induced by the combined effect of storm surge and high astronomical tides during winter, promoting the accumulation of a new thin layer of sand as observed between October 2020 and May 2021 (Fig. 4B). This process would have helped to reset the surface, providing new and finer sediments for the winds to blow and prevent surface armouring. Conversely, aeolian processes seem more likely responsible for the erosion of the surface documented in the period between May 2020 and October 2020. This could also promote the depletion of finer sand fractions and create subsequent surface armouring.

4.2. Vegetation cover characterisation and evolution

After the hook spit formation, vegetation started to slowly colonise the area, showing very few plants and low cover in September 2019

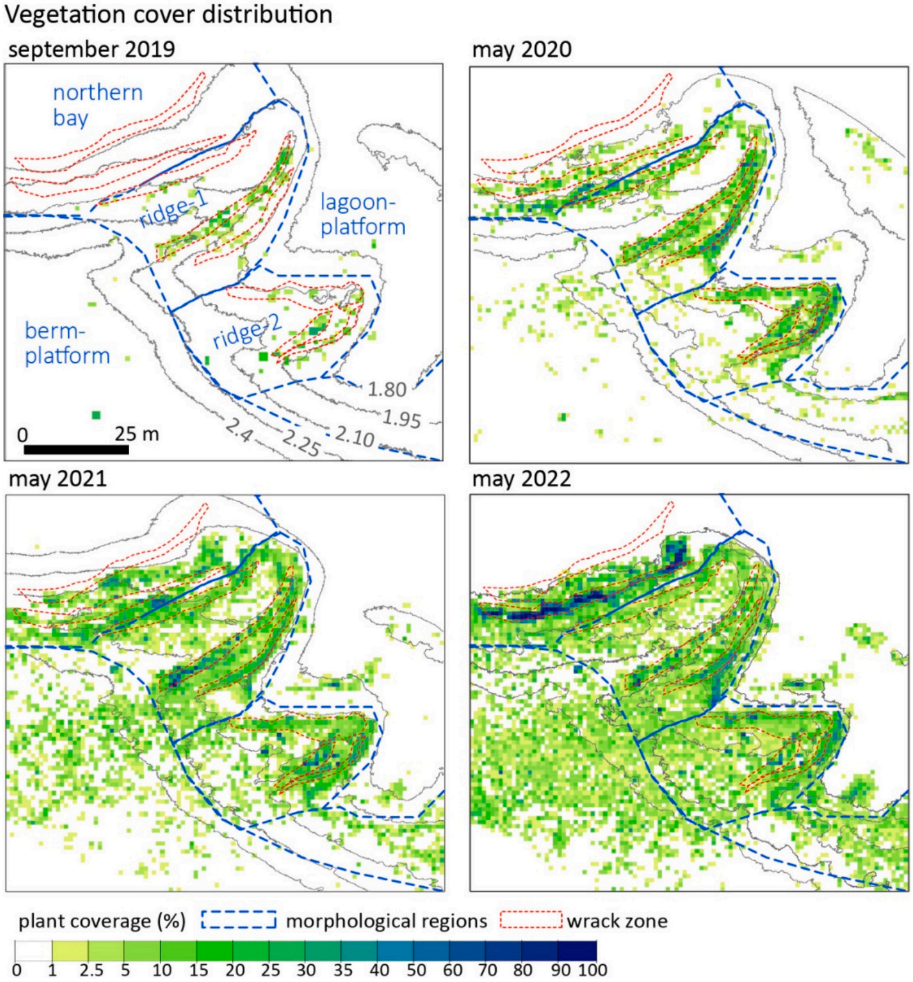

Fig. 5. Maps of the study area showing the temporal evolution of the vegetation cover and the position of the beach wrack as reported in September 2019. Data represent the vegetation cover in percentage at plot level (i.e., 1 m^2). Red dashed lines represent the wrack zones and blue dashed lines the morphological regions.

(Fig. 5). Following this initial stage, vegetation expansion was relatively fast, increasing quasi-linearly over the remaining period. The plant species during all surveys were classified according with the successional stage that they represent, into pioneer, dune builder or sand-binder (Table 1, Supplementary Fig. 1). Vegetation cover values for each morphological region seem strongly-skewed (Supplementary Fig. 2), suggesting a rather heterogeneous distribution of plants, with high variability in values above the mean (Supplementary Fig. 2). Wrack occupied between 21 and 32 % of the morphological units' surface in September 2019 (Table 2).

The total vegetation cover in September 2019 was 0.6 %. At the scale of the 1 m × 1 m cell, coverages of up to 30 % were found (Fig. 5, Supplementary Fig. 2), however mean values were low (0.22 ± 1.81 %). Colonisation initiated at the ridges, with very few to no plants on the berm- and lagoon-platforms and on the northern bay region (Fig. 5, Supplementary Fig. 2). Most of the new plants appeared within the mapped wrack zones, which accounted for up to 87 % of the cover (Table 2). The reduced number of plants found in the first survey facilitated species classification at the individual plant level. The number of species was three, represented by *Polygonum maritimum*, *Elymus farctus* and *Ammophila arenaria*. The first species is considered as a pioneer species while the two other are dune builder species (Table 1, Supplementary Table 1). Most plants colonised the contour lines of 2.1 and 2.25 m at ridge-1 and close to the contour line of 1.95 m at ridge-2 (Fig. 5). Yet, *Polygonum maritimum* plants appeared at significantly lower elevations and distances to the shoreline than *Elymus farctus* and *Ammophila arenaria* plants (Fig. 6). Interestingly, wrack zones along the ridge crests (i.e., higher elevation) (Fig. 5, Supplementary Fig. 3), were mostly colonised by the two dune builder species.

