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Review article

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Ecomorphodynamics of coastal foredune evolution

Laura J. Moore [1] ✉, Sally D. Hacker [2], Josh Breithaupt [3], Sierd de Vries [4], Thomas Miller [5], Peter Ruggiero [6] & Julie C. Zinnert [7]

Abstract

Globally, along sandy coastlines, foredunes support ecosystem services including provision of habitat and protection of communities from waves and storm surge. In this Review, we discuss the interactions between sand transport and vegetation processes (ecomorphodynamics) that give rise to the foredune-building feedback as illuminated by empirical and modelling studies. Foredune shape and alongshore continuity depend primarily on sand supply, vegetation density and growth form. For instance, low-lying, creeping herbaceous species tend to form short embryo dunes, whereas tall, dense grasses that grow vertically tend to form tall, narrow foredunes. Climate and weather events, herbivory and anthropogenic disturbances of varying scale affect the foredune-building feedback. For example, small local scale disturbances, such as herbivory or trampling, cause local vegetation loss and erosion. Management activities, such as beach nourishment, can increase foredune sand supply, leading to foredune rebuilding, although the presence of infrastructure on the back beach can inhibit foredune development. At a regional scale, hurricanes and tropical storms cause substantial dune erosion and overwash, potentially resetting the foredune-building process. Sea-level rise exacerbates the effects of storms, leading to increased erosion, saltwater intrusion and a potential landward shift in foredune location. Future research should prioritize integrated ecomorphodynamic observations and modelling to fill critical knowledge gaps and address the effects of changing climate on the foredune-building process.

Sections

[1]Department of Earth, Marine and Environmental Sciences, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA. [2]Department of Integrative Biology, Oregon State University, Corvallis, OR, USA. [3]Coastal and Marine Laboratory, Florida State University, St Teresa, FL, USA. [4]Department of Hydraulic Engineering, Delft University of Technology, Delft, The Netherlands. [5]Department of Biological Science, Florida State University, Tallahassee, FL, USA. [6]College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA. [7]Department of Biology, Virginia Commonwealth University, Richmond, VA, USA. ✉e-mail: laura.moore@unc.edu

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Introduction

Coastal dunes are a prominent feature of many sandy coasts[1], the latter globally representing one-third of ice-free coastlines[2]. The foredune provides protection from storms[3] by sheltering natural habitats and coastal communities from disturbance and stress[4,5], elevated water levels and wave-induced erosion[6–8]. Foredune shape determines the degree and type of protection provided. For example, tall, narrow foredunes can provide greater protection from short-duration, high-surge events, such as hurricanes, whereas lower, wider dunes can provide better protection from longer-duration, lower surge events, such as nor'easters[9]. Foredunes also store carbon[10,11] and provide critical habitats for many plant and animal species[12–14], supporting various ecosystem services[15,16].

Coastal foredunes arise from intertwined geomorphic and ecological processes associated with sand transport and vegetation growth in sandy beach–dune environments (Fig. 1). Vegetation growth leads to sand deposition and vice versa, triggering interactions and feedbacks — collectively referred to as ecomorphodynamics — that drive the co-development of landscape morphology and ecological communities. Thus, understanding biological–physical interactions is of fundamental importance to effectively manage sandy coastlines[17,18].

In the 1980s, early conceptual models of dune development[19,20] highlighted the importance of interactions between sand supply and vegetation[21]. These insights led to the study of coastal foredune ecomorphodynamics, which integrates ecology, engineering, geography, geology, physics and biogeochemistry across a wide range of spatial (metres to >100 km) and temporal (hours to decades) scales, using a broad range of approaches (Box 1). These interdisciplinary efforts focus on blending characterizations of dune morphology and vegetation community structure using various approaches to understand the dynamics driving the co-development of dunes and plant communities[17,18].

Projected changes in climate[22], sea level[23] and storm patterns[24] will impact coastal foredune processes. Constraining the mechanisms influencing foredune dynamics following disturbance is critical for assessing and improving the management and future resilience of coastal communities. For example, insights can inform dune restoration and dune management efforts[25]. Such efforts range in scale from local initiatives to enhance dune growth[26], construct artificial dunes[27] or limit the height of maintained dunes[28,29], to the systematic management of dune traits (such as shape and vegetation cover) for periods exceeding a century and over distances greater than 100s of kilometres[30,31]. In addition, foredunes have an important role in the large-scale evolution of coastal landscapes, through their influence on the landward transport of sand[32,33] with consequences for future barrier island habitability[28,29].

In this Review, we synthesize the understanding of foredune ecomorphodynamics relevant to transgressive (landward-migrating or eroding), progradational (seaward-growing) and stable coastal settings and present a generalized conceptual model for foredune growth. We focus on dynamics and so omit the broader biogeography of dunes, such as global variations in first-order variables influencing dune development (wind, climate and tectonics). We provide an overview of the geomorphic and ecological processes and feedbacks driving foredune formation, shape and development. We also summarize the influence of disturbance and stress (including the effects of anthropogenic activities) on dune growth. Finally, we provide recommendations for future work to address critical knowledge gaps in the field, such as how climate change will alter sediment transport and vegetation dynamics, and therefore the foredune-building feedback.

The coastal foredune-building feedback

Coastal foredunes arise from a feedback between aeolian sand transport processes and vegetation processes[34,35], whereby vegetation causes sand deposition[36–38] and deposition enhances plant growth[39] (Fig. 2a). The initiation of foredune growth from a flat, sandy beach surface (or overwash plain) requires an increase in back beach elevation (Fig. 2b,I), facilitated by aeolian or hydrodynamic transport and deposition of sand. Once the elevation of the back beach is sufficient for beach vegetation to grow and persist, the dune-building feedback begins and sand accumulation accelerates (Fig. 2b,II). Although factors such as high moisture content can reduce sand supply rates, the presented conceptual model assumes maximum potential (saturated) sand flux. Thus, the model assumes that the wind is carrying as much sand as it can for given conditions and when limitations on the rate of sand supply occur, they decrease relative dune growth rates accordingly.

Generally, plants cause the deposition of sand via two mechanisms[40]. First, sand blowing across the beach–dune landscape is deposited when wind energy is dissipated by a boundary layer formed around the vegetation causing shear stress to fall below a threshold value[41]. Sand is also deposited when grains hit the surface of plants[42]. When present, wrack — organic material that washes onshore — and elevated topography induce similar effects on sand deposition[43]. The influence
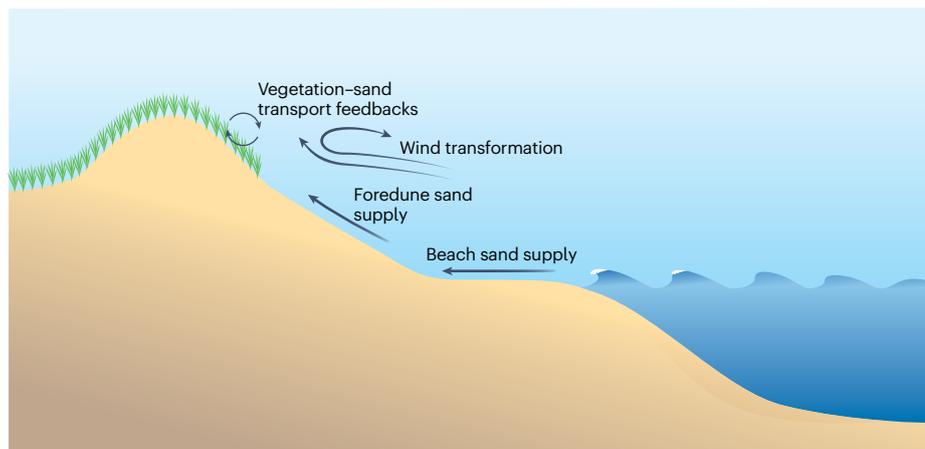
Fig. 1 | Sand transport and vegetation processes across the beach–dune system. Grey arrows represent beach sand supply, foredune sand supply and wind transformation processes. Vegetation reduces the carrying capacity of wind, causing sand deposition, which stimulates vegetation growth, leading to more sand deposition. This self-reinforcing collection of processes is referred to as the ecomorphodynamic foredune-building feedback.

