

Research Article

Time tells: plasticity and developmental asynchrony underlie trait variation in a dune-building grass

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Habitat-modifying plants engineer landscapes through plant-environment feedbacks. The strength of these feedbacks is determined by above- and below-ground traits shaping landscape morphology. Besides interspecific differences, recent findings highlight that intraspecific trait variation, such as shoot density, can also influence landscape morphology. Trait expression often changes throughout a plant's life cycle and in response to environmental conditions. Traits advantageous during establishment in early successional stages may differ from those facilitating long-term persistence in stabilized environments. Yet, it remains unknown how traits change relative to environmental stressors across a landscape successional gradient. We conducted a field experiment planting 120 juvenile *Calamagrostis arenaria* transplants, similar in size and appearance, across three successional habitats (beach, foredune, backdune) at four dune locations, covering its full habitat range. After two growing seasons, surviving transplants were harvested to analyze how establishment success, biomass dynamics and trait expression responded to environmental stressors. Establishment, biomass dynamics, and trait expression in *C. arenaria* varied across successional habitats. Initially, *C. arenaria*'s capacity to cope with burial stress is limited, impeding establishment at the beach. Over time, however, high sediment dynamics in early successional habitats promoted growth. In contrast, stabilized foredune and backdune habitats, despite benefitting establishment, provide less favorable growing conditions, reducing biomass and plant vigor. Traits associated with growth strategy, like below-ground stem length, increased in response to burial stress, indicating plasticity. Conversely, above-ground traits reflecting vigor, e.g. stem diameter and leaf size, changed according to plant size, suggesting divergences in developmental. Collectively, our results demonstrate that trait expression and requirements change throughout the life cycle of a habitat-modifying plant and in response to environmental conditions. While some traits shift with plant development, others show plastic responses to stress. Our results

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suggest that single-season or large-scale studies may overlook key features determining trait expression, essentially shaping emerging landscapes.

Keywords: biogeomorphic feedbacks, *Calamagrostis arenaria*, environmental gradients, plant life cycle, vegetated coastal systems

Introduction

Coastal biogeomorphic ecosystems, e.g. seagrass meadows, salt marshes, mangrove forests and dunes, are vital ecosystems as they provide heterogeneous habitats that support diverse species assemblages, and deliver goods and services, including carbon sequestration or flood protection (Orth et al. 2006, Barbier et al. 2011, Corenblit et al. 2015, Castillo et al. 2021). Spanning across the sea-to-land interface, sandy coastal ecosystems can range from sparsely vegetated and highly dynamic to fully vegetated with more stabilized conditions (Corenblit et al. 2015, Castillo et al. 2021). Yet, harsh physical conditions characteristic of unvegetated sandy coastal systems exert strong selective pressure (Crain and Bertness 2006). Only specialized plants may get established as they possess adaptations that enable them to cope with prevailing physical stresses by modifying their environment to their benefit (Altieri et al. 2013, Castillo et al. 2021), often referred to as ‘ecosystem engineering’ (Jones et al. 1994). For instance, plants intercept wind or water flow aboveground, thereby trapping and accumulating sediments, which stimulates plant growth, promoting further sediment capture (Hesp 2002, Altieri et al. 2013). Belowground, expanding root systems and rhizome formation stabilize accumulated sediments over time, raising local bed levels and ameliorating physical stress as new habitat features are formed (Altieri et al. 2013, Corenblit et al. 2015, Castillo et al. 2021). Mitigation of physical stress eventually facilitates recruitment of less tolerant plant species, which in turn enhance habitat stabilization and promote soil development, effectively driving succession (Hesp 2002, Corenblit et al. 2015, Torca et al. 2019). Over time and with increasing distance to the shoreline, ongoing habitat modification creates a biogeomorphological gradient encompassing a sequence of successional stages (Cowles 1899, Torca et al. 2019).

However, the extent to which habitat-modifying plants, such as seagrasses, marsh grasses, mangroves and beach grasses, shape their environment differs among species. Feedback strength and, thereby, engineering capacity are determined by morphological traits (Bouma et al. 2013, Schwarz et al. 2018). Interspecific variation in trait expressions thus can be a key driver in determining the spatial extent and engineering strength of habitat-modifying plants, thereby controlling the type of landscape that emerges (Van Hulzen et al. 2007, Bouma et al. 2013, Schwarz et al. 2018). For example, common cordgrass *Sporobolus anglicus* and dwarf eelgrass *Zostera noltii* co-occur along parts of the intertidal salt marsh gradient (Van De Ven et al. 2024). Cordgrass’ stiff, but dislodgement-prone shoots, enhance sediment trapping by attenuating

flow more effectively than the flexible shoots of eelgrass. While the dense tussocks formed by mature cordgrass can attenuate hydrodynamic drag effectively, its establishment is strongly hampered by physical stress (Bouma et al. 2005, Van Hulzen et al. 2007, Van De Ven et al. 2023). Conversely, eelgrass tolerates higher hydrodynamic drag, enabling greater spatial expansion, but with reduced habitat-forming capacity (Bouma et al. 2005, Puijalon et al. 2011).

Furthermore, increasing attention is given to the effect of intraspecific trait variation on population performance, community structure, and emerging landscape features (Violle et al. 2012, Westerband et al. 2021). Factors like age, size and genetic variation combined with local resource availability and stress determine a plant’s trait expression (Barton 2024). Different environments, therefore, produce a range of phenotypes, which is the combined expression of any morphological, physiological, or phenological trait, as one or more traits respond to local conditions (Violle et al. 2007). However, the underlying mechanisms driving a plant’s response may differ. A plant can actively adjust one or more traits in response to environmental stress. In its simplest form this is referred to as ‘phenotypic plasticity’ – the ability of a single genotype to produce multiple phenotypes (Bradshaw 1965, DeWitt and Scheiner 2004). For instance, for the salt-marsh forming bulrush *Bolboschoenus maritimus*, phenotypic plasticity allows clones to adjust shoot traits in response to hydrodynamic stress, enabling bulrush to inhabit both wave-exposed and sheltered locations (Silinski et al. 2018). At the population level phenotypic plasticity may vary when multiple genotypes are present, as the extent of change in a trait, or ‘reaction norm’ (DeWitt and Scheiner 2004), is genetically regulated. In this study, however, we do not distinguish between genetic and phenotypic plasticity. Instead, we use the term ‘plasticity’ to refer to trait adjustments in response to environmental stress in a general sense. Moreover, variation in trait expression can also arise passively. Two plants might differ in height because of their age, e.g. juveniles are typically smaller than mature individuals. Alternatively, two plants of the same age might differ in height if one experiences environmental limitations, such as water stress. In this case there is an asynchrony in their development that affects trait expression (Cope et al. 2022, Barton 2024). Plasticity and developmental asynchrony can work synergistically when plastic responses during early development favor traits benefiting growth during later plant life-stages despite experiencing environmental limitations (Westerband et al. 2021). Or they can work antagonistically when initial trait investment during plant establishment leads to mismatches in later stages (Pham and McConnaughay 2015, Dayrell et al.

2018). Despite growing awareness of the role of phenotypic variation on plant performance, there remains considerable uncertainty around its origin, extent, and consequences for habitat-modifying plants (Pazzaglia et al. 2021) – all of which might affect ecosystem functionality.