The next survey (May 2020) shows an increase in vegetation cover to 4.2 % of the total surface with average vegetation cover around 1.45 ± 4.96 % and maximum values reaching up to 60 % at the plot (1 m^2) level (Fig. 5, Supplementary Figs. 2, 3). As for the previous survey, vegetation expansion was higher across the ridges, with plants tending to concentrate around zones that coincide with the wrack mapped in September 2019 (Fig. 5). In fact, cover data from the mapped wrack zones suggests that vegetation continues to concentrate in these zones, which account for up to 83 % of the vegetation cover within the morphological region (Table 2). The northern bay area became a new colonisation region during this period (Supplementary Fig. 2). Here, the relation to the presence of wrack was not so clear because of relatively frequent inundation. Vegetation cover remained very low across the platforms, which displayed a very different colonisation pattern from the other regions (Fig. 5). The berm- and lagoon-platforms were colonised by pioneer species (Supplementary Table 1), which is also the overall dominant group at this initial stage (Fig. 7). The ridges were colonised by communities dominated by a mixture of builder and pioneer species (Supplementary Table 1), with the former concentrating along the crests of the ridges, as also documented by their preference for higher elevations (Fig. 6). The northern-bay was colonised by pioneer plant species at an elevation of around 1.95 m (Fig. 5, Supplementary Table 1). The elevation and distance to the closest shoreline of each identified group community differ very little, showing similar values close or even within the detection threshold of the applied approach. Yet, the variance analyses (Fig. 6) reveal that the differences between the groups were significant, confirming that each group tended to occupy a particular space (Fig. 6).

Table 1
List of identified plants, successional stages, lifespan and typical location across the beach-dune profile where they can be found.

Plant species	Successional stage	Lifespan	Typical location
Cakile marítima Scop.	Pioneer	Annual	Beach backshore
Polygonum maritimum L.	Pioneer	Perennial	Beach backshore
Elymus farctus (Viv.) Runemark ex Melderis	Dune builder	Perennial	Embryo dunes, foredune
Ammophila arenaria (L.) Link	Dune builder	Perennial	Embryo dunes, foredune
Calystegia soldanela (L.) Roem. & Schult.	Sand-binder	Perennial	Embryo dunes, foredune
Eryngium maritimum L.	Sand-binder	Perennial	Embryo dunes, foredune
Otanthus maritimus (L.) Hoffmanns. & Link	Sand-binder	Perennial	Embryo dunes, foredune
Crucianella marítima L.	Sand-binder	Perennial	Foredune
Silene nicaeensis All.	Sand-binder	Annual	Foredune

Table 2
Contribution of the wrack zones to the different regions where they have been identified in September 2019. The first line represents the percentage of surface that wrack occupies within each region. Lines two to five represent the percentage of vegetation cover that corresponds to the wrack zone in each morphological region.

Region		Ridge 1	Ridge 2	Northern bay
Wrack surface (%) $(\frac{\textbf{\textit{wrack surface}}}{\textbf{\textit{region surface}}}\textbf{*100})$		26	21	32
% of wrack vegetation	Sep-19	87	78.3	0
	May-20	83	72.3	36.4
	May-21	65.4	55.4	30.5
	May-22	54	40.7	8.9

Over time, colonisation continued, increasing plant cover across all morphological regions, in particular across the northern bay with the platforms still displaying very low values (Fig. 5). Vegetation cover doubled between May 2020 and May 2021 and reached 12 % of the total analysed surface in May 2022. Cover values at the plot level (1 m^2) also increased, reaching maximum values of 98 % in May 2022. Despite that, the cover of plants remained low with overall average values around 2.93 ± 6.68 and 4.55 ± 9.35 % during May 2021 and May 2022, respectively. Spatially, vegetation cover followed the previous patterns with higher average values across the ridges and lower values across the platforms (Fig. 5, Supplementary Fig. 2) and with the northern bay showing very rapid expansion (Fig. 5, Supplementary Fig. 2). The expansion of vegetation allowed the colonisation of a large part of the area above 1.8 m, an elevation that coincides with the level of the highest astronomical tide (Fig. 6). This is consistent with other studies that show pioneer plant colonisation is typically sustained only above the spring high tide levels (Bauer et al., 2012; Doing, 1985; Tobias, 2015). Yet, it is worth noting that a few pioneer plants were observed below this level probably because of their tolerance to rare inundation. Vegetation expansion induced a more homogeneous cover, reducing the relative importance of the wrack zones whose values dropped by >30 % since the initial survey (Table 2).