In figure: Vegetation–sand transport feedbacks; Wind transformation; Foredune sand supply; Beach sand supply

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Box 1 | Approaches

Coastal dune ecomorphodynamics is a highly interdisciplinary field involving application of various different approaches. Longitudinal[64–66,99] or post-storm[75] field observations of vegetation cover and composition, sand supply and beach–dune morphology allow assessment of relationships between changing vegetation and dune morphological characteristics (see the figure, panel **a**). Controlled common garden, mesocosm and wind tunnel experiments[206] support testing of the effects of various physical and ecological factors (including sand deposition , erosion, nutrient availability and species composition)

on the feedback between vegetation growth and sand capture (see the figure, panel **b**). An array of numerical modelling approaches, including the use of processed-based[35,84,183], reduced-complexity[85,209], empirical[210] and computational fluid dynamics[45] models, are used to test hypotheses arising from observational work[48] and explore feedbacks and interactions within the system (see the figure, panel **c**). These approaches are particularly powerful when explored synergistically, combining multiple methods to investigate particular mechanisms or aspects of foredune dynamics[157].

a Field observations

b Field and laboratory experiments


c Numerical model simulations

- Processed-based models
- Reduced-complexity models
- Empirical models
- Computational fluid dynamics models

of vegetation on wind speed and sand deposition can be substantial[37,38]. For example, sand transport decreased 30-fold after dune grass was planted on an unvegetated foredune[44].

As dune plants grow vertically and horizontally, continued sand deposition leads to the formation of incipient or embryo dunes[21] and the rate of deposition increases (Fig. 2b,II). This deposition stimulates further plant growth, which reduces the shear stress even more and leads to greater amounts of sand deposition, creating a self-reinforcing (positive) feedback between vegetation spread and sand deposition[39]. Together with the effects of topography on wind shear stress, these processes are often referred to as sand capture.

If vegetation cannot maintain an emergent structure, either owing to lack of vertical growth or burial under rapid deposition, foredunes will stop growing or even erode as occurs in the case of nebkha dune formation along arid African coasts[45]. However, uninterrupted net growth of embryo dunes leads to taller dunes (Fig. 2b,III,IV), coalescence and the formation of alongshore, connected foredune ridges. Further growth can lead to the formation of prominent features on the landscape, which can subsequently evolve to become transgressive dune fields[40], well-developed oblique or transverse dune ridges, such as those typical of barrier islands and barrier spits[46], or prograded dune fields[47,48].

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a Overview of foredune development over time
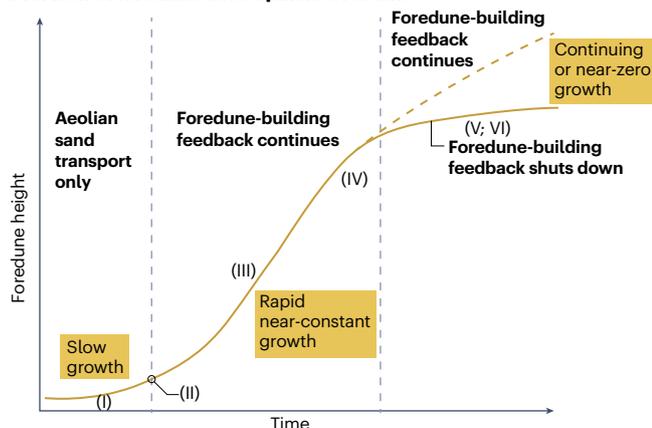
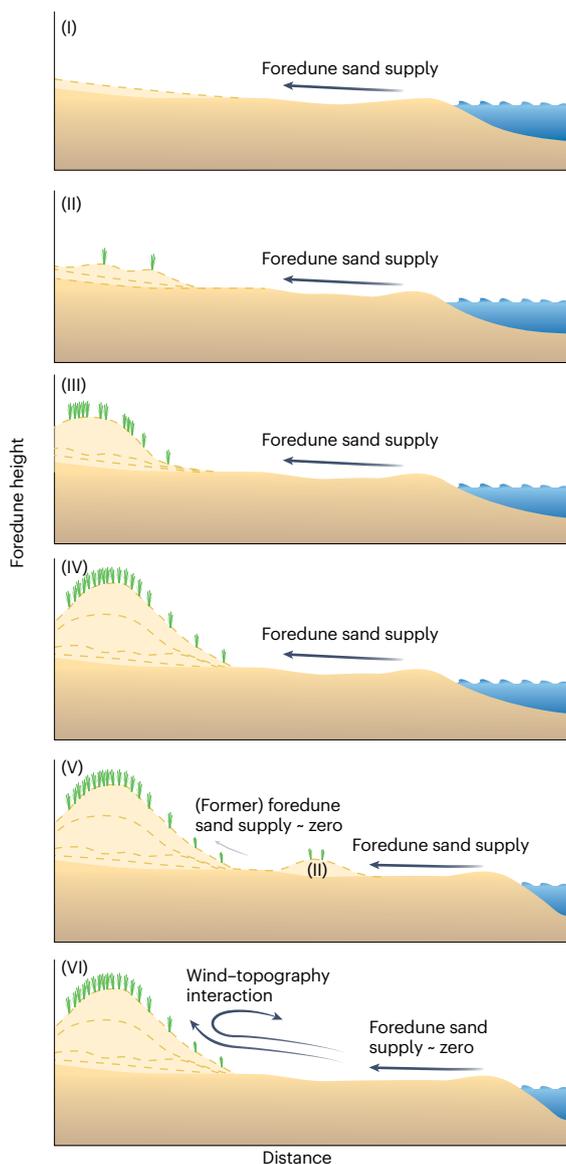## b Generalized foredune profile during each phase of development

Fig. 2 | Foredune growth rate and development. a, Overview of foredune growth over time generalized for conditions of saturated sand flux. Roman numerals correspond to dune profiles in panel **b. b**, Generalized foredune profile during each phase of development: (I) sand accumulates slowly as a result of aeolian sand transport only, (II) embryo dunes form once vegetation establishes and the dune building feedback initiates, (III) rapid near-constant foredune growth at annual timescales gives rise to a taller dune form, (IV) foredune growth continues at annual timescales as vegetation and root systems become increasingly established, (V) foredune growth occurs very slowly, or not at all, when foredune sand supply is intercepted by a newly formed foredune and (VI) foredune growth occurs very slowly, or not at all, when wind–topography interactions reduce foredune sand supply to near zero. In general, foredune growth is slow until vegetation establishes, whereafter foredune growth is rapid, at least for a time.

Storms can interrupt the dune-building process through erosion, overwash or inundation, returning foredune growth to its beginning stage[49] (Fig. 2a,b,I). Mid-cycle rates of vertical foredune growth can be relatively rapid[49] (Fig. 2b,II–IV) owing to high rates of vegetation growth and sand deposition, as well as sand-bound nutrient delivery that further promotes vegetation growth. Later in the growth cycle, if large dunes more appreciably impact the wind field[35], vertical dune growth rates can become negligible[49] (Fig. 2a,b,V). Vertical dune growth can also nearly cease following the development of a new foredune associated with landward foredune migration[50], shoreline progradation[47,48] (Fig. 2a,b,VI) or the emplacement of sand fences[51].

