November 2024

Dear Editors and Reviewers,

We hereby resubmit the revised MS (egusphere-2024-1944), now titled "Narrowing down dune establishment drivers on the beach". The insightful comments from three anonymous reviewers have improved the narrative and the scientific context. We wish to express our sincere gratitude to all reviewers and the associate editor for their dedication and comments.

In the revised Manuscript we have addressed the comments of the reviewers by:

1. Clarifying our experimental approach and scope in terms of ecological processes
2. Elaborating on the design of the establishment experiment and the statistical methods used
3. Enhancing the discussion by incorporating additional scientific literature and adding further context to our findings
4. Refining the wording of certain sentences and conducting additional proofreading to improve the overall writing style of our manuscript

Please find a detailed, point by point explanation of how we addressed the reviewers' comments below.

Yours sincerely,

Jan-Markus Homberger

Referee(s)' Comments to Author:

Reviewer: 1

General comments

Overall, this study is well designed and thought through. The topic of dune initiation and plant establishment is important for coastal research and management. Including both naturally occurring sites as well as an establishment experiment was a great idea to not only compare results, but for comparing managed vs. unmanaged dune systems. There are significant data needs in this community, and this research helps fill the gaps. These species-specific data are novel findings and relevant to the overarching body of knowledge.

Reply: We thank reviewer 1 for this positive and thoughtful feedback on our study.

Specific comments

One thing that's missing from the introduction and discussion are comments on sea-level rise. This could be including the projected annual SLR for the sites in the methods. Which could be added to table 1. However, throughout the paper when discussing the other environmental factors affecting dune establishment, sea-level rise should be included. Section 5 of the discussion would also be a great place to add this information.

Reply: Indeed, including SLR is an important consideration, as it may lead to erosion of beaches. The intertidal zone would then shift landwards reducing the space for vegetation establishment.

However, in the Netherlands sea level rise is currently offset by intensive nourishment activities (Keijsers et al. 2015) and therefore does not pose a direct problem for establishment and dune development. Rather, dunes are expanding seaward (van IJzendoorn et al. 2021). Therefore, we decided against adding this information in Table 1, but we included it in the discussion.

Change: We highlighted that beach erosion can be caused by sea level rise in the introduction (*see: §1 Introduction, p. 1****, line 23***) and added two new paragraphs to the discussion which discuss the effects of sea level rise on establishment and dune initiation and extended our considerations about global and local management approaches (*see: §5 Implications for coastal management, pp. 22-23,* ***lines 525-535****)*. To support the discussion on sea-level rise the following literature was added:

Carter, R. W. G. 1991. Near-future sea level impacts on coastal dune landscapes. Landscape Ecology 6:29–39

Davidson-Arnott, R. G. D. 2005. Conceptual Model of the Effects of Sea Level Rise on Sandy Coasts. Journal of Coastal Research 216:1166–1172.

Davidson-Arnott, R. G. D., and B. O. Bauer. 2021. Controls on the geomorphic response of beach-dune systems to water level rise. Journal of Great Lakes Research.

Garner, K. L., M. Y. Chang, M. T. Fulda, J. A. Berlin, R. E. Freed, M. M. Soo-Hoo, D. L. Revell, M. Ikegami, L. E. Flint, A. L. Flint, and B. E. Kendall. 2015. Impacts of sea level rise and climate change on coastal plant species in the central California coast. PeerJ 3:e958.

Gao, J., D. M. Kennedy, and T. M. Konlechner. 2020. Coastal dune mobility over the past century: A global review. Progress in Physical Geography 44:814–836.

van IJzendoorn, C. O., S. de Vries, C. Hallin, and P. A. Hesp. 2021. Sea level rise outpaced by vertical dune toe translation on prograding coasts. Scientific Reports 11:12792.

Keijsers, J. G. S., A. Giardino, A. Poortinga, J. P. M. Mulder, M. J. P. M. Riksen, and G. Santinelli. 2015. Adaptation strategies to maintain dunes as flexible coastal flood defense in The Netherlands. Mitigation and Adaptation Strategies for Global Change 20:913–928.

