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LETTER

Sediment availability provokes a shift from Brownian to Lévy-like clonal expansion in a dune building grass

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Abstract

In biogeomorphic landscapes, plant traits can steer landscape development through plant-mediated feedback interactions. Interspecific differences in clonal expansion strategy can therefore lead to the emergence of different landscape organisations. Yet, whether landscape-forming plants adopt different clonal expansion strategies depending on their physical environment remains to be tested. Here, we use a field survey and a complementary mesocosm approach to investigate whether sediment deposition affects the clonal expansion strategy employed by dune-building marram grass individuals. Our results reveal a consistent shift in expansion pattern from more clumped, Brownian-like, movement in sediment-poor conditions, to patchier, Lévy-like, movement under high sediment supply rates. Additional model simulations illustrate that the sediment-dependent shift in movement strategies induces a shift in optimisation of the cost–benefit relation between landscape engineering (i.e. dune formation) and expansion. Plasticity in expansion strategy may therefore allow landscape-forming plants to optimise their engineering ability depending on their physical landscape.

Keywords

Ammophila arenaria, biogeomorphic landscapes, clonal expansion, coastal dunes, engineering traits, habitat modification, Lévy movement.

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INTRODUCTION

Movement is essential to life; it determines the fate of individuals through encounters with resources or other organisms, thereby ultimately shaping the dynamics of populations, communities and landscapes (Darwin and Darwin, 2009; Berg, 1993; Turchin, 1998; Nathan *et al.*, 2008; Baguette *et al.*, 2013). Mobile organisms can perceive and respond to their environment, moving towards beneficial or avoiding hostile conditions, while simultaneously balancing energetic costs of movement with expected benefits. This means that how, where and when an organism moves depends both on the environmental conditions in time and space, and the physiological state of the individual (Dickinson *et al.*, 2000; Nathan *et al.*, 2008; Halsey, 2016; Goossens *et al.*, 2020). Although the processes underlying movement are complex, the emerging spatiotemporal movement patterns can be predictable. Movement patterns of many mobile organisms – from large marine predators to unicellular bacteria – can be described using relatively simple random walk models (Berg, 1993; Viswanathan *et al.*, 1996; Bartumeus, 2007; Sims *et al.*, 2008; Ariel *et al.*, 2015; Reynolds, 2018). Brownian motion is the most commonly used model and assumes a Gaussian distribution of step sizes, generating a spatially confined movement pattern. Heavy-tailed models such as the Lévy walk or composite Brownian assume scale-invariant or multi-scale distributions with the resulting movement patterns strongly influenced by the infrequent occurrence of larger step sizes. Which movement pattern an individual follows may directly impact its fitness by affecting its capacity to interact with its physical and biological environment and could therefore be subject to natural selection or environment-dependent optimisation (Viswanathan *et al.*, 1999; de Jager *et al.*, 2011; Ariel *et al.*, 2015; Reynolds, 2018).

While most studies on movement pattern optimisation have been on mobile organisms (e.g. de Jager *et al.*, 2011; Kölzsch *et al.*, 2015; Bartumeus *et al.*, 2016; Reynolds and Ouellette, 2016), clonal plants – typically regarded as sedentary organisms – can also move in space by producing laterally expanding vegetative organs (Cain, 1994; de Kroon and Hutchings, 1995; Oborny *et al.*, 2012). In contrast to mobile animals, which physically move from one location to the next, clonal

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plants can occupy new environments while simultaneously remaining at their previous location (Oborny, 2019). They can maximise nutrients and light uptake by, for instance, increasing shoot density in favourable areas (Slade and Hutchings, 1987; Hutchings and de Kroon, 1994; de Kroon and Hutchings, 1995; Evans and Cain, 1995; Louâpre *et al.*, 2012). However, especially in stressful environments, such as coastal or arid ecosystems, rather than simply responding to conditions, plants can engineer their environment by affecting the distribution of resources such as water, nutrients or sediment (Jones *et al.*, 1997). For instance, plants can enhance local rainwater infiltration in dry environments, and trap water and windborne particles to promote surface accretion in coastal environments (Rietkerk *et al.*, 2002; Bouma *et al.*, 2005; van der Heide *et al.*, 2007; Zarnetske *et al.*, 2012). Whether landscape-forming plants can change their movement strategy depending on environmental conditions, thereby affecting engineering strength, remains unknown.

Here, we hypothesise that clonal movement patterns expressed by landscape-forming plants can be context-dependent, emerging in response to their initial environment and plant-mediated modifications of their environment (see Fig. 1). We expect different clonal expansion strategies to be advantageous in different environmental settings. In physically challenging environments a tight shoot clumping – indicative of Brownian-like expansion (Reijers *et al.*, 2019b) – may enhance engineering strength and protect plants against hydrodynamic forcing or alleviate local anoxia stress (Silliman *et al.*, 2015; Maximiliano-Cordova *et al.*, 2019; Reijers *et al.*, 2019c; de Battisti and Griffin, 2020). However, in more benign environments a Brownian-like pattern may hamper plant expansion and local nutrient limitations may restrict growth potential (Fischman *et al.*, 2019). Previous studies have found that mobile organisms can shift their movement strategy depending on resource availability: expressing Brownian movement patterns under high resource availability, but Lévy-like movement when resources are low and erratically distributed (Nolet and Mooij, 2002; Bartumeus *et al.*, 2003; Wosniack *et al.*, 2017). For landscape-forming plants we expect similar adaptive responses, with individuals expressing Brownian-like, clustered, patterns in physically challenging environments that become increasingly dispersed (i.e. heavy-tailed) as the environment becomes more benign.

We tested this general hypothesis by investigating the clonal expansion patterns of European marram grass (*Ammophila arenaria*), known for building the highest coastal dunes worldwide (Zarnetske *et al.*, 2012). Dune grasses typically colonise the beachfront and rely on trapping wind-blown sand and the subsequent formation of embryonic dunes to escape the damaging effects of seawater flooding. However, excessive sand burial also hampers growth by burying leaves, thereby inhibiting photosynthesis (Maun, 1998; Maun and Perumal, 1999; Brown and Zinnert, 2018). Our recent work in dune grasses demonstrated that, although clonal expansion plays a negligible role in nutrient foraging or sharing in these homogeneously nutrient-poor environments, it plays a key role in determining the capture of sand particles (Reijers et al. 2019a). Interspecific differences in clonal expansion strategy can impact landscape morphology via the plants' engineering strength (Reijers *et al.*, 2019b). The Lévy-type clonal expansion strategy, employed by marram grass during beach colonisation, was found to optimise dune building efficiency by trapping sediment over a relatively large area while minimising the distance it covers with its rhizomal network (Reijers *et al.*, 2019b). However, whether this clonal expansion strategy is an intrinsic trait of the species or whether it holds phenotypic plasticity remains unknown.

Here, we investigated whether marram grass can employ different clonal expansion strategies depending on sediment availability (i.e. aeolian transported sediment). We first conducted a survey in contrasting beach environments (high vs. low sediment availability) to investigate how marram grass organises its shoots under contrasting sediment supply rates. Next, we investigated plant response to contrasting sediment deposition regimes by manipulating deposition in a mesocosm set-up. Our results demonstrate that the expansion strategy of landscape-forming plants is not a fixed trait but that it is plastic. Additional model simulations demonstrate that this plasticity allows for environment-dependent optimisation of the cost–benefit relation between engineering and expansion.

MATERIALS AND METHODS

Field characteristics

We tested whether marram grass (*Ammophila arenaria*) exhibited different clonal expansion strategies under contrasting sediment supply rates by investigating plants growing on the barrier island of Texel (high sand availability, 52°59'37.37" N, 4°43'54.49" E, *c.* 650 m distance to sea) and the back-barrier island of Griend (low sand availability; 53°15'8.55" N, 5°14'38.53" E; *c.* 90 m to sea) (Fig. 2a). The sediment supply rate on the wide beach of Texel reflects a natural coastal beach environment along the Dutch coast with high sediment supply (van Puijenbroek *et al.*, 2017; Silva *et al.*, 2018). In contrast, the beach of Griend is part of a sand nourishment applied in 2016 to reduce island erosion. As a result of the low-fetch (<50 km), tide-dominated conditions, the surrounding tidal flats and proximity to sea, there virtually is no wave-driven sediment supply for aeolian transport (Jackson *et al.*, 2002; Nordstrom and Jackson, 2012).