In some locations, vertical foredune growth appears to continue on decadal timescales[52] (Fig. 2a,b,VI). Continued growth occurs when foredune sand supply is not inhibited by the foredune topography itself, or by new foredunes. For example, where sand-transporting winds are oblique to the shoreline, the effects of topography on the wind field might be limited, allowing dunes to continue growing over long timescales[53]. Variations in the rate of vertical dune growth, its potential limits, and whether equilibrium dune shapes and states exist, remain points of discussion[53].

Feedbacks between sediment transport and vegetation growth drive foredune formation and growth, with rates of growth varying over time as a function of vegetation establishment, sand supply rates and interaction with topography. Storms can reset the dune-building process and, in later stages of foredune development, foredune growth might continue, or be impeded by limits to foredune sand supply.

Physical influences on foredune building

Understanding of dune-building feedbacks and the other ecomorphodynamic processes involved in coastal foredune development requires quantification of the physical processes governing the transport of sand to foredunes, the influence of plants on landward sand flux (sand transport rate per alongshore length) and the biotic responses of dune-building plants to foredune sand flux. This section focuses on physical aspects of these processes and their role in ecomorphodynamic interactions and feedbacks.

Environmental setting

The presence, growth rate and shape of foredunes are strongly influenced by both marine and aeolian processes across the nearshore–beach–dune system[54]. Coastal dunes are typically associated with sand-rich coasts located on the downwind side of large ocean basins or adjacent to previously glaciated areas[55]. Coastal dunes are part of a sand-sharing system involving dynamic linkages between the upper and lower shoreface[56,57] and the beach–dune environment.

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Thus, the geological setting and framework, which influence sediment type and sediment availability, are important boundary conditions for dune building[55]. Regional climate dictates dune distribution[58] and broadly influences dune shape and evolution. Foredunes in the tropics are relatively modest dune terraces, owing to the dominance of low, creeping plant species that grow rapidly (relative to grasses) in the seaward direction via rhizomes[59]. By comparison, mid-latitude dunes, dominated by grasses, typically form relatively robust dune ridges[59]. Lower rates of sand supply and less favourable wind conditions in the tropics likely also contribute to these differences[59]. Variability and trends in metocean climatology (wind, waves and water levels) dictate the frequency and magnitude of dune-building and dune-eroding events[60].

Critical beach–dune interactions

Interactions between beach and dune processes are critical to foredune ecomorphodynamics, especially the landward flux of sand from beaches to dunes. Net sand flux from the nearshore to beaches and from beaches to dunes is a function of the balance between the rate of sand supply and the rate of sand loss to the beach and to the dune (the beach or dune sand budget per time), hereafter termed the beach sand supply and foredune sand supply, respectively.

In the 1980s, researchers used conceptual models, often coupled with empirical data, to describe foredune development in terms of sand availability and storm dynamics. Potential foredune size varies with surf zone, beach type (dissipative to reflective) and associated wave-driven and wind-driven sand transport[19]. The largest foredunes are generally associated with the wide fetches, low beach slopes and high-sand-transport potential of dissipative beaches, whereas relatively narrow, reflective beaches tend to be associated with smaller foredunes[19].

In the 1990s, under the assumption that sand supply is a driving factor for foredune evolution, it was proposed that under positive and high sand supply to beaches (Fig. 3), foredune development is potentially limited by progradation[55,61]. Rapid progradation (such as metres of seaward beach growth per year) can lead to repeated development of new, seaward foredunes owing to plant growth seaward of the established dune, which limits the supply of sand to the immediately landward, former foredune[61]. Conversely, slower rates of beach progradation allow for the development of a single, larger foredune[61], consistent with observations[62] and numerical model experiments[48]. Foredune development (rate of dune-volume growth or rate of crest-height increase) is at a maximum under slightly negative beach sand supply, when there is cross-shore exchange of sand from an eroding beach to the dune[61]. Under more substantially negative sand supply to the beach (owing to sand losses offshore, onshore or alongshore), the availability of sand for aeolian transport to dunes is limited, and thus foredune growth typically ceases and dunes become susceptible to erosion and overwash[61].

Foredune sand supply

Sand supply from beaches to foredunes is a critical factor in foredune development, with the potential to limit or enhance the dune-building feedback. However, quantifying aeolian sand transport from beaches to dunes is challenging. Even available numerical approaches are limited by a lack of input data to produce sufficiently accurate time series of aeolian foredune sand supply for quantitative comparison with observations of dune development. As such, shoreline change rates — representative of beach sand supply — are sometimes used as a proxy for foredune sand supply[63,64] and can explain the majority of variance in coastal dune morphological change at interannual timescales[65,66]. In addition, data analysis and reduced-complexity model simulations also indicate that decadal-scale dune-volume change can be explained primarily by wave-driven alongshore transport gradients[67].

Predictive models can be used to estimate aeolian transport from beaches to foredunes. Generally, transport rate is parameterized as a function of wind speed (or shear velocity), air density and grain size[68] by implementing the concept of a velocity threshold[69,70]. Models of aeolian sand transport capacity that apply this foundational concept of a velocity threshold[55] (Fig. 3) under steady wind and unlimited sand supply conditions[68] often overpredict measured aeolian sand transport rates[71,72]. Advances in the 2000s saw the incorporation of the so-called fetch effect[73], which accounts for changes in sand transport from open-water to sandy-beach to foredune environments via a simple geometric approach[74]. This class of models can quantitatively estimate the frequency of occurrence of appropriate wind, sand and beach conditions necessary to actively build foredunes[60,75].

A wide range of other confounding factors can also limit sand supply. Refining estimates of how often dune-building conditions occur requires accounting for these confounding factors, such as potential interactions between the wind field and growing foredune topography[35], high sand moisture content[76], algal crusts and armoured beach surfaces[77]. Some of these factors are implemented in state-of-the-art sediment transport modelling frameworks, including Duna[78] and AeoLiS[79]. These models are based on advection and mass balance and allow for the simulation of bed surface properties and sand availability, as well as wind forcing across space and time. Therefore, these models provide an opportunity to include the influences of bed surface moisture dynamics[80], grain size sorting[81] and feedbacks between the growth of vegetation and sand transport[35] on foredune sand supply.

Coastal foredune growth has typically been associated with aeolian sand transport processes, whereas foredune erosion is typically associated with marine processes such as wave-induced dune scarping and subsequent transport of dune sand offshore[82], or onshore as washover. Empirical data and numerical modelling experiments suggest that total water levels in the collision regime[3] — when waves reach as far as the dune toe — can cause dunes to accrete owing to wave-driven
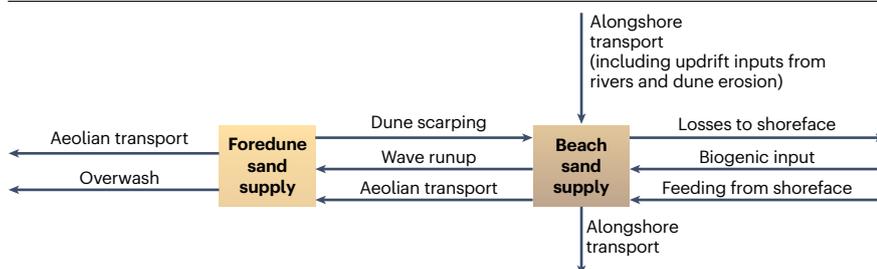

Fig. 3 | Physical processes associated with beach–foredune interactions. Brown squares represent foredune and beach sand supply, and grey arrows represent processes and the direction of sand transport. A range of processes operate across the beach–dune system, supplying and removing sand.

sand transport, indicating that wave impacts are not unconditionally erosional[83]. Estimates based on morphologic-change data sets suggest that on a high energy dissipative beach, marine processes explain between ~10% and 40% of annual dune growth, primarily near the dune toe, with aeolian processes accounting for the remainder[83]. To what extent marine processes also cause appreciable annual dune growth at other locations remains unclear.