Lansu, E. M., V. C. Reijers, S. Höfer, A. Luijendijk, M. Rietkerk, M. J. Wassen, E. J. Lammerts, and T. van der Heide. 2024. A global analysis of how human infrastructure squeezes sandy coasts. Nature Communications 15:432.

Rijkswaterstaat. 2024. Kustlijnkaarten 2024.

Staudt, F., R. Gijsman, C. Ganal, F. Mielck, J. Wolbring, H. C. Hass, N. Goseberg, H. Schüttrumpf, T. Schlurmann, and S. Schimmels. 2021. The sustainability of beach nourishments: a review of nourishment and environmental monitoring practice. Journal of Coastal Conservation 25.

Vousdoukas, M. I., R. Ranasinghe, L. Mentaschi, T. A. Plomaritis, P. Athanasiou, A. Luijendijk, and L. Feyen. 2020. Sandy coastlines under threat of erosion. Nature Climate Change 10:260–263.

The “window of opportunity” statements (including in the title) are a little misleading given the project. There are no phenology or timing of emergence data included, which given the title I would expect. The findings narrow down the drivers and limits of dune initiation for these species. I’d recommend changing the wording throughout to remove “window of opportunity,” or define it clearly. There is a definition on line 42, however the findings are more about the ongoing environmental factors and not disturbance. The definition would need some clarity.

Reply: We agree with this assessment. Indeed, the aim was not to narrow down timing or phenology of the emergence data but rather to quantify environmental conditions that explain long term establishment success and subsequent dune initiation. While the window of opportunity term could potentially be defined in a broader sense, we removed it from the manuscript to avoid further confusion.

Change: We removed window of opportunity from the title with the new title being: “Narrowing down dune establishment drivers on the beach”. We also made some further adjustments in the text removing “window of opportunity” and replacing it by “drivers” or “required conditions” (*see: § Abstract, p. 1,* ***line 17****, §1 Introduction, p. 3,* ***line 63*** *and §4 Discussion, p. 16,* ***line 323*** *and* ***line 332****).* We also removed a reference to a study by Balke et al. 2014, as this work emphasizes the window of opportunity concept (*see: §1 Introduction, p. 2,* ***line 42****)*

It's mentioned in the discussion, but along with Table 2 in the methods, it would be good to include a seed size comparison of the 2 species. Table 2 shows the species differences, but given the objectives of the study this is an important point to include earlier in the text.

Reply: We tried to mimic the natural dispersal of both species. While we introduced both species as spikelets it is important to note that *Ammophila* spikelets typically contain a single floret (Huiskes 1979), while *Elytrigia juncea* contains several florets within a dispersed spikelet. This makes an important difference for the size and weight. In light of this comment and to further clarify we decided to highlight this aspect better in the discussion while also adding relevant information to the table and the supplements.

Change: We added measurements on the floret and spikelet length and adapted the table caption accordingly (*see: Table 3 §2.2.3 Plant Material, p. 7).* We extended the discussion on the size difference between spikelets (see *§4.1 Arrival and success of plant material, pp. 17-18,* ***lines 361 - 367****).* We added figure S3 to the supplementary material showing differences in sizes of the introduced plant material

In Figure 2A it is difficult to distinguish between the 3 levels of "establishment success", I'd recommend using 3 different shapes instead of different sized circles.

Reply: The establishment success in Figure 2A is displayed as a continuous variable rather than a variable with different levels. The size of the circle is relative to the establishment success. Therefore, we decided against changing the shape of the circles, but we adapted the figure for clarity.

Change: We adapted the range for the circle size and adapted the legend to show the size of the circle for an establishment success from 0 – 100 % (see *Figure 3a. §3.3 Establishment success, p. 13)*

Technical corrections

Line 38: Used common name when throughout the rest of the paper the scientific name is used. Both are listed in Table 2, but not in the text.

Change: Changed to scientific name with the common name in brackets (*see: §1. Introduction, p. 2,* ***line 38****).*

Line 203: In section 3.3 of results there is a switch from "monitoring moments" to "monitoring campaigns" - consistency would be helpful here.