In European dune ecosystems, *Calamagrostis arenaria* (formerly *Ammophila arenaria* or marram grass) is the main habitat-modifying species. Under natural conditions, *C. arenaria* initiates dune formation by trapping aeolian sand on the beach, creating small, often short-lived embryo dunes. The subsequent burial invokes upward elongation to escape burial, increasing both plant height and tiller density, which in turn enhances sand-capturing capacity in a self-amplifying sediment-growth feedback loop (Huiskes 1979, Zarnetske et al. 2012, Van Puijenbroek et al. 2017a). With adequate sand input, *C. arenaria* may accumulate sufficient sand to escape seawater flooding, leading to more permanent white dunes (Van Puijenbroek et al. 2017a). Increasing dune height and habitat stabilization eventually inhibit the self-amplifying sediment-growth feedback of *C. arenaria*, and the more benign conditions instead favor the settlement of later successional species, further promoting primary succession along the biogeomorphological dune gradient (Hesp 2002, Bonte et al. 2021). Both obstructed sediment-growth feedbacks in conjunction with an accumulation of harmful soil organisms (Van der Putten et al. 1993) and increased biological competition (Maun 2009) have been connected to the demise of *C. arenaria* in the stabilized backdunes.

The importance of coastal sand dunes as protective barriers against floods and storm surges has regained recognition in the last decades, and dune-building efficiency and (a) biotic feedbacks of dune grasses, in turn, have been widely studied (Van der Putten et al. 1993, Feagin et al. 2015, Bonte et al. 2021). Previous research linked species-specific differences in plant morphology and growth form to sand-capturing efficiency and the emerging dune landscape morphodynamics (Zarnetske et al. 2012, Feagin et al. 2015, Hacker et al. 2019, Reijers et al. 2019b). For instance, studies have found that the clustered high-density growth form of *C. arenaria* increases local sand-capturing efficiency, which leads to high and steep dune morphologies (Zarnetske et al. 2012). In comparison, American dune grasses *Calamagrostis breviligulata* and *Leymus mollis* and European dune grass *Elymus fractus* have a more lateral expansion leading to shorter and wider dunes instead (Zarnetske et al. 2012, Biel et al. 2019, Lammers et al. 2023). Other traits known to affect sand capture and stabilization in dune grasses include above- and below-ground biomass allocation and shoot-specific features such as height, weight, stiffness, and diameter, with in general a greater investment in aboveground biomass promoting sediment capture, while sediment stabilization is associated with belowground investment (Hesp 2002, Poorter et al. 2012, Zarnetske et al. 2012, David et al. 2016, De Battisti and Griffin 2019, Hacker et al. 2019).

Furthermore, recent papers have highlighted *C. arenaria*'s ability to adapt its morphological traits in direct response to environmental conditions (Reijers et al. 2021, Lammers et al.

2023). Namely, *C. arenaria* actively responds to adverse effects of unfavorable sedimentation volumes by adjusting its shoot organization, directly affecting its engineering capacity. When buried, stem internodes elongate to re-emerge above the surface, while the buried stem segments develop adventitious roots and new shoots, effectively functioning as vertical rhizomes (Huiskes 1979, Maun 1998, Ievinsh 2006). Yet, little is known about which mechanisms (Fig. 1A) underlie trait variation in *C. arenaria* and how it affects plant performance and associated dune-forming capacity. Given that planting *C. arenaria* is a widely used dune restoration practice to enhance coastal protection globally (Feagin et al. 2010, Hanley et al. 2013), understanding how this plant responds to varying growth conditions is critical for ensuring its effectiveness. It becomes particularly pressing in light of projected sea-level rise, increasing extreme weather events, and shifting sand budgets (Hanley et al. 2013, IPCC 2023), which may alter coastal environments both abruptly and long term. Beyond implications for coastal protection, modifications to dune habitat characteristics may also alter plant community composition, potentially leading to shifts in local fauna (Maun 2009, Provoost et al. 2011).

In this study, we investigated responses of transplanted juvenile *C. arenaria* to large-scale environmental gradients and small-scale heterogeneity characteristic of coastal dune systems (Fig. 1B). Specifically, we studied how environmental stress gradients influence the establishment success, survival and trait expression of *C. arenaria*. We conducted a field experiment planting juvenile transplants in three successional zones (beach, foredune, backdune) to include *C. arenaria*'s full spatial extent across the dune landscape at four sites on the Dutch Wadden Island Terschelling. We collected data on environmental conditions, monitored plant survival and harvested all living transplants after two growing seasons, to determine trait expression. To separate the role of plasticity from developmental asynchrony we used a single source population of uniform juvenile transplants purchased from a commercial plant nursery. Overall, we expected 1) high physical stress on the beach to limit establishment success and 2) stable conditions in the backdune to hamper survival and vigor. We further hypothesized that plasticity causes *C. arenaria* to adjust its morphological traits in response to environmental gradients, promoting 3) increased below-ground shoot length on the dynamic beach to escape burial, 4) greater shoot numbers in the semi-dynamic foredune to facilitate lateral expansion, and 5) reduced plant height and leaf size in the stabilized backdune to mitigate competitive stress and conserve resources under sediment deprivation.

Material and methods

Field experiment

The field study took place between April 2021 and July 2022 at four dune sites on the Dutch Wadden Island of Terschelling (53°24'N, 05°21'E). At each site, we picked positions in the following three successional zones (henceforth referred to