Modelling coupled beach–dune development

Mesoscale beach–dune models coupling nearshore, beach and dune morphodynamic processes can simulate the full coastal profile at timescales of seasons to decades, in addition to incorporating interactions between sand transport and vegetation. Such modelling platforms, including XBeach-Duna[84], DUBEVEG[85] and Windsurf[86], enhance knowledge of the various drivers responsible for coastal dune evolution. Although not as detailed as computational fluid dynamics approaches[45], these models allow testing of hypotheses related to eco-morphodynamic processes and exploration of the relative influence of various drivers of foredune morphological evolution[87]. For example, XBeach-Duna[84] simulations confirm that foredune height evolution depends on beach sand supply. Other explorations of dune development under various climate change scenarios, including those using the rule-based cellular automata model DUBEVEG[85], predict potential preservation of dune height and volume during landward retreat in response to sea-level rise.

Many physical factors influence foredune building, including environmental setting, beach–dune interactions, foredune sand supply and beach sand supply. The next section discusses the role of biotic influences, which, together with physical factors, control the foredune-building feedback.

Biotic influences on foredune building

Vegetation presence, persistence and growth critically influence coastal dune formation, shape and stability. The effect of plants on dune building varies with plant community structure, productivity and biomass and species-specific responses to regulatory factors of wind-driven and wave-driven sand supply, beach wrack, sea water and salt spray (Fig. 4a). Dune vegetation is also influenced by regional temperature and precipitation conditions and local access to the water table (Fig. 4a). In turn, these regulatory factors are altered by dune-building processes, leading to further changes in the feedbacks between morphodynamic processes and vegetation. This section discusses these regulatory factors, interactions and feedbacks

Dune plant community structure

Dune plant community structure, including species richness and composition, varies globally[88] owing to differences in evolutionary history, climate and environmental variability and human influence[89]. Despite this variability, dune plant communities exhibit similar phylogenetic and functional traits, allowing them to thrive dune environments[90–92]. For example, a global multiscale analysis of dune plant communities found that dune plant species assemblages are phylogenetically related at continental or subcontinental scales (indicating high species diversification and endemism among regions), latitudinal scales (where temperate, subtropical and tropical communities differ owing to large-scale climate variability) and local scales (where plants with similar functional traits are grouped together across dune profile locations that vary sharply in sand supply and mobility, wave action, salt water inundation, freshwater availability and nutrients)[90]. In addition,

anthropogenic activities, such as the introduction of the non-native dune-building European beachgrass, *Ammophila arenaria* (also synonymous with *Calamagrostis*), to the coasts of the US Pacific, Australia, New Zealand, South Africa and Chile[43,93–95], have markedly altered dune shape and triggered changes in community structure and conservation and restoration efforts.

At a local scale, dunes have distinct patterns of zonation with plant communities varying as a function of time-dependent or successional stage cross-shore profile location[88,96]. These zones include the upper beach, foredune, deflation plain (low elevation area between dunes, also termed a swale) and the stabilized and potentially forested backdune. Each of the cross-shore locations is associated with different physical conditions that are important to plant community establishment, species composition and productivity[93,97–101] (Fig. 4a).

The upper beach and foredune experience strong winds, salt spray and potentially high rates of sand supply. Upper-beach communities, in which high tidal flooding and wrack deposition are common, are sparsely vegetated and dominated by mound-forming, creeping and early successional dune plants that thrive in this dynamic habitat[93,98,101]. Under high sand supply, these plant species can form early successional stage embryo dunes. The foredune itself is a secondary successional stage, typically dominated by dune-building grasses along with herbaceous species that can tolerate moderate-to-heavy winds, sand movement and potentially drier and nutrient-limiting conditions[93,101]. Finally, the region on the landward side and behind foredunes is a tertiary successional stage community, in which longer-lived species that are less tolerant of winds, sand deposition, salt spray and saltwater inundation thrive[93,101].

The self-reinforcing feedback between vegetation and sand transport processes leads to additional foredune modifications that are important for plant communities (Fig. 4a). Deposition of wind-blown sand delivers marine-derived nutrients, fuelling productivity, but also potentially limiting water availability owing to increased elevation above the water table[102] (Fig. 4a). In addition, on the landward side of the foredune and into the backdune, plants experience lower winds and sand deposition and have greater access to the water table than at the dune crest, leading to enhanced plant species richness[103]. In the absence of disturbance, plants stabilize the sand surface by forming a layer of litter and vegetation, accelerating soil formation and the growth of shrub and tree communities, which vary in composition depending on the regional climate[104].

Dune plant productivity and biomass

Dune plant productivity and biomass depend on access to nutrients, which vary across profile locations and regionally[105]. Many dune plants are nitrogen (N)-limited[105–108], although some are phosphorous (P)-limited or co-limited by N and P[109,110]. Nutrients can enter the system through atmospheric deposition[111–113] or are associated with nutrient-rich sand and wrack delivered to the beach and foredune via waves and wind[105,114,115] (Fig. 4a). Wrack not only delivers nutrients but also contributes to sand capture and dune nucleation, potentially promoting plant and foredune growth and influencing dune shape[101,116–118]. Field and mesocosm observations confirm the positive impact of nutrient-rich sand and wrack on plant production metrics such as biomass, plant height and leaf number[105,115,119] and species richness[115]. Moisture in fresh wrack might also promote seed germination and enhance microbial decomposition and remineralization of organic matter, releasing nutrients to support pioneering vegetation[119]. Conversely, although rainwater also adds moisture to

dunes, the low moisture retention capacity of sand can create downward leaching and loss of nutrients from the root zone during rainfall in wet climates[108].

Access to fresh water is a determining factor in the zonation and overall productivity of dune plant communities[120,121]. Although dunes are known for their large groundwater reserves, sand is highly porous
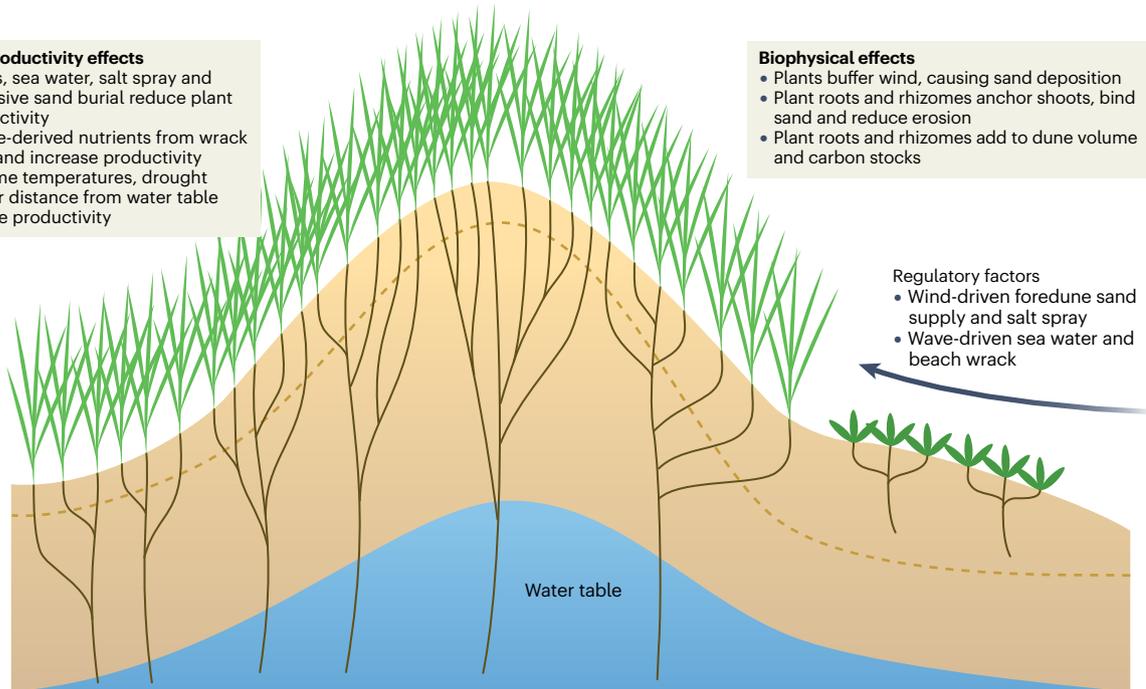
a **Dune plant biophysical and productivity effects**