Field measurements

Following the methods described in Reijers *et al.*(2019b), we selected young isolated plants ($N = 7$ (Texel) and $N = 8$ (Griend), with on average 24 and 50 metre between plants respectively) growing in the pioneer zone. Whereas, the high sediment supply rate on the beach of Texel inhibits the establishment of burial-intolerant species (Maun and Perumal, 1999), on Griend, marram grass was growing in proximity to other salt-tolerant plants (e.g. *Cakile martima, Salsola kali*) (Fig. S1). As a proxy of sediment deposition, we measured elevation differences between the middle of the plant and four points on either edge on a 0.5 m distance using a RTK-GPS system.

We derived the step length distribution with the use of the nearest neighbour connection algorithm on still images using

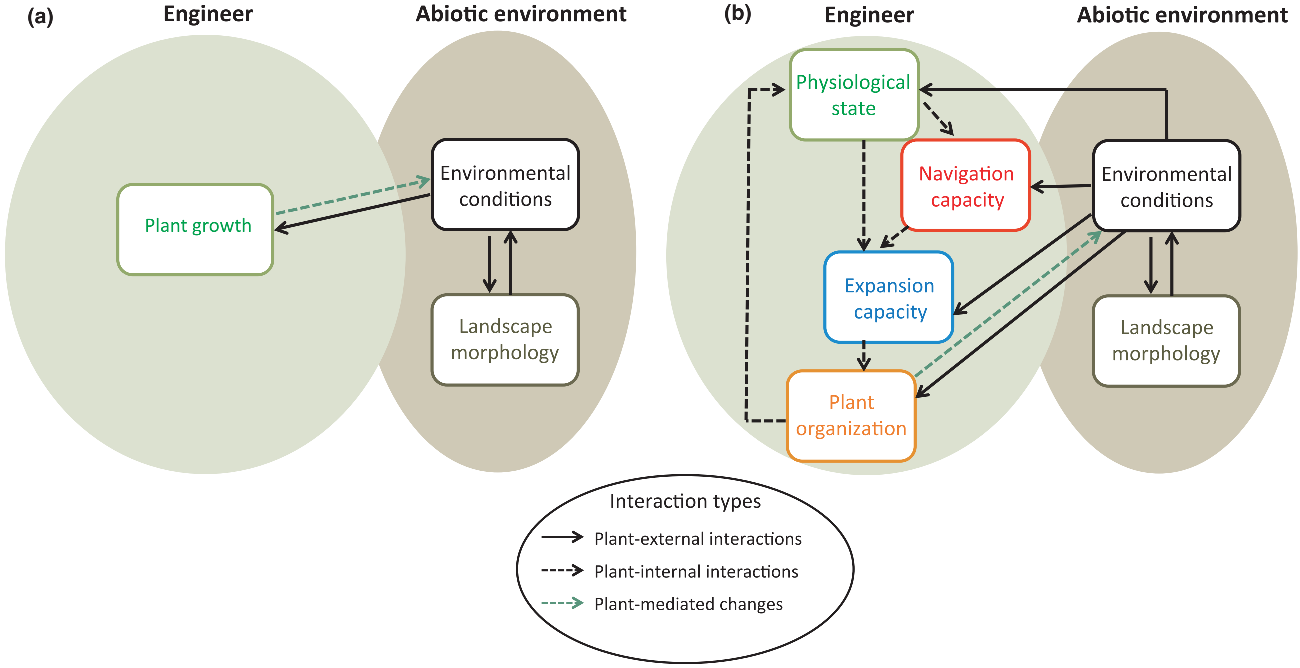
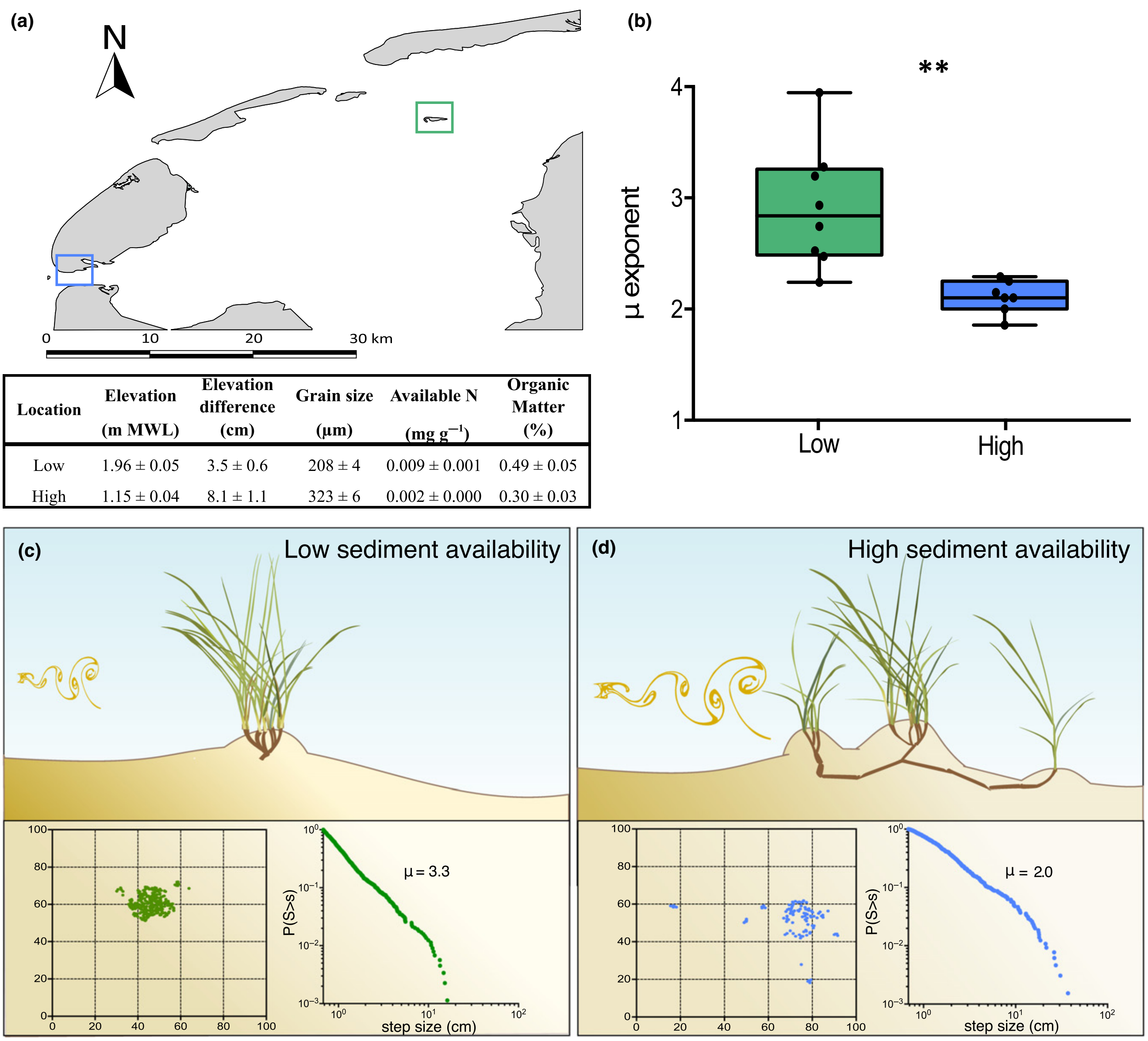