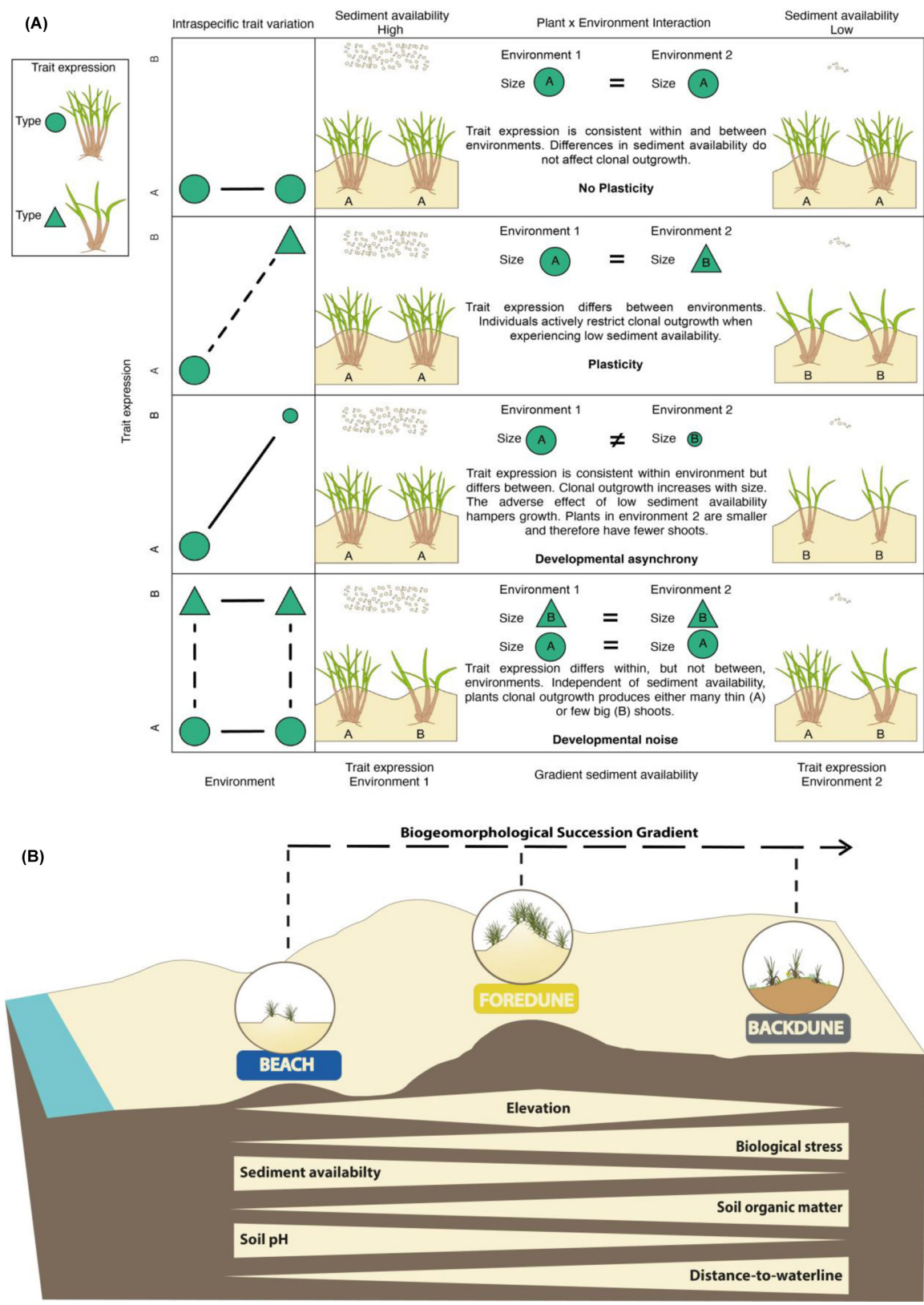


Figure 1. Conceptualization of (A) – the mechanisms causing trait variation in habitat-modifying plants of identical age (left column, circle and triangle = two types of trait expression, solid-black = non-plastic response, dashed-line = plastic response), and (B) – the position of the three successional zones (blue = beach, yellow = foredune, grey = backdune) and associated stress gradients in reference to the biogeomorphological succession gradient.

as 'habitat'), namely: 1) the beach, denoting the upper end of the beach, marked by either embryo dunes or the foot of the first foredunes. Sparsely vegetated, the beach is highly dynamic (net sedimentation 46.4 ± 25.7 cm) and features extensive areas of bare sand where *C. arenaria* co-occurs next to sand couch *Thinopyrum junceum*; 2) the foredune, indicating the semi-stable (net sedimentation 7.29 ± 9.4 cm) area on top of the first foredune ridge featuring denser vegetation cover of the dominant *C. arenaria*; and 3) the backdune, the area located behind the first foredune ridge with signs of succession. In this stabilized zone (net sedimentation 4.1 ± 4.8 cm), *C. arenaria* cover decreases, while mosses, herbs, other grasses, and shrubs notably begin to colonize the area. The four selected sites differ in their morphology (distance-to-sea per habitat, distance between habitats, habitat elevation; Supporting information), as these variables are known to affect bio-physical stress gradients. Per habitat, we haphazardly selected ten experimental plots ($n=40$), where we planted approximately 4-month-old *C. arenaria* transplants (total $n=120$) purchased from a commercial plant nursery (Kwekerij Zwantjes, NL). We selected primarily vegetation-free areas in close proximity of vital-looking *C. arenaria* tussocks and prepared each plot by digging a hole approximately 50×70 cm to remove any remaining plant material (Höfer et al. 2025a). While this approach may have alleviated biological stress potentially benefitting establishment success in the backdune, it reduced initial variability among plots within the habitats improving comparability. Using the prior excavated sand, we first filled the holes to ~ 10 cm depth, where we placed four transplants per plot, including their nursery potting soil, and then filled them up to surface level.

We ended the experiment after the second growing season (July 2022), retrieving all living transplants.

Plant data

At the start of our experiment, we randomly selected 20 transplants to verify uniformity in trait expression and size of the *C. arenaria* before planting by counting the number of shoots (mean 17 ± 1.9 shoots), measuring maximum shoot length (mean 52.4 ± 3.8 cm), stem basal diameter (mean 1.5 ± 0.2 mm), and above-ground biomass (mean 11 ± 1.6 g dry weight after oven-drying, 60°C , 24 h). After planting, we monitored transplant survival by counting all living transplants in the field at three critical time points in *C. arenaria*'s early life cycle: the end of the first growing season (September 2021), the start of the second growing season (April 2022), and the end of the second growing season (July 2022). A transplant survived if we could relocate it and had at least one living shoot. After retrieving all living transplants at the end of the experiment, including their potting soil, we determined plant performance. We chose a combination of plant traits and biomass measurements previously considered important for dune formation or stress adaptation (Feagin et al. 2015, Balestri et al. 2022). In the lab, we assessed eight traits per transplant on the fresh plant material. We started by counting all living shoots (count no.) (Fig. 2A). Next, we selected the three most vital shoots (or fewer if less present) to measure: plant height (cm), measured as the total length from the surface of the potting soil until the end of the longest living leaf tip; above-ground stem length (cm), distance from the most recent node until the base of the first leaf; stem diameter (mm) at the base above the most recent

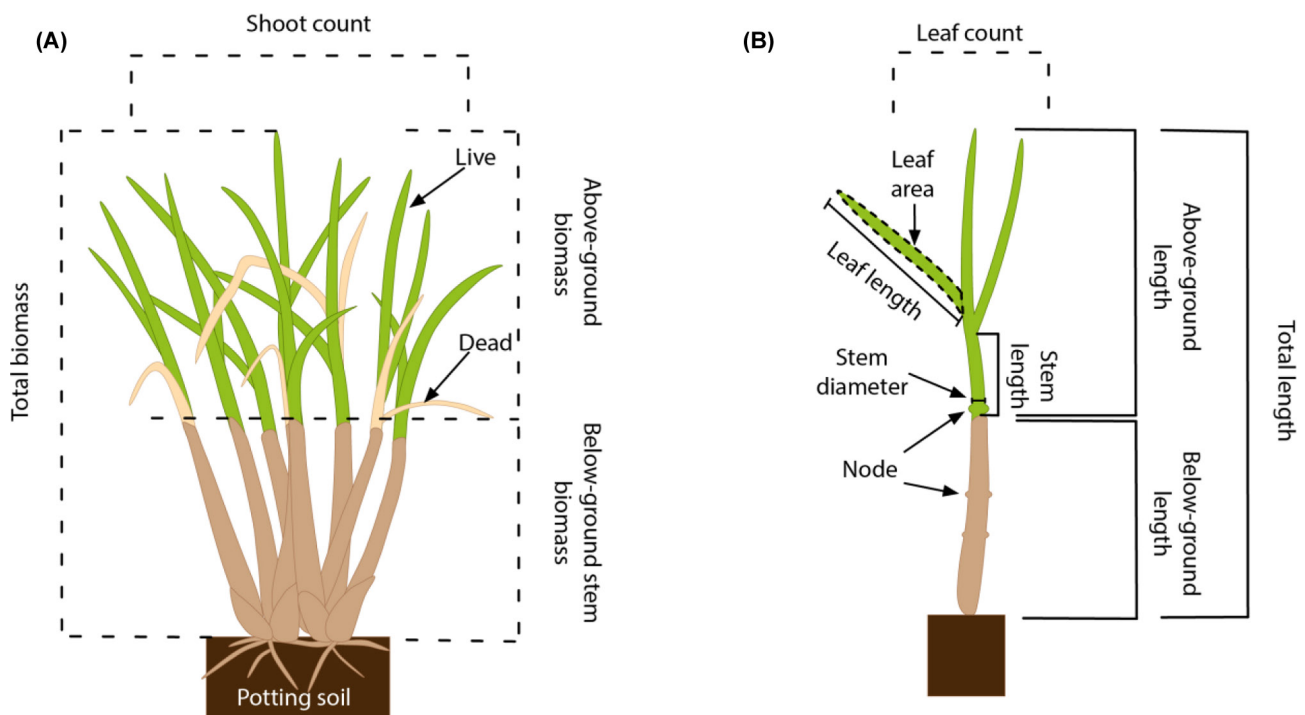


Figure 2. Illustration of measured (A) – whole-plant biomass and traits, and (B) – traits per shoot.

node; the number of leaves per shoot (count no.). From the three shoots, we selected the most vital leaf to determine leaf area (cm^2 of living fraction after 24 h rehydration) in ImageJ (ver. 1.53 K) and specific leaf area (SLA) ($\text{cm}^2 \text{g}^{-1}$ dry weight) after oven-drying (60°C , 24 h). We determined relative below-ground elongation by splitting plant height at the most recent node, marking the transition from rhizomal below-ground material to the above-ground stem, and calculating the ratio between the below- and above-ground shoot length (cm cm^{-1}) (Fig. 2B). Afterward, we separated above- from below-ground biomass and removed the potting soil by clipping all shoots at the position of the youngest node along each stem and at the potting soil surface level (Fig. 3A). We split above-ground biomass into living and dead material and determined total biomass production (g dry weight , oven-drying 60°C , 48 h), discerning above-ground live, dead, and below-ground allocation as their fraction of the total plant dry weight (g g^{-1} dry weight).