Plant productivity effects
• Waves, sea water, salt spray and excessive sand burial reduce plant productivity
• Marine-derived nutrients from wrack and sand increase productivity
• Extreme temperatures, drought and/or distance from water table reduce productivity

Biophysical effects
• Plants buffer wind, causing sand deposition
• Plant roots and rhizomes anchor shoots, bind sand and reduce erosion
• Plant roots and rhizomes add to dune volume and carbon stocks

Regulatory factors
• Wind-driven foredune sand supply and salt spray
• Wave-driven sea water and beach wrack

Water table

b **Species-specific biophysical effects**

AMAR   AMBR   UNPA   PAAM   SPPA   LEMO

75 cm   75 cm   85 cm   50 cm   60 cm   95 cm
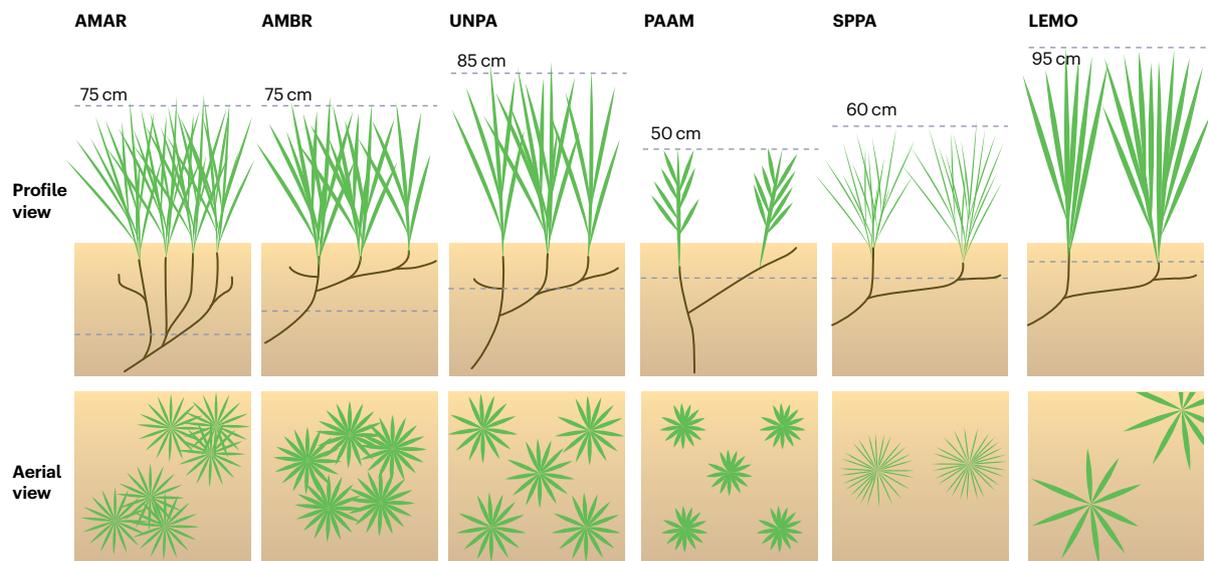
Profile view

Aerial view

Fig. 4 | Biotic processes important to foredune development. a, Dune plant biophysical and productivity effects on a natural foredune. Dune grasses and mound-forming plants occur across the foredune profile. Grey arrow indicates wind-driven and wave-driven regulatory factors. Brown solid lines represent plant roots and rhizomes; blue shading indicates the level of the water table and the dashed brown line represents the foredune height before plant-induced sand deposition and stabilization. **b**, Species-specific biophysical effects. Morphology and growth forms of six species of dune grasses. The sand surface and belowground dashed line represent the hypothesized sand deposition, and aboveground dashed lines and values represent average plant heights. *Ammophila arenaria* (AMAR), *Ammophila breviligulata* (AMBR), *Uniola paniculata* (UNPA), *Panicum amarum* (PAAM), *Spartina patens* (SPPA), *Leymus mollis* (LEMO) from US East and West Coast foredunes. Aerial view represents 0.25 m² area. In general, denser, taller grasses enhance sand deposition more than shorter grasses and mound-forming plants, and support the growth of large volume foredunes. Adapted from ref. 145 under a Creative Commons licence CC BY 4.0.

and plants must be able to access the water table. As such, plants on the dune crest are more water-stressed than those at lower elevations and closer to the water table such as the deflation plain[102] (Fig. 4a). However, some evidence suggests that foredune vegetation can use saltwater, especially during the dry season[122]. Plant species vary in their response to salinity and so for some species excessive salt levels represent a stress, restricting plant functions, such as growth[122–124] and germination[4]. Taken together, these factors raise uncertainties about the response of plants and dune resiliency to sea-level rise[125].

Sand deposition, in addition to being an important arbiter of nutrients and water, also has an important role in how plants allocate resources to aboveground and belowground productivity. Partial burial of plants stimulates rhizomes and roots to grow upward, as with *Ammophila* and *Uniola*, and/or to grow horizontally, as with *Cakile*, *Ipomea* and *Honckenya*, to compensate for sand deposition[39,101] (Fig. 5). Dune plants exhibit contrasting responses to sand deposition[126], from compensatory lengthening of shoots through rebalancing

of root-to-shoot ratios, and increasing investment in aboveground components[127,128], or reapportioning belowground biomass resources for the lengthening of aboveground components[129,130]. There are also ambiguities as to how nutrient availability helps plants respond to sand deposition or burial by especially rapid sand accumulation. For example, some plants, such as *Spartina patens*, can increase internode length in response to sand accretion, regardless of nutrient availability[130], whereas for other plant species, aboveground and belowground biomass allocation and form do not change even with additional nutrients[131].

Species-specific biophysical effects
The species composition of dune plant communities influences sand capture and dune shape at local- to-landscape scales[88,89] (Fig. 4b). For example, dunes of the US Pacific Northwest (dominated by two invasive grass species, European beachgrass *A. arenaria* and American beachgrass *Ammophila breviligulata*[63–65]) and US mid-Atlantic (dominated by four dune grass species, *Uniola paniculata*, *A. breviligulata*, *Panicum*

Fig. 5 | Common dune-building plant species. **a**, *Ammophila arenaria* (European beachgrass, marram grass). **b**, *Ammophila breviligulata* (American beachgrass). **c**, *Panicum amarum* (bitter panicum). **d**, *Leymus mollis* (American dune grass). **e**, *Spartina patens* (salt meadow cordgrass). **f**, *Uniola paniculata* (sea oats). **g**, *Cakile maritima* (sea rocket). **h**, *Honckenya peploides* (sea sandwort). Credit: Sally D. Hacker.