Figure 1 Schematic representation of how ecosystem-engineering frameworks (a) (Jones *et al.*, 2010) and the movement ecology paradigm (Nathan *et al.*, 2008) (b) can be integrated in biogeomorphological research. (a) Ecosystem-engineering framework in biogeomorphic ecosystems. Structural changes by plants can provoke changes in environmental conditions that impact both the engineering plant, landscape morphology and plant-mediated structural changes. (b) We integrated the movement ecology framework into the ecosystem-engineering framework to better reflect the movement-related traits that impact plant organisation and related engineering strength. The movement pattern of an individual (i.e. the plant organisation for clonal plants) is the outcome of four interrelated components (i.e. physiological state, navigation capacity, expansion capacity and environmental conditions). Plant shoot organisation is therefore a product of (i) the internal motivation of an organism to move (the *why*), (ii) the capacity to process information and orient movement (the *where*), (iii) the set of traits that enable an organism to move (the *how*) and (iv) the environment conditions. Plant organisation can, however, change environmental conditions via plant-mediated modifications (green dashed arrow), which in turn can either directly impact plant organisation or indirectly via changes in the movement strategy of the individual. Landscape morphology is ultimately the product of plant organisation (both on the individual and population level) mediated changes to the environment and physical processes (e.g. sediment supply rate, hydrodynamic forcing etc.). The arrows symbolise the relationships among these four components. Adapted and modified from Nathan *et al.* (2008).

a frame of 100 x 100 cm (Reijers and Hoeks, 2019). We first cut off all individual shoots (148 ± 21 and 94 ± 18 for Griend and Texel, respectively) and replaced them with a coloured pin, so we could derive shoots' coordinates (with an accuracy of *c.* 0.34 cm) using a custom-made Matlab tool (Fig. S2). We excavated all plants to verify that per plot all individual shoots were connected via a rhizomal network. If no rhizomal connection was visible, we considered them to be unconnected and discarded them from further analyses. In addition, we measured other plant and soil characteristics including: shoot length and diameter, rhizome depth, leaf nitrogen content, soil grain size, organic matter and plant available nitrogen (see Appendix S1 for detailed description of methods).

Experimental set-up

To separate the effect of sediment deposition from other environmental factors that differed between field locations (Fig. 2a), we set up an outdoor mesocosm experiment in which we subjected marram grass individuals from the same beach environment to different sediment deposition treatments. In spring 2016, we constructed 24 large boxes (2.5 m × 2.5 m × 1 m) in the experimental garden of the Radboud University (Nijmegen, the Netherlands). These boxes were filled with 20 cm base level of drift sand collected from a natural blowout at the Dutch coast (Schoorlse Duinen: 52°41'46.94"N, 4°38'11.22"E; median grain size: 282 ± 0.4 μm in between field locations ($N = 6$)). Rainfall was natural and average daily temperature and light intensity were slightly elevated in the sheltered mesocosms compared to outside conditions (Fig. S3). To ensure water filtration and to prevent plant roots from reaching the underlying soil, each box contained a layer of baked, inert clay pebbles (*c.* 4 cm) at the bottom covered by anti-root fabric. The plants were collected from a young successional beach of the barrier island Terschelling (53°21'23.05"N, 5°10'28.82"E). We planted four individuals (8.0 ± 0.2 shoots tussock^{-1}, 56.9 ± 0.9 cm length; $N = 96$) in a square at a 30-cm distance from each other in April 2016 (Fig. S4). After an acclimation period of 1.5 months (end June 2016) we randomly assigned each box to one of the three sediment deposition treatments: 0, 2 or 4 cm of sand every two weeks. These sediment deposition levels have been applied in other experiments and reflect the average natural burial rate of the species (*c.* 50 cm year^{-1}) and two extremes on either end (0 and 100 cm year^{-1}) (Baye, 1990; Maun and Perumal, 1999; Zarnetske *et al.*, 2012). Over the course of one year, we



Location	Elevation (m MWL)	Elevation difference (cm)	Grain size (μm)	Available N (mg g^{-1})	Organic Matter (%)
Low	1.96 ± 0.05	3.5 ± 0.6	208 ± 4	0.009 ± 0.001	0.49 ± 0.05
High	1.15 ± 0.04	8.1 ± 1.1	323 ± 6	0.002 ± 0.000	0.30 ± 0.03

Figure 2 Field data on the spatial organisation and clonal expansion strategy of marram grass individuals growing in high (wave-dominated; blue colour) and low (tide-dominated; green colour) sediment supply rates. (a) The position of both coastal beaches in the Western Waddensea region (the Netherlands), the blue square indicates the Hors region on the barrier island of Texel, where an ample supply rate of sediment promotes a large coastal dune landscape. The green square indicates the coastal beach on the back-barrier island of Griend where the tide-dominated conditions (note the island is situated in the tidal basin) prevent a constant delivery of coarse-grained sediment to the island. The table below states the environmental characteristics of both sites. (b) The clonal expansion strategy as indicated by the slope (μ) exponent of the step size distribution for plants growing on Griend (low sediment availability; $N = 8$) and Texel (high sediment availability; $N = 7$). The horizontal line indicates the median, box height depicts the first and third quartiles and whiskers represent the max and min values. Statistical differences are indicated using: $P < 0.01$ (**). (c and d) are conceptual depictions of the plants growing under high (c) and low (d) sediment availability. The graphs underneath the picture demonstrate the spatial organisation of one of the clonal individuals (left graph on both panels) and the associated inverse cumulative distribution function and slope (μ) exponent of the clonal expansion strategy (right graph on both panels).

manually added 0, 2 or 4 cm of sieved (5 mm mesh, median grainsize 282 μm) sand every 2 weeks on top of the original 30 × 30 cm square in the middle of the plot. As the plots were – except for wind – subjected to natural conditions such as rainfall, sediment shifted over time. Consequently, final sediment deposition height was *c*. 40 vs. 60 cm and volume 0.3 vs. 1.0 m^3 for the 2 and 4 cm treatments, respectively (Fig. S5).

Mesocosm measurements

We were unable to monitor and track clonal outgrowth of the plants throughout the experiment and instead we analysed final shoot patterns at harvest. The effect of sand deposition on the clonal expansion strategy and the resulting spatial organisation of shoots was analysed using calibrated still images on the 250 * 250 cm plot dimensions. Similar to plants sampled in the field we clipped off all aboveground biomass and replaced each shoot with a coloured pin to mark its position from still images (Reijers and Hoeks, 2019). The vast lateral outgrowth of some of the individuals hampered shoot identification on the individual plant-level based on their aboveground position. By excavating all plants in each experimental plot, we were able to identify the origin of each shoot for $N = 27$ (0 cm), $N = 19$ (50 cm) and $N = 18$ (100 cm). Next to clonal expansion strategy analyses, we measured several other plant and soil parameters including: shoot numbers, shoot growth, leaf and soil C:N ratios, shoot clustering, rhizomal lengths, movement direction and sediment deposition and characteristics (see Appendix S1 for detailed description of methods).

Quantification of clonal expansion strategy – field & mesocosm

Step sizes between shoots for the plants of both the field survey and the mesocosm experiment were estimated on images for which sufficient data were available ($n > 30$ shoots). We applied a simple connecting algorithm (Nearest Neighbour search) that was previously validated for marram grass in natural conditions (Reijers and Hoeks, 2019; Reijers *et al.*, 2019b). In short, the algorithm searches for the nearest neighbour consecutively until all shoots (N) are connected. The algorithm was iterated N times, starting at each individual shoot, and step sizes from the shortest possible route were selected to describe the clonal expansion strategy. We used the inverse cumulative distribution of the derived step size distribution of the pooled data per treatment level to illustrate differences between treatment levels. We tested several heavy-tailed step size models: Brownian, Composite Brownian, log-normal, Lévy and truncated Lévy (see Supporting Information Appendix S2 for a description of different models). In most cases (*c.* 80%) the step size distribution of the individual plants (both field and mesocosm) was best described by a Pareto (Lévy) distribution of step sizes and, in all cases, the model fit was significantly similar to the observed step size data based on a two-sample Kolmochorov–Smirnov (KS) test (see Table S1 and S2 for data-analyses on all individual plants).