Environmental data

At each plot, we collected data on bio-chemical and physical conditions, all suggested to affect survival and morphology of *C. arenaria* (Lammers et al. 2023). In the field, we recorded GPS coordinates using an RTK-GPS (TopCon Positioning Netherlands) at the start of the experiment to determine plot elevation (mNAP) and infer the distance to waterline. Between April and July 2022, we measured five times topsoil compaction (kPa $\sim$ cm 10 depth) in the center and four corners of each plot with a penetrometer (SpotOn Digital Soil Compaction Meter). In the presence of other vegetation, we avoided placing the penetrometer directly on top of it, except in the case of a thin moss layer. We used the standard deviation of the measured compaction over the five visits as a proxy for habitat stability. We estimated net sedimentation (cm) as the distance from the top of the potting soil to surface level using maximum below-ground stem elongation (distance (cm) from potting soil surface to the youngest node) as a proxy for accretion, and maximum height of exposed potting soil (distance (cm) bed level to the top of the potting soil) as a proxy for erosion. Before transplant retrieval, we took a picture of each plot to estimate vegetation encroachment (% plant cover m^{-2} , Adobe Photoshop 2024, ver. 25.1). In the lab, we measured topsoil organic matter (%) via loss on ignition (4 h, 550°C) and pH of soil-water extractions (HI 2300-02 Autoranging meter, Hanna Instrument) using root soil samples ($\sim$ 10 cm depth). Soil samples were collected from a nearby healthy, established *C. arenaria* tussock to standardize sampling. This was considered representative as Reijers et al. (2019a) found plant-available nutrients to be similar within and outside vegetation patches.

Statistical analysis

Survival and biomass dynamics

To test the effect of habitat and time on transplant survival, we employed the paired Wilcoxon signed-rank test for within-habitat comparisons across three time points. For

between-habitat comparison separately for each time point, we used the Wilcoxon rank-sum (package 'rstatix', Kassambara 2019). We investigated if *C. arenaria* biomass production (g dry weight), resource allocation (below:above-ground, g g^{-1}), and relative health (above-ground live:dead, g g^{-1}) are habitat-specific via analysis of variance (ANOVA). We used habitat as the explanatory variable in linear mixed-effect models (package 'lme4' and 'lmerTest', Kuznetsova et al. 2017, Bates et al. 2024) with biomass production as response, and site included as random effect. For resource allocation and relative health, we applied linear fixed effect models, as the random effect of site was not significant. To address potential survivor bias we repeated the biomass production and allocation analysis using only the ten largest transplants (g dry weight) per habitat. To test if plants within the same habitat prioritized above- or below-ground resource allocation we fitted linear-mixed effect models using biomass fraction (biomass fraction (g g^{-1} dry weight), above-ground live, dead and belowground) as explanatory variable, transplant ID as random effect to correct for repeated measures while excluding site as non-significant random effect. All models were inspected for normality and homoscedasticity of model residuals. If required, we applied boxcox (package 'MASS', Ripley and Venables 2009) (between-habitat models) or logit (within-habitat models) transformations to fit assumptions. Significant Satterthwaite one-way ANOVA, type II (package 'car', Fox et al. 2001) for ordinary linear and type III package 'lmerTest' for mixed-effect regression, were followed with pairwise comparison and Tukey adjustments (package 'emmeans', Searle et al. 1980) to separate significant effects.

Plant traits and environment relations

We performed multivariate analyses (package 'vegan', Oksanen et al. 2001) to identify key variables or combinations of variables most important in explaining observed variation in plant traits and environmental conditions, respectively, via principal component analyses (PCA). Afterward, we applied redundancy analysis (RDA) to assess plant performance (growth strategy, relative health and trait expression) across stress gradients using environmental variables as predictors. Prior to the analysis, we tested if our variables followed an approximately normal distribution and showed linear relationships by determining Pearson's correlation. We tested normality and, if necessary, applied boxcox transformation. All variables were standardized using z-scale transformation. The first two pc-axes of the plant trait and environmental PCA, respectively, served as composite variables during further analyses. We examined trait expression and habitat effect on transplant fitness, resource allocation, and health with a two-way ANOVA on linear mixed-effect models using site as random effect. After confirming that site was not significant, we simplified the models to fixed-effect and followed the same assumption testing described for the linear mixed-effect models above. Significance of the interaction term was tested using stepwise variable selection based on Akaike information criterion (AIC).

The significance of the RDA model and each environmental variable in explaining trait plasticity were tested with