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amarum and *S. patens*)[66] demonstrate the influence of geomorphic factors and dune grass species composition on dune shape (Fig. 5). Comparing foredunes at multiple sites in the two regions show that taller and wider foredunes are associated with greater beach sand supply and grass species with higher shoot densities, demonstrating the species-specific influence of vegetation on dune building.

Experimental plantings using different dune grass species also show that plants vary in their dune-building capabilities. For example, along the US mid-Atlantic Coast foredunes vegetated with monocultures of dune grasses that included *A. breviligulata, P. amarum* or *U. paniculata* grew to similar heights, but *A. breviligulata* established and spread more quickly than the other species, resulting in wider foredunes[132–135]. The salt meadow cordgrass *S. patens* also captures sand, but to a lesser extent than *A. breviligulata* and *U. paniculata*[136] (Fig. 4b). Similarly, in the US Pacific Northwest, *A. arenaria* typically creates taller foredunes than *A. breviligulata* or the native grass *Leymus mollis*[137] (also synonymous with *Elymus mollis*) (Fig. 4b). On the US East Coast, associations between *U. paniculata* and mounded dunes versus *A. breviligulata* and continuous dune ridges[138] are explained by the faster vertical growth rate relative to lateral growth rate of *U. paniculata*[139], leading to the initial formation of hummocky foredunes, which coalesce slowly owing to the slower lateral spread of *U. paniculata*[139]. The rate of dune coalescence is further slowed because intervening low areas between hummocks are vulnerable to overwash, leading to localized resetting of foredune building[139].

Species-specific variation in dune shape arises from functional differences in sand capture between plant species[21,63,65,135]. Dune plants have a suite of characteristics including aboveground stems, leaves and inflorescences and belowground stems (rhizomes) and roots. Variation in the number, length, weight, stiffness and arrangement of these plant parts determine how sand is captured and retained on the foredune[21,37,40,63,65,135,140–144]. For example, a comparison of aboveground and belowground traits of six dune grass species suggests that numerous, tall or heavy shoots capture more sand than few, short or thin shoots[34] (Fig. 4b). However, rhizome length and branching patterns determine whether sand deposition occurs more in vertical or horizontal axes across the foredune[145] (Fig. 4b). For this reason, in the US Pacific Northwest, lower shoot densities and higher lateral growth rates of *A. breviligulata* result in widening of the foredune at the seaward margin, whereas denser shoots and restricted lateral spread of *A. arenaria* result in more vertical sand deposition on the foredune face and crest[63,65]. For a given sand supply regime, the different growth forms of these grasses lead to development of gently sloped, wide foredunes when dominated by *A. breviligulata* and steep, narrow foredunes when dominated by *A. arenaria*.

Less is known about the functional differences in sand capture of low-lying, creeping herbaceous species such as *Abronia, Ambrosia, Cakile* and *Honckenya*, which are well known for forming short embryo dunes (Fig. 5). There is limited evidence on how the traits of dominant species might differ across climate or other environmental gradients that influence sand capture[142]. As well, comparisons of sand capture and dune building in diverse species assemblages with those including fewer species remain limited[99,146].

Vegetation dynamics in foredune models
Foredune models vary in their complexity and incorporation of ecomorphodynamic factors and processes. Focusing on ecological drivers, the DOONIES foredune model[147] uses photosynthesis, respiration, sand deposition, dispersal and mortality to simulate the growth of three types of dune plants as a function of physical factors, such as depth to the water table and distance to the ocean. This model also incorporates the effects of biomass on sand deposition and erosion. To varying degrees and using different approaches, a growing number of ecomorphodynamic models incorporate parameterizations for the growth of dune-building vegetation allowing changes in vegetation and dune morphology to interact dynamically. For example, the Coastal Dune Model[35,139], AeoLiS[148,149], DUBEVEG[85] and Duna[84] model vegetation cover as a generalized or species-specific function of sand deposition and erosion, which can be simplified to a representative dune growth rate. In addition, these models include vegetation effects on wind and sand deposition, via parameterizations that reduce the wind shear stress as a function of plant shape and cover[35,148,150].

Foredune development and morphology depend on the biophysical and productivity effects of vegetation, which in turn are controlled by regulatory factors such as wind-driven sand and salt spray and wave-driven wrack, nutrients and seawater inundation, in addition to freshwater access. Disturbance and stress are also important to the dune-building process and are covered next.

The role of disturbance and stress
Disturbance and stress are ubiquitous in beach–dune systems and appreciably affect foredune development[58,151,152] (Table 1). Although stresses tend to alter dune ecomorphodynamics through effects on individual plants and plant communities[153,154], disturbances (such as sand burial, herbivory or trampling, and storms) yield direct effects on both dune morphology and vegetation, thereby altering feedbacks[96,99,151]. Disturbances and stresses occur across a range of spatial and temporal scales, from metres to 100s of kilometres and from days to multiple decades. Disturbance and stress can be frequent but less intense (such as that caused by sand burial, trampling or blowouts), or less frequent but with greater magnitude (such as that caused by storms and sea-level rise)[152,155,156] (Table 1). In some cases, disturbances and stresses generate positive effects, for example, by reducing plant competition[157], promoting plant dispersal[158] or providing nutrients through enhanced wrack deposition[117].

Small-scale, non-storm disturbance and stress
All dune plants are influenced by small-scale disturbance and stress (Fig. 4a). For example, although most dune plants thrive under some amount of sand deposition, very high rates of sand deposition leading to burial can reduce plant productivity and change vegetation community structure[39,159]. Similarly, the effects of droughts, high temperatures and seawater inundation can reduce productivity and biomass[154,160] and change community composition[99]. By contrast, biotic factors, including herbivory, parasites and disease, although less well studied, can affect vegetation dynamics in coastal systems. For example, herbivory by deer can slow recovery of vegetation following storms[161], and other ungulates can enhance recovery of vegetation by increasing plant dispersal[162]. Smaller grazers, such as rabbits[163], wallabies[164], crabs[165] and parasitic nematodes[166], can reduce biomass and diversity in dominant coastal plant species.

Hurricanes and tropical or extratropical storms
Weather events associated with high water levels generated by high winds and high wave energy, such as hurricanes or storms, can erode beaches and dunes, leading to washover deposition, vegetation loss and even localized species extinctions[75,167,168] (Table 1). Storm erosion can trigger foredune blowouts and, in some locations, stimulate the

Table 1 | Examples of foredune disturbances, stresses and responses across spatial and temporal scales

Disturbance and stress type	Smaller spatial and temporal scale			→		Larger spatial and temporal scale
	Sand burial	**Trampling**	**Blowouts**	**Beach nourishment**	**Storms**	**Sea-level rise**
Effect on foredune sand supply, vegetation and topography	Excessive sand deposition buries vegetation decreasing growth and survival, decreasing sand capture, and leading to decreases in dune growth	Loss of vegetation causes increased local sand mobility and erosion, leading to locally reduced alongshore continuity of foredunes	Erosion and scarping cause local vegetation loss and landward transfer of sand, leading to gaps in foredune	Increased beach width potentially increases foredune sand supply, with possible short-term vegetation burial and loss	Storm surge and waves narrow beaches, enhance erosion, leading to overwash and potential vegetation loss	Enhanced storm surge and wave impacts increase erosion, saltwater intrusion and potential vegetation loss
Functional types of foredune vegetation likely to thrive following disturbance	Tolerant to sand burial, salt spray; rapid tiller and rhizome growth; excellent dune-building potential	Fast-growing, weedy annual species; limited dune-building potential	Tolerant to sand burial, salt spray; rapid tiller and rhizome growth; excellent dune-building potential	Tolerant to sand burial, salt spray; rapid tiller and rhizome growth; excellent dune-building potential	Tolerant to sand burial, sea water, salt spray; rapid tiller and rhizome growth; excellent dune-building potential	Tolerant to sand burial, sea water, salt spray; rapid tiller and rhizome growth; excellent dune-building potential
Consequences for foredune-building processes	Foredune-building feedback resumes when vegetation recovers; persistent excessive burial slows foredune building	Reduced effectiveness of the foredune-building feedback, leading to further erosion or blowouts	Foredune-building feedback resumes when vegetation cover and sand supply allow; if blowouts persist, foredune building can cease	Foredune-building feedback might be enhanced if nourished sand properties allow an increase in foredune sand supply	Foredune-building feedback might reset or stall if foredunes are sufficiently lowered; potential landward shift in location of foredune building	Foredune building might be repeatedly reset by frequent overwash; foredune toe elevation might increase or the location of foredune building might shift landward; vegetation loss might slow foredune growth rate