We tested whether the clonal expansion trait differed between treatment levels (field and mesocosm), using the parameter settings of our best candidate model (Lévy). Maximum-likelihood methods were used to estimate the scaling exponent μ of a Pareto distribution and the minimum step size (*s*min) for the mesocosm experiment was estimated using KS statistics (Clauset *et al.*, 2009). For some plants of the field survey the optimal *s*min for fitting a power-law distribution was leading to a relatively large loss of step sizes – as all step sizes below *s*min are omitted from the fitting procedure – meaning that the total number of step sizes would be below 30. For those plants we set the minimum step size at 0.68 cm to account for the methodological measurement error of c. 0.34 cm. All individuals with insufficient step sizes for fitting procedures ($n < 30$) were discarded from the dataset (Reijers *et al.*, 2019b) (Table S1 and S2). This resulted in $N = 8$ (low) and $N = 7$ (high) for the field data and $N = 20$ (0 cm), $N = 14$ (2 cm) and $N = 8$ (4 cm) for the mesocosm experiment. The probability density function of a Pareto (Lévy) distribution is given by:

$$P(s) = \left((\mu - 1)\mathrm{smin}^{\mu-1}\right)s^{-\mu} \tag{1}$$

with *s* being the step size, *s*min the minimum step size from which the power-law starts and μ determines the shape of the step size distribution with $1 < \mu < 3$ being referred to as a Lévy distribution. The parameter μ was estimated from the data using the maximum likelihood estimator (Edwards *et al.*, 2012):

$$\hat{\mu} = 1 + \frac{n}{\sum_{i=1}^{n}(\ln(s_i) - \ln(\mathrm{smin}))} \tag{2}$$

Model fitting, validation and verification were done in Matlab (version 2015b, The Mathworks, Inc.). Differences in clonal expansion strategy (μ exponent) between different field locations and sand addition treatments were analysed using R (version 3.4.0). We used a *t*-test and linear mixed models with location or sand addition treatment as explanatory variable and experimental plot as a random factor for the mesocosm experiment. Tukey HSD post hoc tests were used to separate sand deposition treatment effects for the mesocosm experiment.

RESULTS

Location effects on clonal expansion strategy & plant growth

The clonal individuals sampled on Griend (low sediment) exhibited a more clumped, Brownian-like, expansion strategy ($\mu = 2.9 \pm 0.5$). In contrast, the plants sampled on Texel (high sediment) demonstrated the more Lévy-like expansion strategy ($\mu = 2.1 \pm 0.2$) that was previously reported for *Ammophila arenaria* ($t_8 = 4.0$; $P = 0.003$; Fig. 2b) (Reijers *et al.*, 2019b). In addition, several other plant parameters differed. While the plants growing under low sediment availability were buried less deep (4.2 (Griend) vs. 15.7 cm (Texel)), their shoots were taller and thicker (length: 65 vs. 44 cm; diameter: 2.9 vs. 2.2 cm) (Fig. S6). Sediments were sandy in nature, with median grain sizes of 323 ± 6 and 208 ± 4 μm, and low in nitrogen and organic matter content with 0.008 ± 0.002 and 0.002 ± 0.001 mg N g^{-1} soil and 0.30 ± 0.03 and 0.49 ± 0.05% at Texel and Griend respectively (see Fig. 2a). Although nutrient availability differed slightly between sites (Fig. 2a), we report no differences in leaf C:N ratio (*c.* 26 g g^{-1}) (Fig. S6d).

Effects of experimental sediment deposition on clonal expansion strategy & plant growth

The plants that received no sediment in our experiment exhibited a more Brownian-like expansion strategy ($\mu = 2.7 \pm 0.1$). The plants that received continuous sediment supply (2 or 4 cm every fortnight) exhibited a more Lévy-like expansion strategy, but surprisingly, we report no differences between treatment levels ($\mu = 2.2 \pm 0.0$ (2) and 2.3 ± 0.1 (4); $F_{2,39} = 14.44$; $P < 0.001$; Fig. 3e). Cluster analyses revealed a similar pattern, with the plants that were deprived of sediment having a higher number of shoots per cluster and a shorter

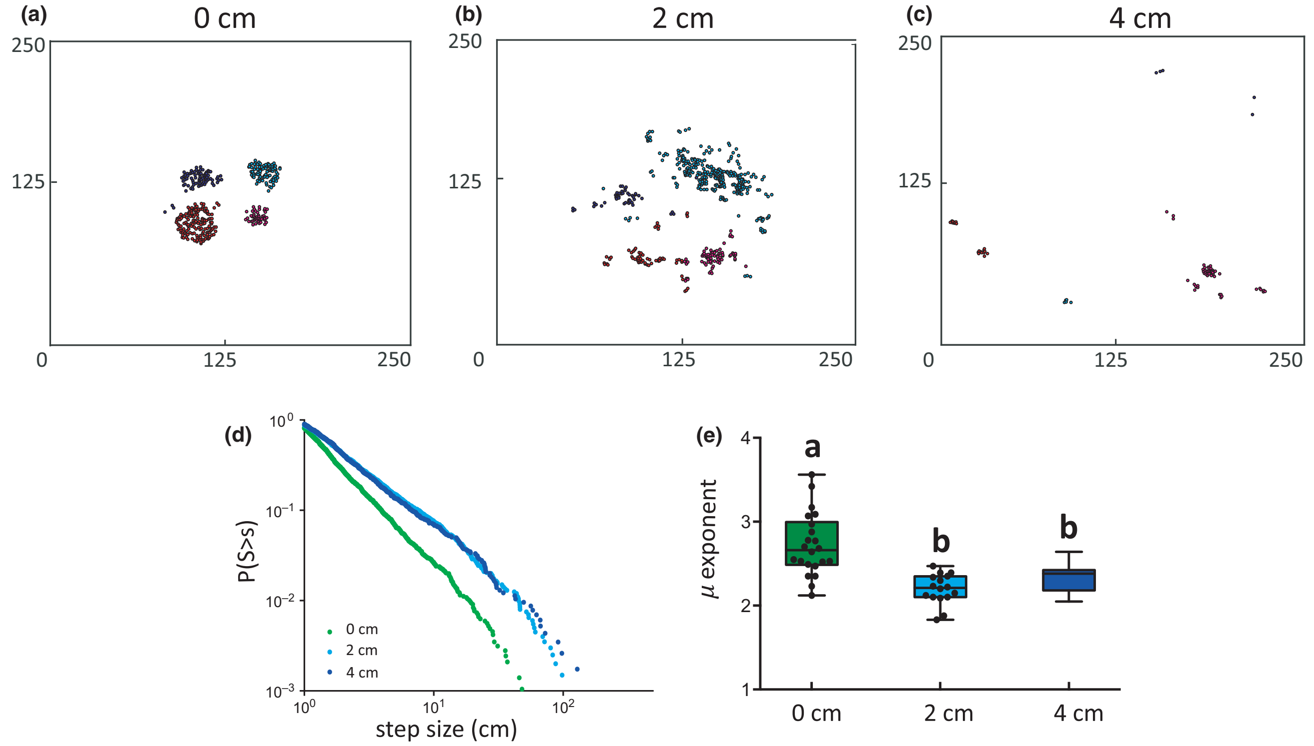


Figure 3 (a–c) Spatial shoot organisation of the *Ammophila* individuals under the different sand addition treatments. The four colours in the plot (i.e. red, blue, turquoise and purple) indicate the four clonal individuals. (a) spatial organisation of the 0 cm treatment (plot 18), (b) spatial organisation of the 2 cm treatment (plot 16) (c) spatial organisation of the 4 cm treatment (plot 1). (d) Inverse cumulative frequency distribution of the estimated step sizes between shoots of the pooled data per treatment (0: green, 2: light blue and 4: dark blue) using a nearest neighbour connecting algorithm on calibrated images of the individual plants (see methods). (e) The power-law or μ exponent of the Lévy distributions for each sand addition treatment. The horizontal line indicates the median, box height depicts the first and third quartiles and whiskers represent max and minimum values. Letters depict post hoc grouping ($P < 0.05$). $N = 20$ (0), $N = 14$ (2) & $N = 8$ (4).