The distribution of plants shows a clearer pattern through time with sand-binder species predominantly populating higher elevations and areas distant from the shoreline (Fig. 6), while dune builders displayed wider ranges. It is also important to note that both species dominated the ridges, where the distance to the adjacent shoreline ranged between 5 and 25 m because of its curved shape (Fig. 4A).

As vegetation cover in the area expanded, so too has species richness, rising from three in September 2019 to nine by May 2021 (Supplementary Table 1). The latter include the emergence of sand-binder species, represented by *Otanthus maritimus*, shifting from pioneer and builder species and colonising bare-sand areas (Fig. 7). Builder species also increased their abundance in May 2022 by colonising bare-sand and areas previously dominated by pioneer species (Fig. 7). Through time, pioneer species tend to be replaced by other plant types, keeping their presence within the vegetation edge along the ridges. Thus, as with many other studies, a clear vegetation succession pattern has been documented.

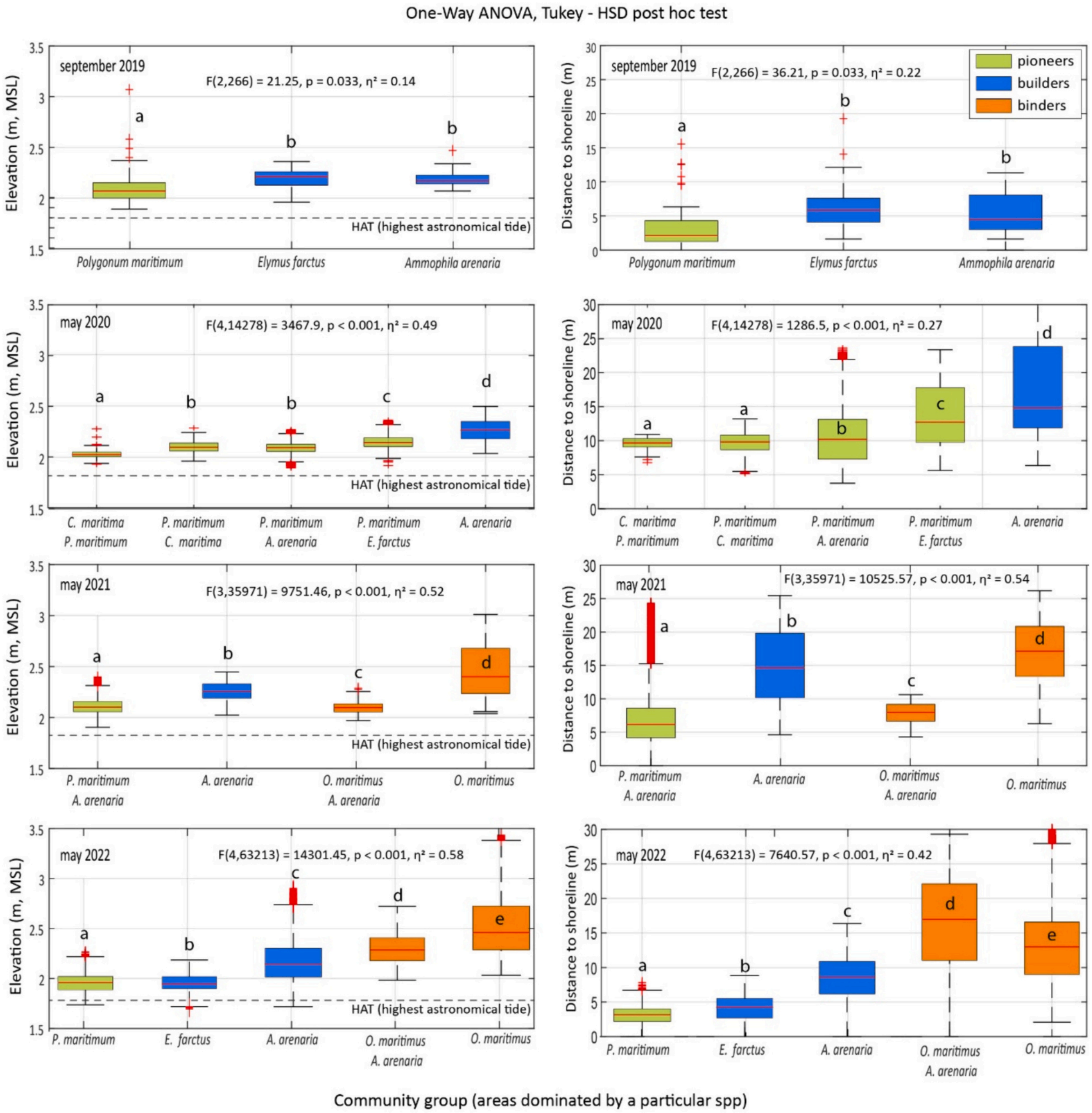

Fig. 6. Boxplots showing the distribution of plant communities (designated by the more abundant species) through time with elevation (left column) and distance to the closest shoreline (right column). Results of the pairwise comparison are reported using non-capital letters.