development of landward-migrating (transgressive) dunefields. Extreme storms can completely remove dunes altogether through overwash and inundation of the foredune system, leaving a wake of washover deposition or loss of sand[3] and resetting the foredune-building process.

The importance of vegetation in mitigating erosion remains unclear, with evidence suggesting that vegetation can not only decrease erosion[169] but also increase erosion, especially if it is newly established via restoration[170]. Plants that are resistant to storms generally have deep roots and grow back to the surface after burial by washover. Other species quickly re-establish from rhizomes, seeds[157,171] or vegetative fragments in wrack[117]. When disturbance and stress are frequent and severe, early colonizers, such as *Cakile* or *Abronia*, tend to dominate, whereas low rates allow mature plant assemblages to persist[4,104,151]. Thus, changes in storm frequency and intensity affect plant species composition and density[104,157,168], and in turn, the dune-building feedback and dune morphology (Fig. 4a). In addition, as dune growth tends to proceed slowly until vegetation becomes established, the relative timescale of storm occurrence versus dune growth rate is critical in determining dune height and vulnerability to overwash processes[35,172].

Anthropogenic activities

Anthropogenic activities generate stress and disturbance in coastal dune systems[58,173,174], leading to alterations of the dune-building feedback. At small scales, trampling of vegetation can stress or kill vegetation[168,175], increasing local sand mobility and erosion and increasing vulnerability to dune blowouts (Table 1). At local-to-regional scales, invasions by regionally novel and non-native species that are planted to stabilize dunes can compete with native species and alter species composition. For example, the sand sedge *Carex kobomugi*, originally planted for dune stabilization, has decreased the abundance of native foredune species in the US northeast, outcompeting native colonizers such as *Ammophila* and *Panicum*[176,177]. Similarly, the European beachgrass, *A. arenaria*, has spread to coastal foredunes worldwide, often through intentional planting for dune stabilization, displacing the native *L. mollis* in the US northwest[63].

Other management activities, such as beach nourishment[178,179], dune grading to improve ocean views, habitat restoration and raking to remove beach wrack[117,118], can disturb vegetation and alter sand availability, wind patterns and dune elevations[174,180,181]. Protecting coastal infrastructure through beach nourishment is a large-scale disturbance[174,182]. Because beach nourishment widens beaches through the addition of sand, it can increase foredune sand supply, resulting in increased dune growth rates[35] and larger dune size[35,61]. However, at the sand engine mega-nourishment site in the Netherlands, dune growth rates declined despite beach widening because of beach surface armouring with course sediment that limited aeolian sand transfer to the dune[183].

Sand fences also disturb foredune development processes[26] by altering wind flow[180] and trapping wind-blown sand near the dune toe, generally promoting natural dune growth[174]. However, fences placed on the back beach in front of the natural foredune can shut down the dune-building feedback within the natural foredune, leading to lower overall dune heights, as the locus of deposition shifts to the fenced zone[184].

In natural systems, dunes can maintain their form and shift landward as conditions change[185]. By contrast, where buildings and other infrastructure are present behind or within the beach–dune system, a landward shift owing to long-term beach-dune migration can lead to coastal squeeze[186]. Infrastructure in the zone landward of coastal foredunes[174] can prevent landward translation, interrupting the foredune-building process, and potentially preventing the regrowth of dunes following storms. Coupled beach–dune modelling

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frameworks[28,29,84,86] that simulate the effects of management actions and infrastructure on coastal evolution yield insights that can inform coastal management to enhance beach–dune resilience to changing physical, ecological and anthropogenic factors.

Disturbances and stresses, from small-scale events such as trampling and herbivory to large-scale events such as hurricanes or beach nourishment, have a pivotal role in the control of sand supply, vegetation and the dune-building process. The next section explores how climate change impacts, such as rising sea level and extreme storms, compound the effects of disturbance and stress, further influencing foredune ecomorphodynamics.

Climate change impacts

Many factors that influence the foredune-building feedback are projected to change in a warming climate[152,187,188]. Changes in some factors, such as wind and precipitation, will vary regionally and projections are uncertain. In turn, variation in vegetation abundance and distribution and the implications for dune ecomorphodynamics in response to such climatic changes are unclear[188]. This section considers the likely effects of changes in temperature, precipitation, wind, storm frequency and sea-level rise on foredune building and the potential resulting impacts on the large-scale coastal evolution of dune-backed coastlines.

Warming temperatures and changing precipitation patterns associated with climate change are likely to alter vegetation abundance and distribution and therefore the dune-building feedback. For example, experiments show that dune grass productivity declines under warming and drought, affecting competitive interactions[154] and fungal symbionts[160]. Moreover, there is a poleward shift in the latitudinal extent of warm season grasses and an equatorward shift in the extent of cold season grasses[189,190], suggesting a link to climate change. Both extreme wet and drought events might differentially impact species based on their tolerance to waterlogging or desiccation[96,191,192]. Extreme drought events, particularly during the summer growing season, could interact with increasing temperatures, resulting in appreciable changes to community composition[99]. However, beach-cast wrack can mitigate reductions in precipitation[193] by enhancing moisture retention within dune systems.

In some locations, climate change might increase the incidence of extreme wind events and the frequency of sand accretion events and overall foredune sand supply[194]. Whether such a change leads to stress and disturbance or simply enhances vegetation and dune growth rates[129] will depend on species-specific thresholds for plant growth (or mortality) as a function of sand deposition and burial. Similarly, foredune sand supply is influenced by changes in wind forcing and shifts in supply-limiting factors, such as beach moisture content[76]. Thus, the timing of wind events relative to the timing (and intensity) of precipitation events also influences sand accumulation rates. Where changes in the timing or intensity of precipitation delivery lead to wetter beaches during sand-transporting wind conditions, foredune sand supply will decrease[83,186], likely decreasing sand accumulation and vegetation growth rates and therefore dune growth rates.

Changes in the delivery and location of beach-cast wrack can alter nutrient delivery to beach–dune systems, as wrack is an important source of nutrients[105,114,115]. Potential climate-change-induced increases in atmospheric deposition of nutrients, especially nitrogen and phosphorus, could also occur[195]. Changes in nutrient input could promote plant growth and abundance, changing plant growth strategies in ways that either enhance or reduce the effectiveness of the foredune-building feedback[120,130].

In some ocean basins, the frequency and intensity of tropical storms and hurricanes are projected to increase[24,196,197]. These changes along with increases in background shoreline erosion rates[198] and higher water levels with sea-level rise will further exacerbate storm effects[199]. Increases in storm frequency will cause more frequent, and more alongshore-extensive, interruptions to the ecomorphodynamic foredune-building feedback. Such interruptions can lead to a tendency for foredunes to alternate between being low (following a storm) and relatively high (given sufficient time in between storms to grow) or to become trapped in a persistently low state when storms occur too frequently for foredunes to redevelop[172,187].