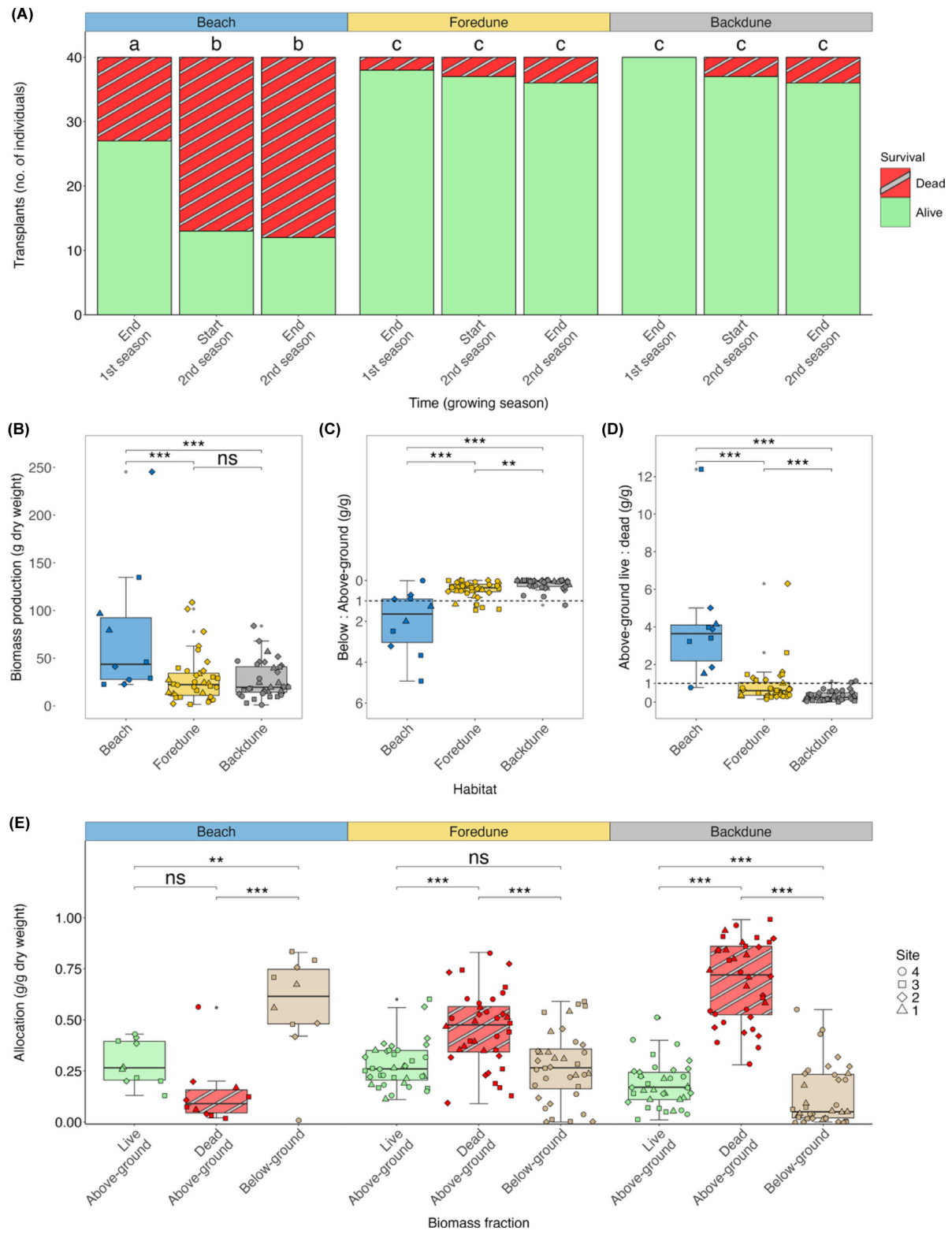


Figure 3. Plant performance across the dune landscape. (A) Transplant survival (no.) per habitat at three critical time points during early life cycle. (B) Whole plant biomass production (g) per habitat. (C) Biomass allocation (ratio below- versus above-ground biomass per habitat (g g^{-1})). (D) Relative health (live versus dead above-ground biomass per habitat (g g^{-1})). In (C) and (D), black dashed line (ratio = 1) indicates equal distribution. (E) Within habitat biomass allocation, discerning above-ground live, above-ground dead, and below-ground fraction (g fraction g^{-1} total dry weight per plant). The points indicate the number of samples per habitat. Their shape refers to the experimental site. Asterisks depict post hoc differences between groups ('ns' $p > 0.05$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$).

ANOVA-like permutation test (999 permutations) and evaluated using adjusted R^2 values. Those values further served as references during forward model selection based on the significant increase in adjusted R^2 and pseudo-F values to compare model fit. We checked multicollinearity among the environmental variables in the RDA models using the variation inflation factor (VIF) test. We repeated the analysis, again using only the ten largest transplants to test for survivor bias. All statistical analyses were conducted in R ver. 4.2.3 (www.r-project.org). Figures were made with packages 'ggplot2' (Wickham 2016), 'ggpbur' (Kassambara 2023), 'ggh4x' (Van Den Brand 2025), 'ggpattern' (Fc et al. 2022), and 'GGally' (Schloerke et al. 2025).

Results

Establishment, survival and biomass dynamics per habitat

Establishment success and over-winter survival were highest in the backdune ($n=40$ mortality end 1st season 0%; $n=37$, mortality start 2nd season 7.5%) and foredune ($n=38$ mortality end 1st season 5%; $n=37$, mortality start 2nd season 7.5%), respectively, while the beach environment limited establishment and over-winter survival ($n=27$ mortality end 1st season 32.5%; $n=13$, mortality start 2nd season 67.5%; Wilcoxon rank-sum test end 1st season adjusted $p < 0.001$, start 2nd season adjusted $p < 0.001$; Fig. 3A). By the second growing season, survival on the beach improved significantly ($n=12$ mortality end 2nd season 70%; Wilcoxon rank-sum test $p=0.773$). However, significantly smaller transplants survived overall in the foredune ($n=36$, dry weight 28.35 ± 25.57 g) and backdune ($n=36$, dry weight 26.7 ± 19.15 g) compared to the beach ($n=12$, dry weight 74.44 ± 70.68 g; $F_{2,76} = 10.63$, $p < 0.001$; Fig. 3B). Biomass allocation changed significantly with habitat (below:above-ground (g g^{-1}), $F_{2,79} = 20.82$, $p < 0.001$, Fig. 3C), shifting from prioritizing below-ground on the beach ($F_{2,27} = 15.04$, $p < 0.001$, Fig. 3E) to a balanced distribution in the foredune ($F_{2,105} = 15.32$, $p < 0.001$). Whereas backdune transplants mainly invested in above-ground biomass ($F_{2,105} = 68.42$, $p < 0.001$), they also accumulated significantly higher proportions of dead relative to living material above-ground (live:dead (g g^{-1}), $F_{2,79} = 20.82$, $p < 0.001$, Fig. 3D). Notably, considering only the ten largest transplants per habitat, maximum biomass production (g) did not differ among habitats (Supporting information). Patterns of biomass allocation, however, remained consistent with those observed for the full dataset, albeit less pronounced (Supporting information). This indicates that allocation differences were not confounded by the survival of smaller individuals in the foredune and backdune. All test results are provided in the Supporting information.

Trait variation in relation to biomass dynamics

The first two principal components explained 74.2% of trait variation in the surviving transplants, separating two main

trait dimensions. Traits associated with above-ground vigor varied along PC1 (60.6%), and transplants with a negative loading on PC1 tended to grow larger, with longer and thicker stems and more numerous, larger leaves than those with a positive loading (Fig. 4A). Traits reflecting growth strategy were captured by (PC2 13.6%), positively relating to rapid growth indicated by greater below- relative to above-ground elongation (i.e. below:above length) and specific leaf area (Fig. 4A). For detailed information on single trait values, Pearson's correlations, and PCA, see the Supporting information.

Multiple linear regressions of biomass measurements on the two trait dimensions, habitat, and their interaction revealed significant albeit varying effects. Variation along the first trait dimension revealed that lower above-ground vigor ($\text{PC1} > 0$) showed significant negative relations to biomass production (Fig. 4B), relative investment into below-ground biomass (Fig. 4C), and living relative to dead above-ground biomass (Fig. 4D), respectively. Biomass production declined stronger on the beach and in the foredune than in the backdune (Trait $\times$ Habitat $F_{2,76} = 6.58$, $p < 0.01$). Conversely, biomass production was unrelated to variation along the second trait dimension (PC2), which reflected growth strategy traits (PC2). On the beach and foredune, greater relative below-ground length ($\text{PC2} > 0$) corresponded to a relatively lower investment in above-ground biomass (Trait $\times$ Habitat $F_{2,76} = 4.19$, $p < 0.05$, Fig. 4D). In backdune transplants, adopting a rapid growth decreased the proportion of living above-ground biomass relative to dead, opposite to the patterns observed for the beach (Trait $\times$ Habitat $F_{2,76} = 6.04$, $p < 0.01$; Fig. 4F).

Effect of environmental gradients on trait expression

In total, 66.7% of the heterogeneity in the multivariate dune environment related to habitat stabilization with ongoing dune landscape modification (PC1 50.2%) and increasing distance to waterline (PC2 16.5%, Supporting information). Coupled with *C. arenaria* performance, redundancy analysis (RDA) revealed that the dune environment significantly influenced transplants (full model $F_{7,74} = 9.59$, $p=0.001$), with net sedimentation, soil pH, soil compaction, elevation and soil organic matter comprising key environmental variables explaining 42.6% (adjusted R^2) of variation in trait expression and biomass dynamics (Table 1A). RDA1 (38.2%) captured co-variation in above- and below-ground trait development, which positively related to net sedimentation, soil pH and soil compaction but formed a tradeoff with soil organic matter and dune elevation (Fig. 5). Variation in growth strategy and resource allocation (RDA2 4.7%) differed with dune elevation, vegetation encroachment, soil pH, and net sedimentation. Compared to assessing plant performance without the context of environmental conditions (PCA, Supporting information), RDA made more nuanced distinctions in the variation of resource allocation from both relative below-ground length and stem traits and leaf area from shoot count. Unlike the beach, transplants from the foredune and backdune only clustered at sites 1 and 3