Change: Changed "campaign" to "moment" (*see: §3.3 Dune initiation, p. 12,* ***line 299****).*

Line 246: I think you mean 'wrack' not 'wreck'

Reply: Indeed. Corrected (*see: §4.1 Arrival and success of plant material, p. 17,* ***line 353*** *and* ***354****).*

Reviewer: 2

General comment

The authors have chosen to study an important topic. We have a limited understanding of the controls on seedling emergence and subsequent dune initiation. While the topic is important, I do not believe that the methods employed as described are at a collection interval that is appropriate for the hypotheses. The abiotic conditions being measured are collected and related to seedling emergence, but the conditions occurring within the time between the collections/emergence which impact if not control emergence triggering are not considered/measured. For example, dormancy is broken in many plants by a combination of suitable conditions being met across a critical number of consecutive days to trigger emergence – the same is to be expected here, but not accounted for in how the work is designed and then discussed. There is a major assumption that the difference between the conditions between collections (which appears to be month to month+) drive the emergence. This is a huge assumption that would need to be justified by the literature or acknowledged in an honest way with the discussion. With this in mind, the meaning of and implications of the results are hard to interpret. This is a biological or ecobiological topic, but the biological does not appear to be the focus in how the methods were designed (timescale) or discussed (emphasis of the context of the work) making it unclear if the results mean anything and if they do how they add to our previous understanding of this system. The methods must be improved to understand the reliability and meaning of this work.

***Reply**:* We thank Reviewer 2 for their thoughtful and constructive feedback, as well as for recognizing the relevance and importance of our study. We appreciate the critical concerns raised regarding the methodology and the relationship between the environmental conditions measured and the ecological responses observed. We acknowledge that a clearer definition of the ecological processes we were measuring would improve the manuscript, particularly regarding the interpretation of seedling emergence and subsequent dune initiation.

The aim of our experiment was to examine establishment from a realized niche perspective over a time scale relevant to dune initiation. As the reviewer correctly points out, there are multiple environmental and biological filters that influence plant success at different life stages, starting from germination (which requires dormancy to be broken), to survival and growth. All of these life stages are expected to be influenced by the measured environmental conditions, which is supported by the literature cited in our introduction. However, it is important to clarify that our study does not explicitly separate these life stages, and the shoot numbers observed in the field represent the net result of these processes. We tried to highlight this aspect better throughout the manuscript by adjusting the definition of the ecological process.

We also acknowledge the reviewer's concern regarding the temporal resolution of our data collection. While temporal conditions can influence processes like dormancy and germination, our study was primarily focused on the role of spatial differences in environmental factors, summarizing results over 750 plot replicates. While moisture, salinity, and bed level changes vary over time, they are also strongly influenced by spatial differences, as discussed in the introduction (*see §1 Introduction, pp. 2-3,* ***lines 54 - 62***). To address the limited temporal resolution of our study, we averaged all variables over time to capture broader trends (*see: §3.3 Establishment success, p. 12,* ***lines* 204 - 207**). We revised the discussion to stress our focus on spatial patterns and acknowledge limitations of low temporal resolutions. In the following we will outline detailed point-by-point changes.

Intro

- Line 25 - is misleading and should be reworded or a citation should support the claim that nourishment "is used for…stimulating new dune development and improving the climate-resilience of dunes." Dunes are often not included in nourishment designs at all and so while net positives in sediment supply to the dunes may occur and can be a benefit, this occurring is an unintentional benefit.

Change: We adapted the text highlighting that nourishments are not carried out to create dunes but rather dunes can result from nourishments (*see: §1 Introduction, p. 2,* ***line 26****).*

Methods

- Methods are missing the 'study site' equivalent for relevant information on the biology of the two study species. This would improve putting the work into context.

Reply: We appreciate the suggestion.

Change: We created a new paragraph in the study area section of the Methods (*see: §2.1* Study areas, *pp. 4-5,* ***lines*** *92-105)* highlighting key characteristics and differences between *Elytrigia juncea* and *Ammophila arenaria* with regards to their growth form, habitats and establishment strategies, all while adding relevant scientific literature.