4.3. Sand accumulation patterns

The coevolution of the vegetation cover, the morphology and the sediment accumulation within the zone dominated by aeolian processes (dashed black line polygon in Fig. 4) was evaluated for the periods when significant vertical changes were observed, namely September 2019 to May 2020, May 2021 to October 2021. The combined effect of topography and vegetation cover over sedimentation (Fig. 8A–C) reveals that during the earlier stages of evolution of the incipient dune, sedimentation occurs within two clear elevation thresholds, ranging between the HAT (~1.8 m) and the ridge crest (~2.4 m), coinciding with the zones selected by the plants to grow (Fig. 8A). Plants tended to colonise higher elevations through time, expanding towards the berm-platform, and facilitating accumulation at higher elevations (Fig. 8). The results suggest that higher average accumulation values are associated with denser vegetation (Fig. 8A). This apparent relationship was also expressed in terms of dependency through a linear regression analysis, which shows that 42 % of the sand accumulation variance is explained by the variability of the vegetation cover at early stages (Supplementary Fig. 4). Results also show that most of the accumulation occurred around areas of low vegetation cover (below 20 %). This is explained by the high abundance of plots with low vegetation cover, which account for most of the accumulation in the area (Supplementary Figs. 5, 6). Through time, the relationship with the vegetation becomes non-linear (Supplementary Fig. 3), with maximum average accumulation peaks occurring between coverages of 20 and 60 % (Supplementary Fig. 5) and very dense vegetation areas with very little accumulation (Supplementary Fig. 5). Vegetation cover values below 5 % have a small contribution to the average accumulation of sand (Fig. 8). However, their greater abundance makes them more important than the very dense plots in terms of total contribution (Supplementary Fig. 5). Maximum total accumulation values concentrated around vegetation cover values of ~20 %.

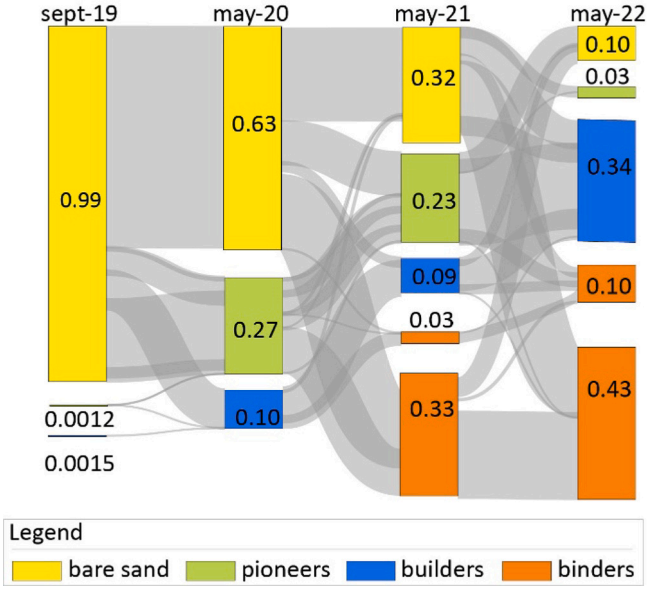

Fig. 7. Summary of the observed community shifts or successional stages across the study area. The shifts were estimated considering the last survey situation as reference. Therefore, the numbers represent the proportion of successional stage through time. Diagram created using open source SankeyMATIC.

The patterns of sand accumulation were further analysed, exploring the combined effect of the surface slope and the vegetation cover (Fig. 8D–F). The surface slope values increased over time (Fig. 8D, E), likely related to local sand accumulation within plants, forming small nebkhas with steep slopes. The first survey shows a smoother topography where sand accumulation appears to show a bimodal response. Higher values of average accumulation were found at plots combining high vegetation cover and low slopes, or at plots where lower coverages and higher slopes coincide (Fig. 8D). This pattern suggests that morphology plays an important role on sediment accumulation at the early stage after initial plant establishment, inducing sand retention at zones with no or little vegetation. This pattern is not detectable in the following stages, with a clear trend of accumulation occurring in zones of denser vegetation and steeper surface slopes (Fig. 8E).

These results, in combination with detailed information from vegetation cover and sediment accumulation within mapped wrack zones (Supplementary Fig. 3), also show that vegetation does not require sedimentation to colonise, survive and expand. In the areas of wrack accumulation, pioneer plants give way to dune builders with high vegetation cover values, despite negligible active sedimentation.