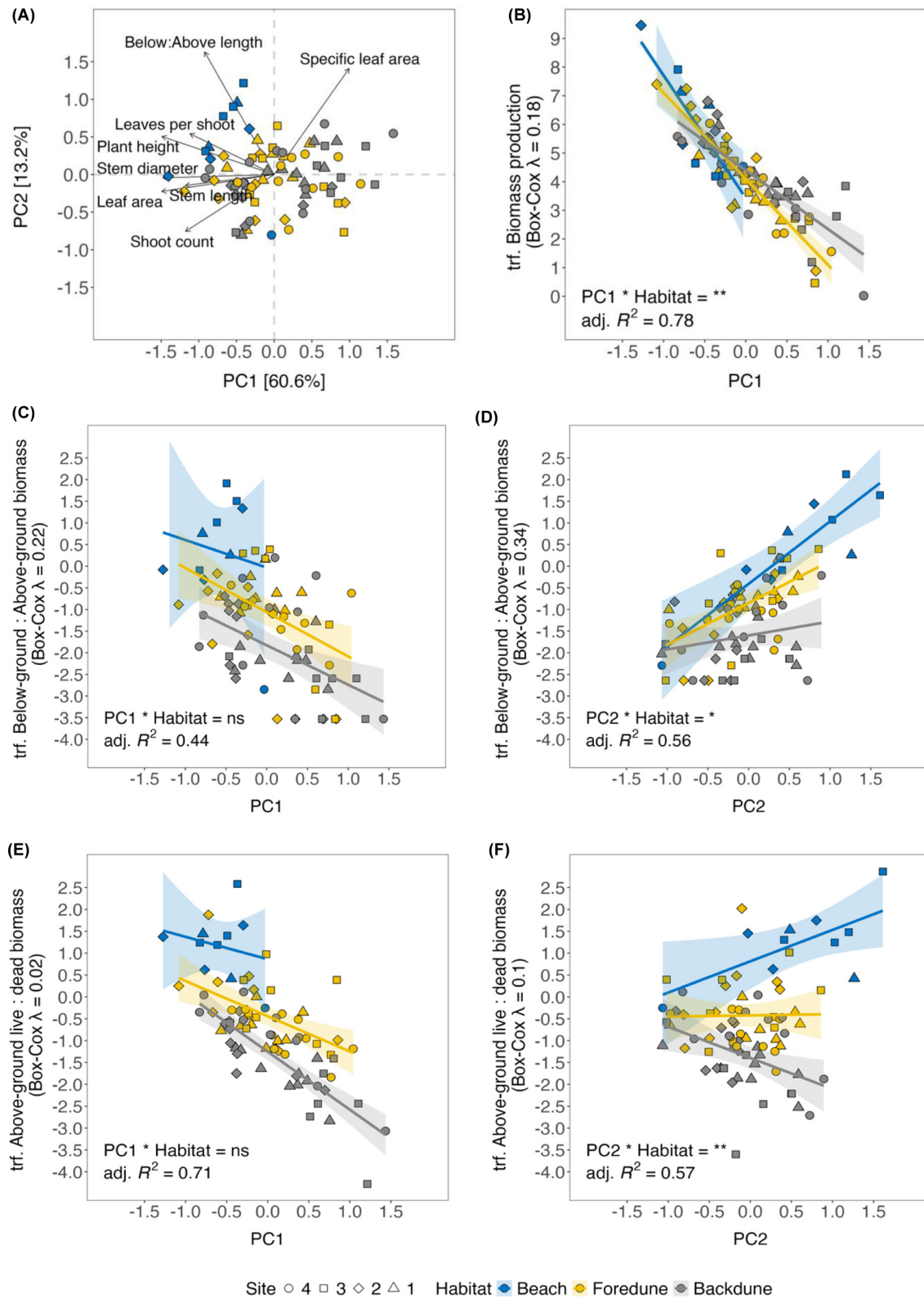


Figure 4. Multivariate analysis showing (A) – PCA results of the plant traits as expressed by all transplants. Multiple linear regression utilizing the first two trait pc-axes and habitat on transformed (B) – biomass production ($g\ dry\ weight$) and PC1. (C) Biomass allocation (ratio below- versus above-ground, $g\ g^{-1}$) and PC1; (D) biomass allocation (ratio below- versus above-ground, $g\ g^{-1}$) and PC2; (E) relative health (ratio above-ground live versus dead biomass, $g\ g^{-1}$) and PC1; (F) relative health (ratio above-ground live versus dead biomass, $g\ g^{-1}$) and PC2. Adjusted R^2 and significance of interaction terms are included per model ('ns' $p > 0.05$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$).

Table 1. Statistical output of ANOVA-like permutation test results listing the separate significance test for each marginal term with all other terms present in the (A) full model considering all environmental predictors, (B) reduced model after forward variable selection.

	RDA model	Environmental predictor	df	Variance	pseudo-F	Pr(>F)
(A)	<u>Full model</u> Plant performance ~	+ Elevation	1	1.66	23.48	0.001***
		+ Distance waterline	1	0.21	2.91	0.054 ^{ns}
		+ Soil compaction	1	0.38	5.41	0.002**
		+ Net sedimentation (trf)	1	1.68	23.67	0.001***
		+ Soil organic matter	1	0.48	6.75	0.003**
		+ Soil pH	1	0.18	2.47	0.057 ^{ns}
		+ Vegetation encroachment	1	0.17	2.42	0.062 ^{ns}
		Residual	74	5.24		
(B)	<u>Reduced model</u> Plant performance ~	+ Net sedimentation (trf)	1	1.6	21.56	0.001***
		+ Soil pH	1	0.51	6.81	0.002**
		+ Elevation	1	0.27	3.66	0.017*
		Residual	78	5.8		

(Supporting information). When restricted to the ten largest transplants per habitat, RDA revealed comparable trait–environment relationships with net sedimentation, soil compaction and pH positively related to greater below-ground biomass allocation and lower accumulation of dead biomass (Supporting information).

Model reduction via forward variable selection singled out net sedimentation, soil pH and dune elevation as key factors for the reduced model explaining *C. arenaria* growth strategy and phenotypic expression (Table 1B). The reduced model supports the notion of burial intensity and dune stability as the main environmental gradients determining growth strategy and developmental trajectory in *C. arenaria*. For supporting information on single-trait relations to environmental gradients, unconstrained analysis of plant parameters and RDA analysis (Supporting information).

Discussion

Understanding the causes and consequences of variation in plant establishment, performance and trait expression in habitat-modifying plants is vital for predicting the dynamics of biogeomorphic coastal systems such as dunes. Here, we found that during *C. arenaria*'s early life cycle, physical stress significantly impeded establishment and survival, illustrated by the high loss of only beach transplants in the first year. Notably, these same conditions ultimately promoted predominantly fast-growing plants on the beach compared to the foredune and backdune. Trait expression reflected opposing axes for vitality and growth strategy. Above-ground traits associated with vitality were tightly related to plant size. Shoot count and below-ground elongation, traits reflecting growth strategy, changed in response to burial stress. Overall, micro-environmental conditions reflecting sediment stability best explained trait expression, yet only weakly related to habitat zonation. Since *C. arenaria*'s dune-forming capacity relies on below-ground traits to enhance erosion resistance (De Battisti and Griffin 2019) and above-ground traits to influence wind attenuation and sediment capture (Zarnetske et al. 2012), these findings offer valuable insights into how environmental conditions shape its contributions to dune dynamics.