- Study site is missing grain size information which is relevant for interpreting dune initiation results around critical wind speeds and angle of repose for expected morphologies and sediment supply

Change: We included information on the median grain size for Terschelling (*see: §2.1* Study areas, *p. 3,* ***line 83****)* and the Sand Engine (*see: §2.1* Study areas, *p. 3,* ***line 89****).*

- I have a lot of questions about the experimental design relative to the driver being tested and understanding the relevance of the results. How are the authors accounting for differences in abiotic conditions across the four areas, 2 sites, and then within them?
- In S2 the authors define the environmental conditions as 'similar,' but this needs to be defined in the actual methods and more specifically as it is critical to understanding how the experimental design may impact the results.
- The authors are citing Houser and so must be aware that there are differences in abiotic conditions relevant to plants that can occur on the order of meters and must be accounted for in experimental design (by limiting plots to close quarters, using a paired design, explicitly monitoring the driving conditions daily, etc).
- As written, I understand that the plots are block designed and 1 meter apart from the next closest, but across what span in the similar areas for which there appear to be 10 per table 3 – the area might be 'similar' but plots 50 m apart in the same area on opposite ends are likely different so that data should be presented that shows the abiotic conditions are comparable as measured in the field beyond TWI and DTM (presented in supplementary). I assume that the authors have accounted for all of this,

> but this needs to be made clear and so methods improved for clarity and reproducibility. How can the authors convince a reader that differences in abiotic conditions are equivalent and so what they are presenting as results are as they describe relative to their hypotheses as opposed to just a documentation of inherent beach/dune heterogeneity?

Reply: In our study, we addressed potential confounding effects both within and across study areas through a systematic experimental design and the inclusion of random effects in the statistical analysis.

For the experimental design, we adopted a stratified approach: We first delineated areas (i.e. strata) with similar expected environmental conditions, based on relevant environmental proxies (Topographical Wetness Index, change in elevation and height above mean sea level), and then allocated 15 blocks per area and study site. Within each strata (or similar area), we further distributed block locations across both coordinate and covariate spaces using the method of Grafström and Tillé (2013). This spatially balanced sampling minimizes potential impacts of spatial autocorrelation, improving our estimates. Our aim was not to ensure that environmental conditions were identical but to ensure that a broad range of environmental conditions were represented across all study sites, while also covering a typical range within each individual site.

In the statistical model, which forms the basis for the results reported, we accounted for potential differences across and within sites by including random effects. These random effects were applied at both the study area level (site-specific) and at the block level (local random effects). This allows us to statistically control for the random variation introduced by unmeasured variability arising from spatial differences at these levels and isolate the effects of the abiotic drivers under investigation. In doing so, we ensure that our results capture broader patterns rather than being overly influenced by site-specific conditions.

Change: We further elaborated on the methodology of the experimental design and the statistical analysis. We addressed reviewer concerns by:

- Providing more detailed explanation on the stratified design including the derivation of covariates from DTMs and the reasons for choosing the design (*see: §2.2.2 Design establishment experiment, p. 6,* ***lines 125 – 128*** *and* ***lines 131 - 140****).*
- Providing additional information and reasons for choosing the doubly spaced algorithm for spreading the blocks in coordinate and covariate space (*see: §2.2.2 Design establishment experiment, p. 6,* ***lines 128 - 130****).*
- Extending the explanation of the random effects and how they could account for within and across site specific differences in abiotic conditions for the statistical models (*see: §2.4.2 Establishment success, p. 9,* ***lines 218 - 225****).*
- Extending the description of the measured environmental conditions (*see: §3.2 Establishment success, p. 12,* ***lines 275 - 279****).*

- How is the position of the plants in turn impacting shielding and so sediment supply and elevation change measured being accounted for in the block design?

Reply: We recognize that the positioning of plants within each plot could impact shielding effects. Especially in the case of plots located downwind we expect a possible influence on the sediment supply and the elevation changes upwind.

In our block design we aimed for controlling spatial variability, and we allocated each treatment only once per block. While we considered spacing the plots at a greater distance, practical constraints—such as avoiding pre-existing vegetation and pathways - meant that a minimum spacing of 1 meter was the only feasible option.