Finally, sediment accumulation was explored from the perspective of the identified plant communities, assessing the average and total accumulation per mapped community group (Fig. 9). The results show that for the period between September 2019 and May 2020, groups dominated by pioneer species accumulated very little, while mixed groups of dune builders and pioneer plants, as well as, communities with abundant dune builders, were highly efficient in trapping sediment. This response can be associated with the location of the communities, with the pioneers restricted to the fetch-limited northern bay. This is also confirmed by the accumulation computed for the mapped wrack zones,

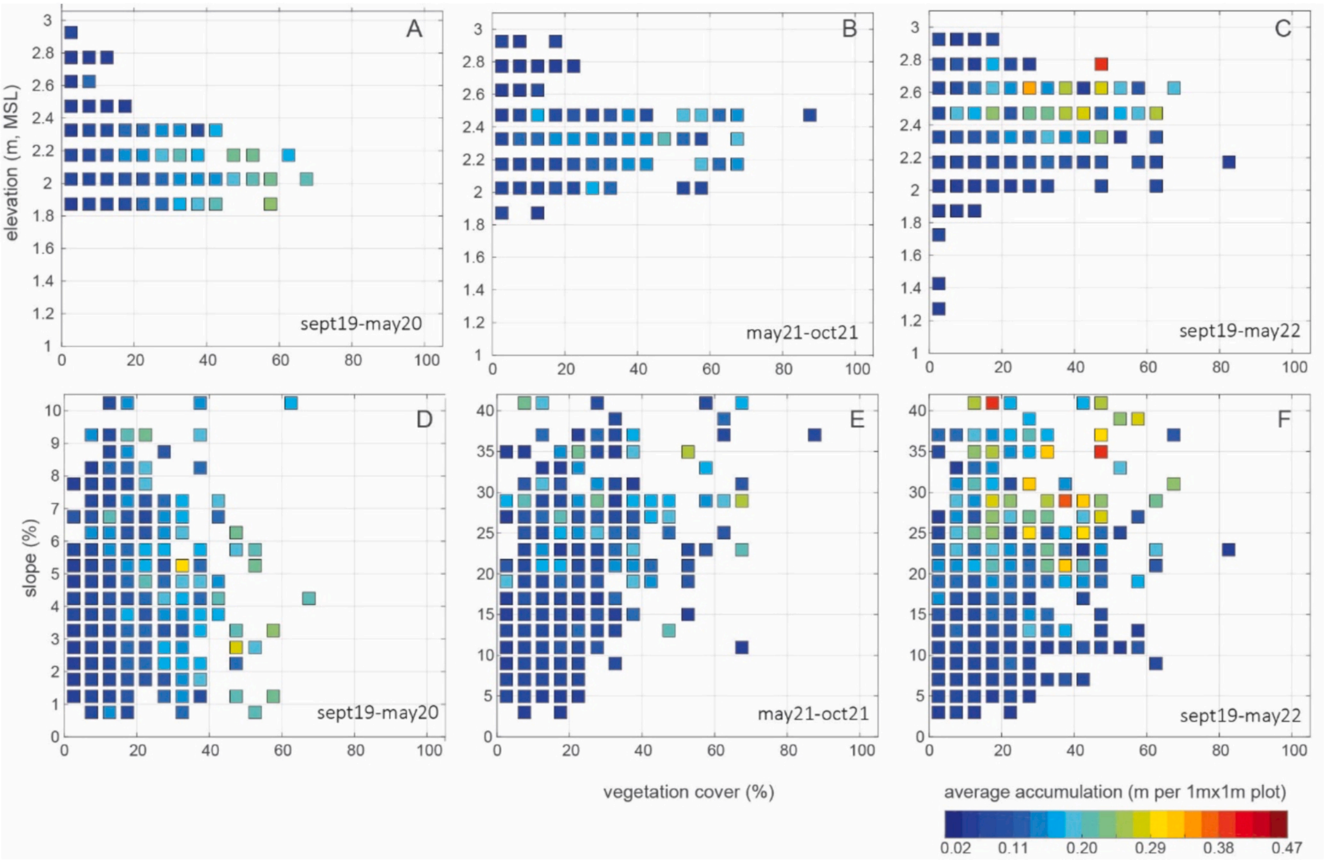

Fig. 8. Plots showing the patterns of average sediment accumulation at the level of the 1 m^2 plot (coloured squeares, with reference to colour-bar), depending on the vegetation cover (x-axis in all plots), the elevation (y-axis in A–C) and the surface slope (y-axis in D–F). Plots A and D show the results for the interval September 2019 to May 2020, plots B and E the interval between May 2021 and October 2021, and plots C and F the net overall change.