Establishment success does not guarantee survival and growth

We found that establishment success is a poor predictor of survival and growth for *C. arenaria* transplants. Similar to other coastal habitat-forming plants, during early life stages, *C. arenaria* struggled to cope with physical stress, especially burial, hampering establishment in highly dynamic conditions (Balke et al. 2011, Durán and Moore 2013, Lammers et al. 2024). While low burial stress initially favored establishment, these advantages diminished over time, negatively affecting survivorship and vigor. On the narrow beach, low sedimentation limited dune growth and led to high over-winter mortality due to hydrodynamic stress (Van Puijenbroek et al. 2017a, 2017b, Moore et al. 2018). In the partly- and fully-stabilized foredune and backdune, reduced sediment input likely disrupted the sediment-growth feedback and increased biological stress (Wallén 1980, Van der Putten et al. 1993, Zarnetske et al. 2013), which lowered biomass production and, ultimately, survivorship. These observations suggest a time lag in the adverse effects of stressors on *C. arenaria*, with sequential impacts from burial, hydrodynamic exposure, and biological stress ultimately negating initial benefits. Overall, our findings align with observations from other coastal ecosystems (Bayraktarov et al. 2016), demonstrating that for habitat-modifying plants like *C. arenaria*, establishment and development dynamics require assessment over longer periods.

Trait expression relates to development and growth strategy

After two growing seasons, the initially uniform trait expression differed greatly between transplants, reflecting variation in two main trait dimensions. First, above-ground stem and leaf traits associated with plant vigor shifted synergistically. Their consistent negative relationship with biomass dynamics and above-ground vitality across the dune gradient supports our second hypothesis that stable conditions hamper survival and growth over time. Second, traits indicative of growth strategies – favoring rapid below-ground elongation (i.e. relative below-ground length) or above-ground resource acquisition (i.e. specific leaf area) – exhibited a weak negative correlation. While these traits did not relate to biomass production, they reflected habitat-specific patterns of resource

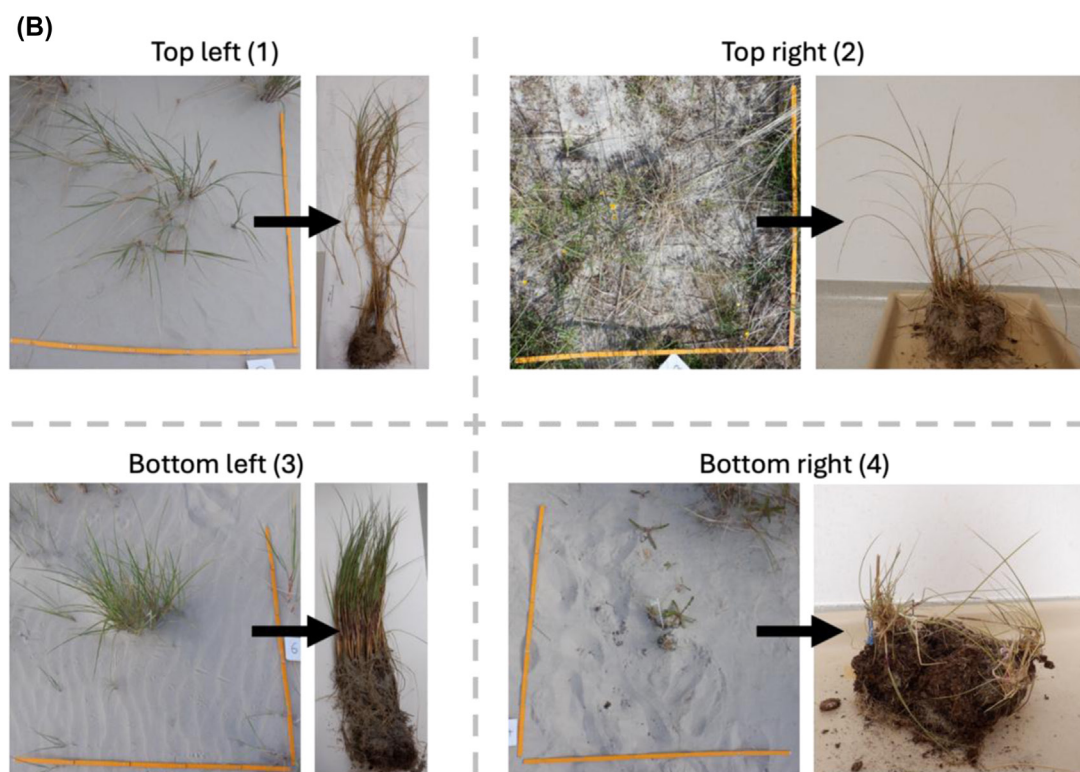
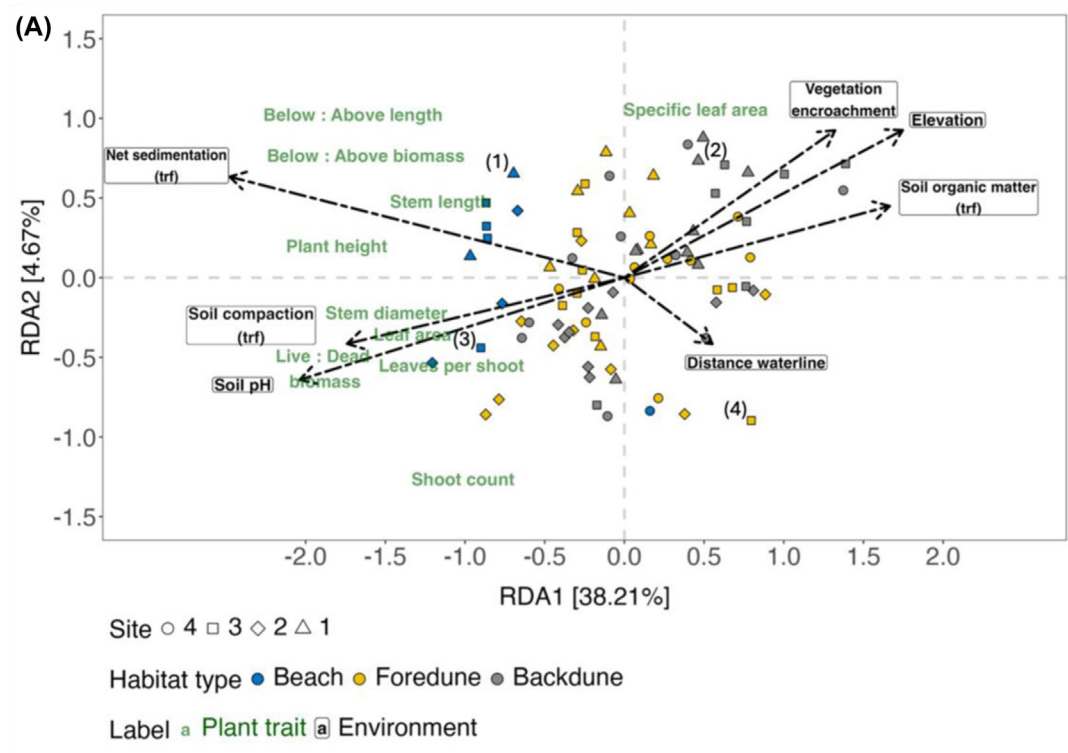


Figure 5. Plant performance across the dune successional gradient. (A) Redundancy analysis (scaling = symmetric) depicting patterns in how trait expression and biomass allocation (green labels) of the transplants (blue = beach, yellow = foredune, grey = backdune) in response to environmental gradients (black labels). Arrow direction and length indicate the correlation and strength of each variable with the RDA axes. The closer a point is to a variable label (green or black), the stronger its association with that variable. (B) Pictures of transplants representative of the four quadrants in the RDA plot (black numbers) taken at the end of the experiment in the field (left) and lab (right).

allocation and plant vitality. The significant negative relation of the first trait dimension to biomass production suggests traits vary due to size, thus developmental asynchrony, whereas the second trait dimension does not relate to plant size, suggesting plasticity (Pham and McConnaughay 2015, Dolezal et al. 2021). Similar to other plants (De Battisti et al. 2020, Walker and Zinnert 2022, Bricca et al. 2023), below-ground and above-ground traits in *C. arenaria* were at least partly decoupled and may explain why some studies report sediment deposition enhances tillering (Zarnetske et al. 2013, Reijers et al. 2021), whereas others found no effect on tillering but increased below-ground biomass production and leaf area (Biel and Hacker 2021). This response suggests that the benefits *C. arenaria* derives from sediment-growth feedback are subject to a threshold beyond which investment in vertical growth comes at the expense of lateral expansion (Nolet et al. 2018, Ievinsh and Andersone-Ozola 2020, Biel and Hacker 2021).