Despite the mostly sparse vegetation within the plots (approx. 12 cm in height, with an average of 23 shoots per 50 x 50 cm plot), vegetation still may influence wind velocity and sediment transport. Wolfe and Nickling (1993, 1996) discuss that even sparse vegetation can lead to wake interference flow. This may particularly be relevant in areas with more pronounced plant growth. Although vegetation development varied across the plots, with only some showing significant shoot growth across all plots, it is possible that these wake effects altered sediment deposition patterns and influenced elevation changes.

Moreover, Hesp et al. (2019) showed that, even with low vegetation cover (~10–12%, equivalent to 90 shoots/m²), bed level changes can occur at a distance of more than 2 meters from the vegetation downwind. Therefore, we anticipated that within a single block, plots positioned downwind from those with higher vegetation development to possibly experience increased sediment deposition and elevation changes.

Change: We adapted the methods to highlight the choices we made regarding upwind plot effects, controlling for shielding in the setup of plots and statistical analysis:

We added the plot orientation with respect to geographic north and wind exposure standardization (*see: §2.2.3 Plant material, p. 7, **line 159***), further emphasized the randomization of the treatments in the context of shielding (*see: §2.2.3 Plant material, p. 7, **line 160***), and highlighted how random effects addresses correlation in the statistical analysis (which may arise due to shielding) (*see: §2.4.2 Establishment success, p. 9, **lines 218 – 225***). Finally, we added to the discussion on bed level change the possible impact of upwind vegetation on downwind vegetation (*see: §4.2 Establishment success in response to environmental drivers, pp. 20 - 21, **lines 463 - 475***).

- The height differences are being ascribed to the plants but increased deposition or sediment supply can trigger plant response such as emergence resulting from in increased retention. It is just as likely that differences in burial are driving emergence, survival, and density, as it is that changes in the emergence, survival, and density in turn impact the burial – this does not need to be tested necessarily, but I do not see it being addressed/discussed despite its importance.

Reply: We thank reviewer 3 for raising this as an important point to discuss. Indeed we cannot separate the effect between the two directly. It is likely that both factors mentioned here play a role.

Change: We extended the discussion highlighting that limited amounts of burial could trigger a positive plant growth response (*see: §4.2 Establishment success in response to environmental drivers, p. 18,* ***lines 383 – 384*** *and lines* ***386 - 387****)*, we also discuss that increased shoot numbers can lead to increased trapping (*see: §4.3 Conditions for dune initiation, p. 22,* ***lines 510 - 511****)*. To further support this discussion we also added a figure to the results depicting the interactive effect of bed level change and shoot numbers on dune initiation as predicted from the statistical model (*see: §3.3 Dune initiation, p. 15, Figure 4b*).

- Line 122 – "We then corrected this number for spontaneous shoot emergence in the control plots." Great, this is important to control for. How was this done so that others can repeat the methods?

Change: We changed the sentence to: "To account for spontaneous shoot emergence, we corrected shoot numbers by subtracting the number of shoots emerged in control plots from treatment plots, setting treatment shoot numbers to 0 for negative numbers" (*see: §2.3.1 Shoot numbers and dune initiation, p. 8****, lines 171 – 172****.)*

- In line 125 establishment is defined as "We expressed plant establishment success as the corrected number of shoots present in a plot at the last monitoring round relative to the amount of introduced plant material in March 2022." Please rework this definition to include info accounting for emergence from seed and rhizome being studied.

Reply: In response to this and the general comments by reviewer 2 we adjusted our definitions to further clarify what we mean by the term "establishment success".

Change: Removed "(shoot emergence, survival and shoot density)" from the Abstract (***line 9***); replaced "shoot emergence, survival and growth" with "establishment success (i.e., the net effect of germination, shoot emergence, survivorship and growth)" (*see: §1 Introduction, p. 3,* ***line 68****;*, removed "long-term survival" (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***line 168****)*, removed the sentence "We defined plant survival as shoot presence at the last monitoring moment." (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***line 174****)* and adjusted our definition of establishment success highlighting that several ecological processes are included: "Therefore, our definition of establishment success includes the net result of several ecological processes such as the germination from seeds, emergence from rhizome fragments as well as subsequent shoot emergence from the soil, survivorship and growth." (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***lines 177-178****)*. We also added that we consider the net effect of establishment to the discussion "In this study we did not separate the life stages of the species, but rather described establishment success as a result of patterns observed over a longer time in the field" (*see: §4.2 Establishment success in response to environmental drivers, p. 20,* ***lines 442 - 443****)*.