Changes in the frequency of dune erosion caused by storms can also cause shifts in the dominant dune-building species, with associated changes in the ecomorphodynamic foredune-building feedback and therefore foredune shape. For example, persistent perennial grasses, such as *A. arenaria*, are less resilient to frequent erosion events than annual species, such as *Cakile*. Potential future dominance of *Cakile* over *A. arenaria* would shift dune form towards lower, less well-stabilized dunes[200]. These foredune fates could be avoided where beaches and foredunes can retreat together intact[201], and where beach and foredune sand supply are sufficient for the foredune toe to increase in elevation as sea level rises[81,202].

Importantly, foredunes have a critical role in the large-scale evolution of coastal landscapes as the height and alongshore continuity of foredunes influence the landward transport of sand[3]. Dune dynamics are especially critical to long-term landscape evolution on barrier coastlines, for example [33]. When foredunes are low − a state that might become more prevalent with rising sea level and increasing storm occurrence − overwash processes can transport sand landward, resulting in a landward shift in the boundary between sand and back barrier marsh[32]. Fluctuations between low dune states and high dune states can lead to punctuated, stop-and-go style landward island retreat[33]. In addition, construction of dunes to prevent storm impacts to roads and infrastructure can prevent delivery of sand by overwash to the island interior[203]. This can result in island drowning from the backside and shortening of the length of time that islands remain habitable[28,29].

Climate-change-induced shifts in temperature, precipitation, wind, storm frequency and storm intensity could alter the foredune-building feedback, affecting future dune shape and alongshore continuity. Alterations to foredune shape and continuity can alter the future habitability and evolution of coastal landscapes.

Summary and future directions

Sand transport and vegetation processes along sandy coastlines are highly interconnected through an ecomorphodynamic foredune-building feedback, which ultimately determines foredune structure, functions and services[15]. Physical processes driving sand transport are governed by a sand-sharing system between offshore sediment sources, beaches and foredunes and influenced by waves, wind, beach moisture and sand properties. Vegetation is regulated by wind-driven and wave-driven beach and foredune sand supply, beach wrack, sea water and salt spray as well as regional temperature and precipitation conditions and local access to the water table. Disturbances and stresses, including those driven by weather events, anthropogenic activities and climate change, have additional consequences for foredune erosion, overwash and subsequent dune rebuilding with implications for large-scale coastal evolution.

The relative contributions of metocean, geomorphic and ecological drivers are critical in determining spatial and temporal variations

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Glossary

Aeolian processes

Erosion, transportation and deposition of sand by the wind.

Beach sand supply

The amount of sand transported from the nearshore or alongshore to the beach, usually by wave action.

Community structure

A set of characteristics that shape a community, including the number, composition and abundance of species.

Disturbance

A natural or anthropogenic event that disrupts community structure by physically, chemically or biologically altering organisms or their resources.

Dune sand supply

The amount of sand transported from the beach to the dune via wind or wave action.

Ecomorphodynamics

Interactions and feedbacks between sand transport processes and ecological processes that drive

changes in landscape morphology and ecological communities.

Embryo dunes

A small-scale accumulation of sand representing an early stage of dune formation found on overwash plains or in front of foredunes, also referred to as incipient dune or nebkha.

Foredune

The seaward-most, fully formed dune, parallel to the shoreline on a sandy barrier or beach.

Sand capture

The accumulation of sand owing to a combination of wind speed reduction and decreased remobilization, induced by vegetation, wrack and/or topography.

Stress

Physical, chemical or biological constraints that reduce growth, reproduction or survival of organisms through processes such as sand loss, drought, nutrient limitation or disease.

in coastal foredune morphology, yet these factors have rarely been considered together[65,66,152]. Longitudinal, comparative field surveys capturing changes in dune growth rate, dune shape and species composition across multiple sites will contribute to understanding the relative influence of regional drivers on coastal foredune morphology. Such comparative surveys will provide a foundation for using models to investigate mechanisms and test hypotheses regarding the effects of future changes in temperature, precipitation, storminess and sea-level rise on foredune building and shape and the geographic distribution of coastal dunes. Comparing numerical model simulations with observational evidence and comparing outputs from separately developed numerical models could appreciably enhance our understanding of dune ecomorphodynamics and accelerate model development and performance.

Many numerical models — including DOONIES[147], the Coastal Dune Model[35,139], AeoLiS[148,149,183], DUBEVEG[85] and Duna[84] — now simulate the ecomorphodynamic co-development of dunes and vegetation communities. These models typically operate at the mesoscale, using approximations and representations of physical processes. For example, changes in critical bed shear stress are approximated as a function of sediment properties (such as moisture content and grain size). Better integration of beach morphodynamics and dune dynamics in coastal dune models is needed. Such improvements require explicit simulation of the interactions between growing topography and the wind field, such as temporal variation in flow directions relative to the

shoreline. Implementing state-of-the-art computational fluid dynamic representations into mesoscale ecomorphodynamic models can support more detailed water and wind flow field simulations, improving our understanding of these dynamic systems[204,205]. Capturing the detailed physics involved in sand transport will improve forecasts of foredune growth and erosion at event-to-decadal timescales relevant to coastal management. However, such model advances will require improved input data for wind, sand flux and metocean conditions and better understanding of the factors determining the role of marine processes in dune growth.

In general, ecomorphodynamic dune models still represent vegetation productivity and growth in simplified ways, such as through changes in vegetation cover[35,84,148]. Expanding and enhancing the representation of vegetation within ecomorphodynamic models is critical[150]. For example, methods are needed to translate species-specific plant morphology and growth form from field data into shear stress reduction in ecomorphodynamic dune models. More detailed community-level parameterizations of multiple species assemblages in models are needed to better determine whole community effects on dune morphodynamics, and how climate-change-induced shifts in plant community structure might affect dune shape. Tackling such challenges will require field observations and experiments specifically designed to produce results that can be translated into model parameters, necessitating close collaboration and coordination between ecologists and geomorphologists.

Numerical models, observations and experiments since the early 2000s have facilitated advances in understanding the species-specific role of plants in dune building[206]. However, many aspects of dune vegetation ecology remain poorly understood. For example, uncertainty remains regarding the degree to which foredune vegetation will be able to tolerate saltwater intrusion from sea-level rise and the lack of freshwater availability from changing precipitation patterns, especially under elevated temperatures or changes in sand deposition and burial[154]. It is also unclear how shifts in atmospheric nitrogen deposition and wrack delivery of nutrients will affect plant productivity and community structure[105]. Advances in understanding these aspects of dune vegetation ecology can guide dune restoration and conservation efforts and improve understanding of likely changes in the latitudinal range of dune species driven by changing climate.

Harnessing the power of synergistic modelling and observational efforts offers the highest impact for advancing understanding of foredune ecomorphodynamics. Creating a new generation of ecomorphodynamic dune models parameterized based on empirical data, informed by computational fluid dynamics approximations and coupled to ecological models capable of simulating the growth and response of dune vegetation to changing conditions will substantially advance understanding in the field. The complexities arising from the wide range of spatiotemporal scales and interconnected processes involved in foredune building will pose a challenge to such model development. Iterative model development based on selective expansion or reduction of detail, such as reduced-complexity approaches[207] and strategic testing of model predictions against observations (and vice versa)[208], could be valuable. Such developments will enhance predictive capacities to identify tipping points in coastal foredune state and investigate the effect of climate change and intensifying anthropogenic activities on beach–dune systems.

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