distance between clusters (Fig. S7). While total number of shoots per experimental plot was the same for the 0 or 2 cm treatments (*c.* 400 shoots; GLM: estimate = -0.04 ± 0.024, $z = -1.61$, $P = 0.108$), the plots that received 4 cm had three times less shoots (*c.* 130 shoots; GLM: model estimate = -1.16 ± 0.035, $z = -32.96$; $P < 0.001$; Fig. S8a). However, we found no differences in shoot numbers between treatment levels for the plants that we used for further analyses on shoot organisation ($n > 30$ shoots; $N = 23$ (0 cm), 17 (2 cm) and 10 (4 cm)), with an average shoot number of *c.* 116 ± 10. Shoot growth rate was positively correlated with sand deposition with the highest rate for the plants receiving 4 cm (0.9 (4) vs. 0.5 cm (2) and 0.3 cm day^{-1} (0); $F_{2,21} = 22.33$; $P < 0.001$; Fig. S8b). Similar to shoot numbers, total plant biomass was comparable for the treatments receiving 0 cm (1449 g FW) or 2 cm (1547 g FW), but lower for treatments supplied with 4 cm of sand (861 g FW) ($F_{2,61} = 4.59$; $P = 0.014$; Fig. S8c). Under sand deposition, plants needed to vertically outgrow the accumulated sediment and this resulted in a higher belowground:aboveground biomass ratio for the plants in the two treatments receiving sand compared to those receiving no sand (2.5 g g^{-1} (4), 1.0 g g^{-1} (2) vs. 0.5 g g^{-1} (0); $F_{2,61} = 29.74$; $P < 0.001$; Fig. S8d). This deposition response is also reflected in the larger proportion of longer, vertically expanding rhizomes (between 15 & 80 cm) (Fig. S9). Although we report no differences in soil C:N ratios (Table S3), leaf C:N ratios were significantly lower in the 4 cm treatment compared to the other treatment levels (22 g g^{-1}(4) vs. 35 and 36 for 2 and 0 cm, respectively). Lastly, analyses on shoot angle distribution demonstrate a uniform distribution in the no sand treatment, but a correlated distribution in both sand addition treatments, with less shoots emerging in the centre areas with the highest sand accumulation (Fig. S10).

DISCUSSION

Our study demonstrates that the clonal expansion strategy, and resulting shoot organisation, is not a hardwired species-specific trait of landscape-forming plants, but instead emerges in response to the environment. As plant organisation can be a direct driver of landscape-forming processes (Schwarz *et al.*, 2018; Reijers *et al.*, 2019b), our results imply that feedback interactions between the physical landscape and plant organisation are driven by movement-related processes (see Fig. 1 for a schematic representation). Specifically, we found marram grass, both in the field and in a mesocosm set-up, to express a Brownian-like, clumped expansion pattern in low sediment conditions. However, when sediment availability and resulting deposition was high, plants exhibited a more Lévy-like expansion pattern. Using a simple model as a heuristic tool (Box 1,

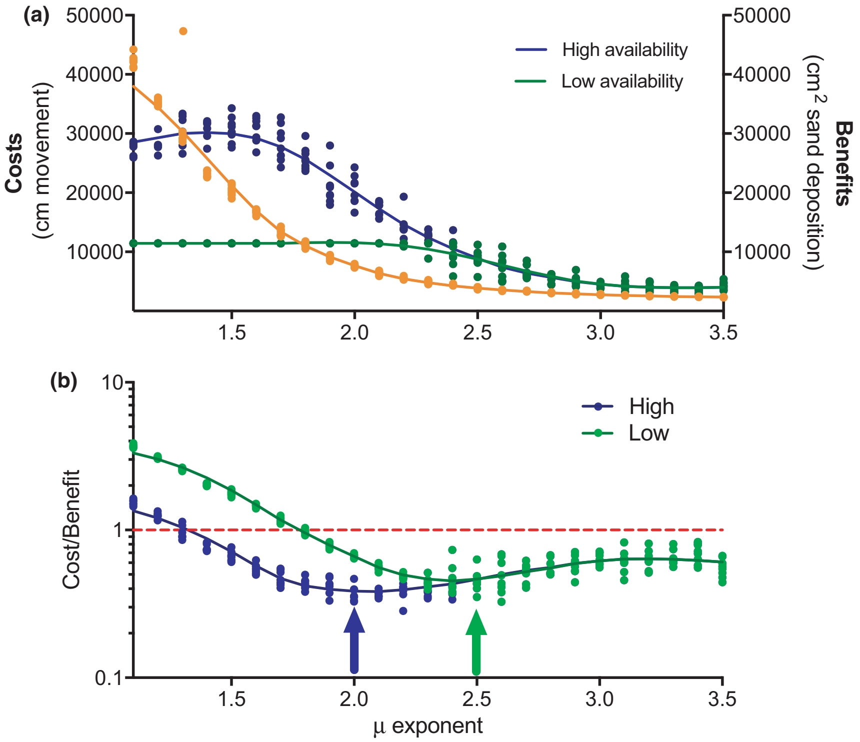


Figure 4 The relation between total distance covered through clonal expansion and the resulting area of sand deposition (a) for a range of clonal expansion strategies from very dispersed (μ ~ 1.1) to tightly clumped (μ ~ 3.5). This cost–benefit relation can switch under low deposition regimes as the maximum area of sand deposition is acquired at a more clumped strategy than under high sediment availability (b). For details on these models simulations see Box 1 and Appendix S3

Fig. 4), we illustrate that this environment-dependent shift in expansion strategy could affect the engineering efficiency of the species. Under low sediment availability, the cost–benefit relation between plant expansion and ecosystem engineering may shift, because maximum engineering capacity (benefit) is acquired under lower costs of expansion. Hence, our work highlights the importance of studying trait variability in landscape-forming species for understanding the formation and resilience of biogeomorphic landscapes, as we show that movement-related engineering traits hold phenotypic plasticity

Box 1. Environment-dependent cost–benefit relation between engineering and expansion

We ran model simulations to illustrate the effects of sediment restriction on the cost–benefit relation between the total distance covered by a clonal dune grass (costs, left y-axis, Fig. 4a) and the area of sand deposition (benefit, right y-axis Fig. 4a). For this, we used a previously published simple biophysical model that simulates clonal expansion as an uncorrelated random walk process and subsequently models wind flow attenuation over the resulting spatial shoot pattern (Reijers *et al.*, 2019b, see Appendix S3 for model specifications and limitations). We ran the model for a range of clonal expansion strategies (x-axis, Fig. 4a and b) from more dispersed expansion (μ ~ 1.1), to more intermittent, Lévy-like strategies (μ ~ 2) and more Brownian, clumped strategies (μ > 2.5). We simulated two potential scenarios: (I) sediment deposition is not restricted (i.e. unlimited potential area of sediment deposition: Fig. 4a and b blue lines) and (II) sediment deposition is restricted (here set at a third of the maximum area of sand deposition obtained under scenario I: Fig. 4a and b green lines). While simulations under scenario I (blue line) illustrate that total sediment deposition is highest at a more dispersed strategy (μ ~ 1.5), it decreases when the clonal expansion strategy becomes more clumped. Under scenario II (green line) the highest potential area of sediment deposition is acquired under a more intermittent clonal expansion strategy. Our model results demonstrate that different environmental conditions, such as high or low sediment supply rates, can change the cost–benefit relation (Fig. 4b), because sand deposition (benefit) becomes limited, whereas costs of movement are unchanged (Fig. 4a). The optimal expansion strategy for rapidly trapping sediment in colonising dune grasses then depends on the trade-off between engineering and expansion and may change under changing environmental conditions (Fig. 4b, arrows indicate the optimum for high (μ ~ 2) and low (μ ~ 2.5) sediment availability).

that allows for adaptive responses under changing environmental conditions.