Furthermore, our findings support the growing recognition that plant's environmental requirements shift throughout their life cycle (Balke et al. 2013, 2014, Del Vecchio et al. 2020), a crucial factor for predicting the dynamics of biogeomorphic coastal systems. Previously, much attention has focused on the establishment of seeds or plant fragments (Balke et al. 2013, 2014, Lammers et al. 2024). However, plants undergo several developmental stages from seedling to maturity, during which investment priorities change (Dolezal et al. 2021). For *C. arenaria*, previous work found no differences in juvenile shoot trait development across a biogeomorphic succession gradient after one growing season, yet mature plants displayed marked differences in recovery after disturbance (Höfer et al. 2025a). In contrast, we found clear trait divergence after two growing seasons, despite initially indiscernible trait expression. These results highlight the benefits of multi-season studies in capturing key life stages determining trait expression in habitat-modifying species like *C. arenaria*.

Environmental gradients steer growth strategy and trait expression

Environmental gradients coincided with changes in *C. arenaria* vigor and resource allocation. Above- and below-ground trait expression converged in response to ambient burial stress independently of plant size, indicating plasticity governs trait variation. This finding partly supports our third and fourth hypotheses, namely, high burial stress results in greater below-ground stem length relative to above-ground shoot length, whereas semi-dynamic conditions promote lateral expansion (Ievinsh 2006, Ievinsh and Andersone-Ozola 2020). We further found plant vigor to decrease with habitat stabilization (Emery and Rudgers 2014). In addition to known factors like reduced sedimentation, accumulation of soil pathogens, and increased competition (Van der Putten et al. 1993, Day et al. 2001, Maun 2009), this finding suggests that slower-growing, less vigorous plants are more likely to survive initially in the backdune than on the beach. Contrary to our fifth hypothesis, trait expression reflecting above-ground vigor

showed no discernable differences among habitats. Instead, they were closely related to plant size suggestive of adverse growing conditions having hindered developmental processes (Dolezal et al. 2021). Surprisingly, we found trait convergence and above-ground vigor to relate only weakly to habitat zonation and distance to sea (Van der Putten et al. 1993), with habitat-specific trait clustering occurring only at two of the four sites. This disconnect may have occurred because the two sites lacking clear clustering, the shortest and longest dune profiles respectively, underwent dune rejuvenation by mechanically opening the outer dunes, reinitiating sand transport in the late 1990s to early 2000s (Löffler and Hooff 2011). Subsequently, beach sand was transported and deposited further inland, explaining the higher soil pH observed at these sites, which likely alleviated biological stress as higher pH is unfavorable for later successional species (Maun 2009). Less encroachment, in turn, meant more bare soil and thus higher chances of occasional sand deposition, triggering sediment-growth feedback loops even in the backdune. Consequently, environmental gradients were less pronounced between habitats at these sites, which likely caused the more similar trait expression.

Lastly, in this study, we used a single source population, allowing us to exclude common confounding factors like age and seedling development on trait expression, but not genetic variation. As trait measurements were only available for surviving individuals, our analysis may be affected by survivor bias, with certain trait expression overrepresented due to their association with higher survival or growth (Valladares et al. 2007, Laughlin et al. 2018). Although this selective survival may have contributed to observed trait-environment relationships (Valladares et al. 2007, Laughlin et al. 2018), the initially uniform trait expression among transplants supports our interpretation that the observed patterns in trait divergence mainly reflect environmentally induced responses. Variation in trait expression among the ten largest individuals across habitats further indicates that different trait combinations were associated with higher growth under varying environmental conditions (Valladares et al. 2007, Laughlin et al. 2018). Generally, our findings strongly suggest that plasticity partly drives trait variation. However, we argue that to fully understand the origin of trait variation for *C. arenaria* performance and its dune-building capacity, the responses of multiple genotypes to the same environmental gradients across a range of geographical locations need to be compared over multiple growing seasons in for instance a common garden experiment (de Villemereuil et al. 2022).

Plasticity affects plant fitness

Plasticity is a key mechanism enabling organisms to cope with rapid environmental changes, aiding in population persistence under climate change, colonization of new environments, and species invasiveness (Nicotra et al. 2010). However, whether plasticity enhances adaptation or leads to maladaptive responses that reduce plant fitness remains uncertain. In cordgrass, for instance, a shift to a lower specific leaf area under salinity stress promotes a conservative

growth strategy, supporting colonization across a larger inundation range in salt marshes (De Battisti et al. 2020). We found that despite growing in stabilized dune systems generally described as unfavorable to *C. arenaria*, transplants still exhibited high specific leaf area. Yet, these transplants ultimately exhibited low vigor, suggesting that adopting an acquisitive growth strategy was likely maladaptive, possibly resulting from our experimental design where transplants were planted inside their potting soil. Our findings underscore the need for caution in coastal restoration projects when temporarily manipulating growth environments, such as applying fertilizers or using burial stress-reducing measures like fencing (Miller et al. 2018, White et al. 2024). Though such interventions may enhance early establishment, they can inadvertently alter plant strategies (Dayrell et al. 2018). This risk increases when planting designs or fertilization potentially undermine long-term restoration success (Balestri et al. 2022). Recent work also suggests that the effectiveness of alternative planting approaches, moving from uniform monocultures to interspecific facilitation-maximizing designs, depends on abiotic conditions. Beneficial for growth under more benign circumstances, but ineffective under stress (Fischman et al. 2019, Lammers et al. 2024). Thus, understanding how habitat-forming species like *C. arenaria* respond to (a) biotic factors is key to optimizing planting strategies and ensuring sustained benefits from dune systems.

Conclusion

In this study, we demonstrated that in *C. arenaria*, trait expression is closely regulated by its growth environment during early development stages. Both plasticity and developmental asynchrony are likely mechanisms governing variation in plant growth strategy and vigor. However, further experiments are required to reliably distinguish genetic variation from phenotypic plasticity, to determine the extent of developmental asynchrony, and to assess potential survivor bias. In essence, our findings support the growing recognition that intraspecific variation in habitat-modifying plants is highly sensitive to microenvironmental heterogeneity (Westerband et al. 2021) and early life cycle development. Utilizing proxy gradients like distance-to-sea for environmental conditions (Hesp 1991) or single-season studies can obscure the effects of small-scale heterogeneity in environmental stressors and mask changes throughout developmental trajectory (Dolezal et al. 2021). This underscores the need for caution in using appropriate spatial and temporal scales when assessing phenotypic variation in habitat-forming plants for predicting the dynamics of biogeomorphic coastal systems.

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Author contributions

Solveig Höfer: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Lissie de Groot:** Investigation (supporting); Project administration (supporting); Writing – review and editing (supporting). **Helge Giezeman:** Investigation (supporting); Writing – review and editing (supporting). **Eva Kloppenborg:** Investigation (supporting); Writing – review and editing (supporting). **Eva Lansu:** Investigation (supporting); Writing – review and editing (supporting). **Nathan Scanlan:** Investigation (supporting); Project administration (supporting); Writing – review and editing (supporting). **Max Rietkerk:** Writing – review and editing (equal). **Martin J. Wassen:** Writing – review and editing (equal). **Tjisse van der Heide:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Valérie C. Reijers:** Conceptualization (equal); Formal analysis (equal); Investigation (supporting); Methodology (equal); Supervision (equal); Project administration (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from DataverseNL: <https://doi.org/10.34894/3IJRTN> (Höfer et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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