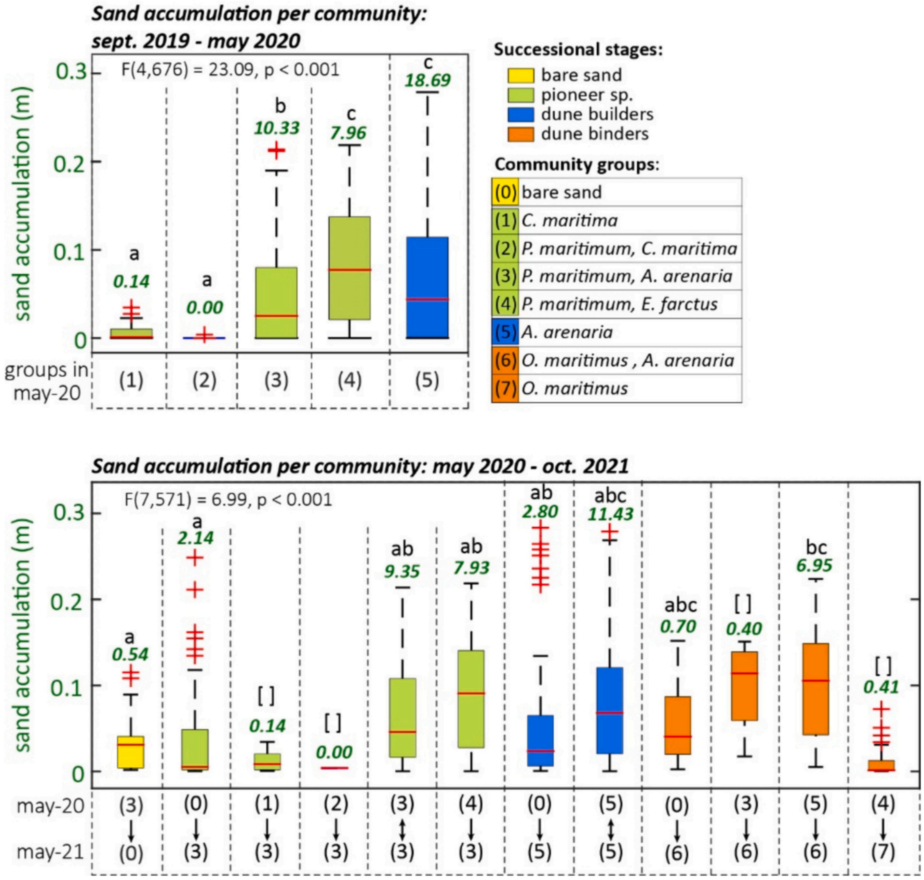

Fig. 9. Sand accumulation per mapped community (group) between September 2019 and May 2020 and from May 2020 to October 2021. The lower panel also included the shifts of communities from May 2020 to May 2021. As in the previous figures, yellow colour stands for bare-sand (group 0), green represents pioneer plant communities (groups 1 to 4), in blue are the dune builders (group 5) and in orange the sand-binders (groups 6 and 7). The number (in green colour) on top of each box-plot represents the total amount of sand accumulated by each group. The results from the pairwise comparison between groups are given in small black letters. Groups with small samples (<10) were not included in the ANOVA analysis (indicated with [ ] in the figure).

where accumulation took place only in wracks located along the ridge crests and adjacent to the lagoon-platform (i.e., wracks 4 to 6, see Supplementary Fig. 3), area already mentioned as a possible sediment source.

For the period between May 2020 and May 2021, higher average and total accumulation values were associated with builder and pioneer communities that maintained their identity, presented small changes or shifted from builder to sand-binders (Fig. 9). As for the first period of analysis, lowest total accumulations were associated with annual pioneer communities (group 1 and 2) while intermediate values were observed in the case of communities colonising new areas. It is important to note that the lower values associated with the shift between pioneer/builder mixed community (group 4) into a sand-binder (group 7) appears mostly related to the location that this community colonised, at the berm-platform where limited sand transport and accumulation was reported. The importance of location to sediment accumulation by vegetation is, again, also evident in the accumulation in the wrack zones, with only the zones adjacent to the lagoon-platform recording some accumulation between May 2021 and October 2021, despite the high vegetation cover across most wrack zones (Supplementary Fig. 3).

5. Discussion

The initiation of an incipient foredune in the study area was firstly facilitated by the generation of new accommodation space through the elongation of a sandy peninsula spit. Elongation materialised through the formation of new spit hooks, represented by new curved berm-ridges advancing eastwards (Figs. 1, 4). Seaward, the new spit-terminus was protected by a wide and high berm-platform. Berm-ridges enabled dune initiation, functioning as the core features for plant colonisation, which was also assisted by the presence of wrack zones. Sand accumulation begun to take place, reinforcing the inherited morphology and promoting the vertical growth of the ridges after one year (Fig. 4). Additionally, a second slower type of dune initiation could be recognised related to low-coverage and reduced sediment accumulation observed across the berm-platform. Significant plant establishment across this platform only took place after three years and sedimentation was almost negligible (Figs. 5, 4). Overall, the results support the occurrence of strong interactions between physical and biotic processes since the very early stages of dune formation. Plant surface colonisation appears primarily controlled by two conditions: topography and occurrence of a wrack zone. As expected, plant establishment promoted the retention of transported aeolian sand along the ridges. Relatively low cover reinforced the topography of the inherited ridge morphologies through a rather continuous vertical growth, despite the occurrence of accumulation local maxima around clumps of the dune builder *Ammophila arenaria* and the perennial pioneer *Polygonum maritimum*, with the latter being replaced by other types with time.

5.1. *Sediment supply limitation*

Sediment input to coastal dunes is limited by a number of factors that control sediment transport on beaches and the amount of sand reaching the dunes (Nickling and Davidson-Arnott, 1990). Of particular relevance to areas with relatively coarse sediments, as it is the case for Ancão Peninsula (Costas et al., 2018), are the processes related to beach surface armouring that induce depletion of sand available for transport to the dunes (Costas et al., 2020).