Previous studies have demonstrated that the engineering ability of species can be related to its species-specific expansion strategy (Hacker *et al*., 2012; Bouma *et al*., 2013; Schwarz *et al*., 2018; Mullins *et al*., 2019; Reijers *et al*., 2019b). However, so far in the field of ecosystem-engineering and biogeomorphology, engineering traits have been mostly considered as invariant properties of species, even though intraspecific variability and environment-dependent trait expression can have far-reaching consequences for ecosystem dynamics and functioning (Hughes & Stachowicz 2004, de Battisti et al. 2020). Here we investigated how environmental conditions impact the expansion strategy of a dune building grass. To visualise the interactions between movement-related processes, ecosystem engineering and landscape morphology we used the movement ecology framework (Fig. 1) (Nathan *et al*., 2008). Based on this framework we argue that the physiological state of the individual – which is essentially a complex vector of many states governed by genetic constraints, environmental stimuli and the past state of the individual – determines the direction and length of movement (Karban, 2008; Nathan *et al*., 2008). Using data from our field survey, mesocosm experiment and additional model simulations, we will discuss below: (1) how the environment affects the movement strategy, (2) what mechanisms can be responsible for observed changes and (3) the implications for dune building processes.

Our field survey demonstrated that marram grass can exhibit different expansion patterns with a more Brownian-type, clumped pattern when sand supply is limited and a more patchy, Lévy-type shoot organisation when sand availability is high (Fig. 2b). Differences in sediment deposition (Fig. 2a) were reflected in the burial depth of the rhizomal network, with the rhizomes from Griend (low sediment) being close to the surface (*c*. 5 cm), whereas the plants from Texel (high sediment) were buried three times deeper (*c*. 15 cm) (Fig. S6c). However, next to sediment deposition rates differences in hydrodynamic regimes with Griend being tide- and Texel wave-dominated, also affect other sediment characteristics, such as grain size, moisture content and plant nutrient availability (Fig. 2a) (Jackson *et al*., 2002; Nordstrom and Jackson, 2012). Our mesocosm setup enabled us to disentangle the effect of sediment deposition from other environmental characteristics. Differences in grain size, for instance, can affect soil moisture content and nutrient availability, but in our experiment we excluded these effects using sand from the same source (Table S3). Although differences in soil moisture in the field can be caused by proximity to sea or due to the formation of freshwater lenses under embryonic dunes (Stuyfzand, 2017; Silva *et al*, 2018), these effects were absent in our experimental setting. Therefore, observed differences in soil moisture likely result from differences in infiltration and evaporation depending on sediment deposition rates (Table S3). While, clonal plants have been found to switch from dispersed to more clumped expansion under high nutrient availability (de Kroon and Hutchings, 1995; Ye *et al*., 2006), we found no differences in nitrogen leaf content between sites (Fig. S6d). Beach grasses in general, and along Dutch coastlines in particular, are nitrogen limited (Hassouna and Wareing, 1964; Reijers et al. 2019a).

In dune grasses, feedbacks between root production in response to burial, enhanced N leaf allocation and increased N uptake in young roots, can maximise photosynthetic rates and thereby increase plant biomass production (Brown and Zinnert, 2018). This implies that direct nitrogen foraging may be less important in dune-building grasses, as nitrogen can by acquired indirectly through sediment trapping. Indeed, in our mesocosm experiment we report higher nitrogen levels in plants growing under high sediment deposition (4 cm) (Fig. S8e).

Contrary to our expectations, we found no differences in expansion strategy between the two sand deposition treatments (2 and 4 cm every fortnight) (Fig. 3). A previous study on the growth response of *A. arenaria* under various sand deposition treatments, reported a strong decrease in lateral expanding tillers under high sediment deposition (Zarnetske *et al*., 2012). Although we found that sediment addition required plants to allocate more resources belowground (Fig. S8d) to vertically outgrow the accumulated sand (note the bimodal distribution under 50 or 100 cm of sand in Fig. S9), they also developed more long, laterally expanding rhizomes (Fig. 2, Fig. S9). We suggest these contrasting results to be explained by differences in experimental setup. In our experiment, we applied new sediment on top of the plants to mimic natural deposition by sand trapping, as opposed to adding sand to the entire plot. However, especially in the 4 cm treatment this centre-based application of sand created a growing conical sand pile and this process passively affected shoot position by pushing shoots outward (Fig. S4). Apart from this physical effect on shoot position, the deposition method allowed the plants to respond by developing vertical expanding rhizomes to reach sand surface (Fig. S9), but also by forming long lateral rhizomes to escape areas of high sand accumulation. This rhizomal growth response – together with the strong clustering of newly emerging shoots on these rhizomal ends – leads to the observed patchy, Lévy-like organisation (Figure 3, Fig. S7).

Based on our results, it appears that the Levy-like movement emerges as a response to burial stress. Although dune formation may allow beach grasses to escape the detrimental effects of seawater flooding, excessive sand deposition may also negatively impact their growth by burying leaves, thereby inhibiting photosynthesis (Maun, 1998; Kent *et al*., 2005). We found plants subjected to 4 cm of sand to suffer from burial stress, growing three times less shoots than the plants receiving no or 2 cm of sand, and having a much lower total biomass (Fig. S8a and c). Although, some individual plants were able to withstand excessive sand burial and had comparable shoot numbers to the other treatment levels (for plants with > 30 shoots used for further analyses, there were no differences in shoot numbers between treatment levels), many individuals in the 4 cm treatment succumbed or had very low shoot numbers ($n < 10$). In addition, we found marram grass to change its movement behaviour depending on sediment deposition, favouring to move away from excessive burial by changing its navigation angle or by increasing the length of laterally expanding rhizomes (Fig. 3; Fig. S10). In contrast, in the absence of sediment, the plants expanded equally in all directions. We expected the added burial stress in the 4 cm treatment to enforce a more Brownian, clumped strategy in the species as a result of the higher energy requirement in vertical growth (Zarnetske *et al*., 2012). Instead, marram grass always exhibits a growth strategy consisting of tight shoot clusters that branch from their rhizomal parts (Fig. S7) (Hacker *et al*., 2019). Without sediment deposition these clusters are on average closer together, resulting in a more Brownian-like pattern (Fig. S7). When sediment deposition occurred – irrespective of the volume of sand – the plants responded by spacing these clusters further apart and a having a lower number of shoots per cluster (Fig. S7). The average distance between shoots in a cluster (which accounts for the small step sizes of the distributions in Fig. 3d) was, as we expected, similar for all sediment deposition treatments.

We propose that this shift in strategy optimises species' sand trapping capacity and therefore its dune building ability under different environmental setting. Model simulations (Box 1, Fig. 4) illustrate that the observed Brownian strategy may be more favourable in low-sediment conditions as it stimulates local sand trapping efficiency, thereby ensuring that the available sand reaches the plant. In contrast, the Lévy strategy that emerges in response to high sediment deposition rates accelerates dune formation when sediment supply is high by enforcing a higher sediment trapping potential. Opposed to mobile species that forage for resources in their environment, sedentary landscape-forming species often attract resources to their local environment through biophysical feedback interactions (Rietkerk *et al*., 2002). This shift in movement strategies we observed in marram grass – with Brownian expansion when resource availability was low and engineering restricted and a more Lévy expansion strategy when resource availability was high and engineering could occur over a larger area – serve as a stepping stone for understanding eco-evolutionary feedbacks in biogeomorphic landscapes.

CONCLUSIONS

Our study demonstrates that marram grass has the ability to process environmental information to navigate away from unfavourable conditions (i.e. moving away from high burial rates (Fig. S10)) and to adjust its moving capacity (i.e. the rhizomal length; Fig. 3; Fig. S9) depending on sediment availability (Fig. 1). Thereby, our findings provide experimental evidence that individual landscape-forming plants can steer spatial shoot organisation and that this behavioural self-organisation affects their engineering strength. This trait variability has important consequences for the morphodynamics of biogeomorphic ecosystems. First of all, the existence of intraspecific engineering trait variation in combination with adaptive responses allows for eco-evolutionary feedbacks, where different biogeomorphic landscapes emerge as a result of changing environmental conditions or a shift in species (Godfrey, 1977; Violle *et al*., 2012; Moran *et al*., 2016; Schwarz *et al*., 2016; Goldstein *et al*., 2018; Dakos *et al*., 2019). Sea level rise, for instance, squeezes beaches, which lowers sediment availability and in turn may impact dune grass' trait distribution and ecosystem dynamics. Second, as species-specific shoot patterns are dependent on environmental conditions, we suggest that they can be indicative of stress at the individual level and potentially serve as early warning signals to predict ecosystem resilience (Rietkerk *et al*., 2004; Kefi *et al*., 2014; Dakos *et al*., 2015). However, they could also be indicative of environmental heterogeneity that, for instance, promotes strong clustering in beneficial patches (de Kroon and Hutchings, 1995). We therefore emphasise the importance of linking plant organisation patterns to underlying environmental conditions (Fischman *et al*., 2019). Finally, our results highlight the existence of adaptive movement strategies in clonal plants, with the same species expressing Brownian-like random expansion patterns or Levy-like, correlated movement strategies. Therefore, our study adds to the growing body of literature emphasising the need to study context-dependency of movement strategies (Nathan *et al*., 2008; Abe and Shimada, 2015; Bartumeus *et al*., 2016; Mizumoto and Dobata, 2019), by demonstrating that sedentary organisms can adopt different movement strategies in response to their environment.

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AUTHORSHIP

V.R. and T.v.d.H. designed the study. V.R., S.H., A.d.R., C.L. and C.v.d.V. conducted the practical work. V.R., S.H., K.S., J.v.B., J.v.d.K. and T.v.d.H. analysed and interpreted the data. V.R. wrote the first draft of the manuscript, all authors contributed substantially to revisions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

Abe, M.S. & Shimada, M. (2015). Lévy walks suboptimal under predation risk. *PLoS Comput. Biol.*, 11, e1004601.

Ariel, G., Rabani, A., Benisty, S., Partridge, J.D., Harshey, R.M. & Be'er, A. (2015). Swarming bacteria migrate by Lévy Walk. *Nat. Commun.*, 6, 8396.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.*, 88, 310–326.

Bartumeus, F. (2007). Lévy processes in animal movement: an evolutionary hypothesis. *Fractals*, 15, 151–162.

Bartumeus, F., Campos, D., Ryu, W.S., Lloret-Cabot, R., Méndez, V. & Catalan, J. (2016). Foraging success under uncertainty: search tradeoffs and optimal space use. *Ecol. Lett.*, 19, 1299–1313.

Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C. & Catalan, J. (2003). Helical Lévy walks: Adjusting searching statistics to resource availability in microzooplankton. *Proc. Natl Acad. Sci.*, 100, 12771–12775.

de Battisti, D. & Griffin, J.N. (2020). Below-ground biomass of plants, with a key contribution of buried shoots, increases foredune resistance to wave swash. *Ann. Bot.*, 125, 325–334.

Baye, P.R. (1990). Comparative growth responses and population ecology of European and American beachgrasses (Ammophila spp.) in relation to sand accretion and salinity.

Berg, H.C. (1993). *Random Walks in Biology*. Princeton University Press. 168 pp.

Bouma, T., De Vries, M., Low, E., Peralta, G., Tánczos, I.V., van de Koppel, J. & Herman, P.M.J.(2005). Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. *Ecology*, 86, 2187–2199.

Bouma, T.J., Temmerman, S., van Duren, L.A., Martini, E., Vandenbruwaene, W., Callaghan, D.P. *et al.* (2013). Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. *Geomorphology*, 180–181, 57–65.

Brown, J.K. & Zinnert, J.C. (2018). Mechanisms of surviving burial: Dune grass interspecific differences drive resource allocation after sand deposition. *Ecosphere*, 9, e02162.

Cain, M.L. (1994). Consequences of foraging in clonal plant species. *Ecology*, 75, 933–944.

Clauset, A., Shalizi, C.R. & Newman, M.E. (2009). Power-law distributions in empirical data. *SIAM Review*, 51, 661–703.

Dakos, V., Carpenter, S.R., van Nes, E.H. & Scheffer, M. (2015). Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20130263.

Dakos, V., Matthews, B., Hendry, A.P., Levine, J., Loeuille, N., Norberg, J. *et al.* (2019). Ecosystem tipping points in an evolving world. *Nature ecology & evolution*, 3, 355–362.

Darwin, C. & Darwin, F. (2009). *The Power of Movement in Plants*. Cambridge, UK: Cambridge University Press.

de Jager, M., Weissing, F.J., Herman, P.M.J., Nolet, B.A. & van de Koppel, J. (2011). Lévy walks evolve through interaction between movement and environmental complexity. *Science*, 332, 1551–1553.

de Kroon, H. & Hutchings, M.J. (1995). Morphological plasticity in clonal plants: the foraging concept reconsidered. *J. Ecol.*, 83, 143–152.

Dickinson, M.H., Farley, C.T., Full, R.J., Koehl, M., Kram, R. & Lehman, S. (2000). How animals move: an integrative view. *Science*, 288, 100–106.

Edwards, A.M., Freeman, M.P., Breed, G.A. & Jonsen, I.D. (2012). Incorrect likelihood methods were used to infer scaling laws of marine predator search behaviour. *PLoS One*, 7, e45174.

Evans, J.P. & Cain, M.L. (1995). A spatially explicit test of foraging behavior in a clonal plant. *Ecology*, 76, 1147–1155.

Fischman, H.S., Crotty, S.M. & Angelini, C. (2019). Optimizing coastal restoration with the stress gradient hypothesis. *Proc. R. Soc. B*, 286, 20191978.

Godfrey, P.J. (1977). Climate, plant response and development of dunes on barrier beaches along the US east coast. *Int. J. Biometeorol.*, 21, 203–216.

Goldstein, E.B., Mullins, E.V., Moore, L.J., Biel, R.G., Brown, J.K., Hacker, S.D. *et al.* (2018). Literature-based latitudinal distribution and possible range shifts of two US east coast dune grass species (*Uniola paniculata* and *Ammophila breviligulata*). *PeerJ*, 6, e4932.

Goossens, S., Wybouw, N., Van Leeuwen, T. & Bonte, D. (2020). The physiology of movement. *Movement Ecol.*, 8, 5.

Hacker, S.D., Jay, K.R., Cohn, N., Goldstein, E.B., Hovenga, P.A., Itzkin, M. *et al.* (2019). Species-specific functional morphology of four US Atlantic coast dune grasses: Biogeographic implications for dune shape and coastal protection. *Diversity*, 11, 82.

Hacker, S.D., Zarnetske, P., Seabloom, E., Ruggiero, P., Mull, J., Gerrity, S. *et al.* (2012). Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact. *Oikos*, 121, 138–148.

Halsey, L.G. (2016). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *J. Exp. Biol.*, 219, 1424–1431.

Hassouna, M. & Wareing, P. (1964). Possible role of rhizosphere bacteria in the nitrogen nutrition of Ammophila arenaria. *Nature*, 202, 467–469.

Hutchings, M.J. & de Kroon, H. (1994). Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research*, 25, 159–238.

Jackson, N.L., Nordstrom, K.F., Eliot, I. & Masselink, G. (2002). 'Low energy'sandy beaches in marine and estuarine environments: a review. *Geomorphology*, 48, 147–162.