The lack of correspondence between periods with frequent strong winds and sediment accumulation in the study area suggests the dominance of supply limiting conditions. The first period of analysis, between September 2019 and May 2020, registered notable vertical changes, even though vegetation cover was still low. Assuming that wind velocity is not a limiting factor for transport, we can hypothesise that the greater mobilization of sand towards the incipient dune at this early stage was related to the recently generated spit end and the subsequent availability of sand. Through time, this surface likely became sand depleted (de Vries et al., 2014), limiting the accumulation of sand during the following periods (May 2020 to October 2020 and October 2020 to May 2021). Sand availability seems to have been restored between May 2021 and October 2021, when sand accumulation reinitiated. Despite less frequent strong winds, the supply of sand during this period could be associated with sediment surface reworking or replenishment with new sand layers by high runup and/or surge levels. This influence can be fundamental for dunes growing in the vicinity of inlets and could also help to explain the intermittency in sediment supply towards the incipient dune (Galiforni-Silva et al., 2020).

5.2. Vegetation distribution patterns

Dune initiation by vegetation has been described as the result of a series of processes that control the delivery and germination of seeds (Hesp, 1983; Maun, 1998) and the subsequent development of dunelets or nebkhas around seedlings (Woodhouse, 1978). Therefore, it is expected that the spatial distribution and cover of vegetation communities will determine where and how dune growth occurs (Hesp, 2002; Tobias, 2015), highlighting the impact of biophysical interactions to the evolution trajectories of coastal barrier states (Stallins, 2005).

Our results highlight the determinant role of marine processes to dune initiation, not only due to the presence of wrack that likely increased diaspore and nutrient availability, but also by providing new accommodation space and favourable topographies for the vegetation to colonise and to eventually promote dune growth. Identified plants and plant communities showed a clear preference for elevations above a critical value, providing protection from marine inundation. Vegetation initially colonised the former berm-ridges, while lower areas (i.e., lagoon-platform morphological region and northern bay) remained non-vegetated for a longer period. This response resembles the two stable states for coastal dunes, described as a function of storm frequency and magnitude that determines if dunes will be able to grow high (resistant-dune) or low (overwash-flat) (Goldstein and Moore, 2016). When the effects of frequent inundation dominate, coastal barriers may become trapped in a perpetual state of low elevation, inhibiting aeolian and biological processes that drive dune recovery (Durán Vinent and Moore, 2015). Our results also suggest that marine inundation probability, which depends on the morphology inherited from wave-related processes, in combination with favourable sediment supply, determine whether a dune will have a chance to develop or not. In fact, the results show that the low areas may eventually be colonised by plants when inundation ceases to reach them, providing the conditions for aeolian sand trapping and vertical growth, provided that sediment supply is available. Similar conclusions were reached by other works, highlighting the role of storms and beach morphology over the development of embryo dunes (Hesp, 2002; Montreuil et al., 2013; van Puijenbroek et al., 2017a).

Observations document the rapid initiation of a dune, once perennial vegetation surpasses a minimum cover that promotes sediment trapping and fixation during active sediment transport events, as observed at the beach ridges. This reinforced the inherited morphologies (berm-ridges) that become dominated by aeolian processes to eventually generate dune ridges, resembling the morphological type 1 defined by Hesp (1989). Conversely, the flat low areas between the ridges and the flat high surface of the berm-platform, did not show clear signs of dune initiation over the period of analysis (i.e., significant vertical growth and vegetation cover). On the lagoon-platform, the limitation seems related to its low elevation, which is very close to the plant elevation threshold. Contrastingly, elevation does not seem to be limiting for the berm-platform. In fact, this platform tended to remain protected from marine inundation because of the width of the beach. The delay in plant colonisation across this higher area suggests a limitation related to the occurrence of successful plant seedlings. This delay in colonisation, in combination with the low accumulation observed, explains the formation of a different morphological dune type, resembling the terrace type 2, proposed by Hesp (1989). Therefore, two very distinct patterns of dune initiation (ridge and terrace), were identified in the study area, resulting from distinct plant temporal (rapid vs slow) and spatial (dense vs scarce) distributions, and two distinct inherited morphologies (berm-ridge vs berm platform). Previous works highlighted the importance of plant colonisation patterns to dune initiation, distinguishing two main types (1 and 2 aforementioned), depending on whether colonisation is initiated from discrete pioneer plants or laterally continuous seedling colonisation (Hesp, 1989). Plant distribution across the study area seems determined by the area of colonisation rather than by the type of species, with greater coverages associated with the occurrence of nutrient-rich wrack lines. This influence has been documented in other studies, where storm wrack occurrence has been found to enhance the growth of certain dune grasses and boost the geomorphological recovery of dunes (Hilton and Konlechner, 2011; Joyce et al., 2022). Experimental research verified that plants growing in a treated substrate (enriched with seagrass litter wracks) grew faster and were twice as large as those growing without treated substrates (Del Vecchio et al., 2013). The contribution of the wrack to the rapid and dense vegetation growth also supports the idea that vegetation growth and expansion is not necessarily controlled by sediment supply. After all, coastal dune plants will likely colonise any surface if minimal conditions are met (Maun, 2004).