Jones, C.G., Lawton, J.H. & Shachack, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.

Jones, C.G., Gutiérrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G. & Talley, T.S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, 119, 1862–1869.

Karban, R. (2008). Plant behaviour and communication. *Ecol. Lett.*, 11, 727–739.

Kefi, S., Guttal, V., Brock, W.A., Carpenter, S.R., Ellison, A.M., Livina, V.N. *et al.* (2014). Early warning signals of ecological transitions: methods for spatial patterns. *PLoS One*, 9, e92097.

Kent, M., Owen, N.W. & Dale, M.P. (2005). Photosynthetic responses of plant communities to sand burial on the machair dune systems of the Outer Hebrides, Scotland. *Ann. Bot.*, 95, 869–877.

Kölzsch, A., Alzate, A., Bartumeus, F., de Jager, M., Weerman, E.J., Hengeveld, G.M. *et al.* (2015). Experimental evidence for inherent Lévy search behaviour in foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150424.

Louâpre, P., Bittebière, A.-K., Clément, B., Pierre, J.-S. & Mony, C. (2012). How past and present influence the foraging of clonal plants? *PLoS One*, 7, e38288.

Maun, M. (1998). Adaptations of plants to burial in coastal sand dunes. *Can. J. Bot.*, 76, 713–738.

Maun, M.A. & Perumal, J. (1999). Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecol. Lett.*, 2, 14–18.

Maximiliano-Cordova, C., Salgado, K., Martínez, M.L., Mendoza, E., Silva, R., Guevera, R. *et al.* (2019). Does the functional richness of plants reduce wave erosion on embryo coastal dunes? *Estuaries Coasts*, 42, 1730–1741.

Mizumoto, N. & Dobata, S. (2019). Adaptive switch to sexually dimorphic movements by partner-seeking termites. *Science advances*, 5, eaau6108.

Moran, E.V., Hartig, F. & Bell, D.M. (2016). Intraspecific trait variation across scales: implications for understanding global change responses. *Glob. Change Biol.*, 22, 137–150.

Mullins, E., Moore, L.J., Goldstein, E.B., Jass, T., Bruno, J. & Durán Vinent, O. (2019). Investigating dune-building feedback at the plant level: Insights from a multispecies field experiment. *Earth Surf. Proc. Land.*, 44, 1734–1747.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. *et al.* (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci.*, 105, 19052–19059.

Nolet, B.A. & Mooij, W.M. (2002). Search paths of swans foraging on spatially autocorrelated tubers. *J. Anim. Ecol.*, 71, 451–462.

Nordstrom, K.F. & Jackson, N.L. (2012). Physical processes and landforms on beaches in short fetch environments in estuaries, small lakes and reservoirs: a review. *Earth Sci. Rev.*, 111, 232–247.

Oborny, B. (2019). The plant body as a network of semi-autonomous agents: a review. *Philosophical Transactions of the Royal Society B*, 374, 20180371.

Oborny, B., Mony, C. & Herben, T. (2012). From virtual plants to real communities: a review of modelling clonal growth. *Ecol. Model.*, 234, 3–19.

Reijers, V.C. & Hoeks, S. (2019). Assessing the clonal expansion strategy of landscape-forming plants. *Protocol. Exchange*. https://doi.org/10.21203/rs.2.9545/v1

Reijers, V.C., Lammers, C., de Rond, A.J.A., Hoetjes, S.C. & Lamers, L.P. & van der Heide, T. (2019a). Resilience of beach grasses along a biogeomorphic successive gradient: resource availability vs. clonal integration. *Oecologia*, 1–12.

Reijers, V.C., Siteur, K., Hoeks, S., van Belzen, J., Borst, A.C.W., Heusinkveld, J.H.T. *et al.* (2019b). A Lévy expansion strategy optimizes early dune building by beach grasses. *Nat. Commun.*, 10, 2656.

Reijers, V.C., van den Akker, M., Cruijsen, P.M.J.M., Lamers, L.P.M. & van der Heide, T. (2019c). Intraspecific facilitation explains the persistence of Phragmites australis in modified coastal wetlands. *Ecosphere*, 10, e02842.

Reynolds, A.M. (2018). Current status and future directions of Lévy walk research. *Biol. Open*, 7, bio030106.

Reynolds, A.M. & Ouellette, N.T. (2016). Swarm dynamics may give rise to Lévy flights. *Sci. Rep.*, 6, 30515.

Rietkerk, M., Boerlijst, M.C., van Langevelde, F., HilleRisLambers, R., de Koppel Johan, V., Kumar, L., Prins Herbert, H.T. & de Roos André, M.(2002). Self-organization of vegetation in arid ecosystems. *Am. Nat.*, 160, 524–530.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & van de Koppel, J. (2004). Self-organized patchiness and catastrophic shifts in ecosystems. *Science*, 305, 1926–1929.

Schwarz, C., Gourgue, O., van Belzen, J., Zhu, Z., Bouma, T.J., van de Koppel, J. *et al.* (2018). Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nat. Geosci.*, 11, 672–677.

Schwarz, C., Ysebaert, T., Vandenbruwaene, W., Temmerman, S., Zhang, L. & Herman, P.M. (2016). On the potential of plant species invasion influencing bio-geomorphologic landscape formation in salt marshes. *Earth Surf. Proc. Land.*, 41, 2047–2057.

Silliman, B.R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T. *et al.* (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proc. Natl Acad. Sci.*, 112, 14295–14300.

Silva, F.G., Wijnberg, K.M., de Groot, A.V. & Hulscher, S.J.M.H. (2018). The influence of groundwater depth on coastal dune development at sand flats close to inlets. *Ocean Dyn.*, 68, 885–897.

Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W. *et al.* (2008). Scaling laws of marine predator search behaviour. *Nature*, 451, 1098–1102.

Slade, A. & Hutchings, M. (1987). The effects of light intensity on foraging in the clonal herb Glechoma hederacea. *J. Ecol.*, 75(3), 639–650.

Stuyfzand, P. (2017). Observations and analytical modeling of freshwater and rainwater lenses in coastal dune systems. *Journal of Coastal Conservation*, 21, 577–593.

Turchin, P. (1998). Quantitative analysis of movement – measuring and modeling population redistribution in animals and plants. Sinauer assoc. Sunderland (mass.).

van der Heide, T., van Nes, E.H., Geerling, G.W., Smolders, A.J.P., Bouma, T.J. & van Katwijk, M.M. (2007). Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems*, 10, 1311–1322.

van Puijenbroek, M.E., Nolet, C.,Groot, A.V.D., Suomalainen, J.M., Riksen, M.J., Berendse, F. & Limpens, J.(2017). Exploring the contributions of vegetation and dune size to early dune development using unmanned aerial vehicle (UAV) imaging. *Biogeosciences*, 14, 5533–5549.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012). The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.*, 27, 244–252.

Viswanathan, G.M., Afanasyev, V., Buldyrev, S., Murphy, E., Prince, P. & Stanley, H.E. (1996). Lévy flight search patterns of wandering albatrosses. *Nature*, 381, 413.

Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999). Optimizing the success of random searches. *Nature*, 401, 911–914.

Wosniack, M.E., Santos, M.C., Raposo, E.P., Viswanathan, G.M. & da Luz, M.G.E. (2017). The evolutionary origins of Lévy walk foraging. *PLoS Comput. Biol.*, 13, e1005774.

Ye, X.-H., Yu, F.-H. & Dong, M. (2006). A trade-off between guerrilla and phalanx growth forms in Leymus secalinus under different nutrient supplies. *Ann. Bot.*, 98, 187–191.

Zarnetske, P.L., Hacker, S.D., Seabloom, E.W., Ruggiero, P., Killian, J.R., Maddux, T.B. *et al.* (2012). Biophysical feedback mediates effects of invasive grasses on coastal dune shape. *Ecology*, 93, 1439–1450.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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