Analysing the evolution of the vegetation cover and the patterns of sediment accumulation across the study area evidences the capacity of vegetation to enhance dune growth, especially at the local scale. Different responses were identified, during dune establishment and early growth stages. The early stage shows two main modes of accumulation, one explained by higher vegetation coverages (>40 %) and the other explained by relatively steep slopes (>5 %) and lower coverages (<30 %). Through time, and with the subsequent change in topography and vegetation cover, accumulation started to occur around very steep slopes (>20 %) and vegetation coverages >20 %. These results suggest, on one hand, that surface roughness and topography play a significant role during the early stages of dune development, influencing topographic changes. On the other hand, their impact cannot be isolated from the presence of vegetation and their interactions as dune morphology matures. The latter is related to the intrinsic eco-geomorphic feedbacks that reinforce landform unit topography, with steeper slopes around vegetation mounds as a result of the capacity of vegetation to trap sand and grow in pace with sand accumulation (Bonte et al., 2021). A positive relationship between initial dune volume and subsequent nebkha dune growth has been found in field observations (van Puijenbroek et al., 2017b), suggesting a similar effect to the one noted in the present work related to the surface roughness/topography.

The low abundance of plots with high vegetation cover results in their relatively minor contribution to the total accumulation of sand across the area. A more homogeneous distribution of the accumulated sand is promoted over low coverages (5–30 %). In addition, the progressive growth of the vegetation in pace with sediment accumulation driven by variable wind directions and speeds, tends to further promote spatial distribution homogeneity, with mounds adapting and changing shape through time.

The results also support the greater contribution of dune builder species to local (i.e., maximum) and total sand accumulation. Two aspects need to be highlighted in this regard. The first is that plants that were more efficient in trapping sand were found at more exposed areas, where sediment transport likelihood was greater. Exposure has been also pointed out as a key factor in enhancing the growth of nebkha dunes (van Puijenbroek et al., 2017b). The second is that pioneer species, and in particular perennial pioneers, showed similar levels of efficiency when located along areas with active sediment supply. However, these tend to be replaced by builders or binders within 1–2 years, making it difficult to isolate the impact of each species to the total accumulation of sand during the species turnover. Yet, dune builder species exhibited greater efficiency in developing this function than annual and short-lived perennial pioneer species, with the annual ones reporting the lowest accumulation values. Overall, it seems that if vegetation colonises areas with active sediment transport, it will trap moving sand with lower coverages, promoting sand transfer and distribution through the incipient dune, while higher coverages will likely induce local accumulation (cf. Hesp et al., 2019). Observations are in line with previous works, suggesting that dispersed plant expansion strategies in the early colonisation phase yielded the highest cumulative area of sand deposition, compared to more patchy spatial organisations (Reijers et al., 2019).

6. Conclusions

This study has demonstrated that local morphological characteristics and processes, such as elevation, distance to shoreline and sand accumulation/erosion drive spatial plant colonisation and expansion preferences. In turn, plant distribution patterns, in combination with other surface roughness elements, and sediment availability determine incipient foredune types.

Overall, the following conclusions can be drawn:

(i) Following the initial stage of vegetation establishment, which primarily occurred on and around berm-ridges, vegetation expansion was relatively fast, increasing quasi-linearly with time. The vegetation establishment followed a fairly classic successional pattern, with pioneer plants followed by dune builders and then dune binders.
(ii) The distribution of plants shows a clear pattern, with binder species occurring on higher elevations and zones distant from the shoreline, while dune builders displayed large tolerance ranges.
(iii) In the initial stages of dune formation, vegetation cover significantly influenced sediment accumulation patterns. Higher values of average sand accumulation occurred around areas with high plant cover and low slopes or around areas with low cover and milder slopes. However, as the dune system matured and complexity grew, the relationship between vegetation cover and accumulation became nonlinear, with accumulation being mostly captured in areas of relatively low vegetation cover (<30 %).
(iv) Temporal and spatial plant colonisation patterns were largely controlled by the presence of wrack, which appear to promote rapid colonisation and dense cover of vigorous plants, even where sedimentation was negligible.
(v) Incipient foredunes were established in two locations; at berm-ridges where the presence of wrack aided plant establishment and growth likely due to the presence of seed material and the provision of nutrients, and on the berm-platform. Significant plant establishment across this platform only took place three years after its formation and sedimentation was almost negligible.
(vi) The inherited morphologies of the berm-ridges and the berm-platform also affected the incipient foredune morphological development, with berm-ridges evolving into type 1 ridges and morphologies on the platform evolving into type 2 terraces.

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CRediT authorship contribution statement

Susana Costas: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Luisa Bon de Sousa:** Methodology, Data curation. **Juan B. Gallego-Fernández:** Writing – review & editing, Investigation, Formal analysis. **Patrick Hesp:** Writing – review & editing. **Katerina Kombiadou:** Writing – review & editing, Visualization, Formal analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Susana Costas reports financial support was provided by Foundation for Science and Technology. Luisa Bon de Sousa reports financial support was provided by Foundation for Science and Technology. Katerina Kombiadou reports financial support was provided by Foundation for Science and Technology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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