- Line 128 - bed height was measured looking at two plot corners. I am assuming that this is 2 of 4 examined, but what two relative to the predominant wind direction? If you collected upwind corners from some and downwind from others then they are not necessarily comparable (apples to apples). Were the same corners measured each time? If you collected upwind corners one collection and then downwind another and took the difference then you would almost assuredly see a net increase in height because of shielding and nebkha formation. I assume all this was accounted for, but it needs to be stated for reproducibility and clarity.

Reply: The main wind direction in the Netherlands comes from the SW, therefore we opted for measuring the elevation at the SE & NW corners. We always measured the same corners during repeated data collections.

Change: We highlighted that we oriented plots with respect to geographic North to standardize wind exposure (*see: §2.2.3 Plant Material, p. 7, **line 159***). We clarified that we always measured the same SE & NW corners (*see: §2.3.2 Bed level change, moisture and salinity, p. 8, **lines 182 - 184***).

- It is not clear how maximum salinity and max moisture measurements were used in analyses and if this is max per plot, area or site. In general, it is hard to understand what data was collected and from where each of the four collections,

Reply: During each monitoring campaign measurements were taken for all five plot per block. This includes shoot counts, soil moisture, salinity, and the height of the NW & SE corners. Measurements were not taken per block but rather per plot. Hence, at each measurement campaign we re-visited all plots and measured in 750 plots. The exception for this is the last measurement campaign where only blocks were re-visited that contained shoots at any point of the measurements (see line 120, i.e., 635 plots). We described the plot number and measurements more explicitly in the methods section to clarify. When it comes to the maximum salinity, minimum soil moisture and maximum bed level change we used the value measured per plot and monitoring period. Reviewer 3 pointed out that this appears to be a minor point as these conditions should be related with the average conditions measured. We therefore removed this analysis.

Change: We clarified that abiotic conditions and shoot numbers were determined per plot (i.e., 750 plots during the first three monitoring moments, 635 plots in the last one) (*see: §2.3.1 Shoot numbers and dune initiation, p. 8, **line 169-171***) and (*§2.3.2 Bed level change, moisture and salinity, p. 8, **lines 180-181***). We removed the analysis of max salinity, min moisture and max change in bed level from the manuscript and supplements.

- I do not believe that the authors collected salinty, elevation and moisture data from about 700 plots each collection, but that is what i'm assuming because of how the methods are presented. Was salinity, height, moisture measured from each block, plot, area? A paragraph at the start of the methods making it clear what was collected where and when across all data would be very helpful to improve clarity.

Reply: The assumptions of the reviewer are correct: it really involved gathering data from 750 plots per collection round. The experiment was created to capture spatial differences and therefore carried out over a large spatial scale and did indeed involve substantial data collection efforts. We mentioned the scale of the study more explicitly in the methods (as outlined above).

Change: In addition to the changes outlined in the previous reply we highlighted the focus on the spatial scale (*see: §1 Introduction, p. 3, **line 72**; §2.4.2 Establishment success, p. 9, **lines 204 – 205*** and *§4. Discussion, p. 16, **line 325***)

- It is not clear how often data were being collected from the field. I am assuming the data mentioned in section 2.3 was collected in 4 collections, in 2022 once in May/June, August and October.

Reply: It was indeed collected during 4 collections, once during May/June, once in August, once in October and the final collection was taken during January/February of 2023. We adjusted the description to be more explicit.

Change: To be more explicit we highlighted that the data was collected during four monitoring campaigns (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***lines 167-168***) and that abiotic conditions were measured per plot in parallel to counting shoot numbers (*see: §2.3.2 Bed level change, moisture and salinity, p. 8,* ***lines 180 - 181***)

- In general, without this information it is hard to understand if the methods are appropriate. If the authors only collected this data 4 times then I have concerns about if the experimental design is appropriate for the hypotheses; the authors are examining salinity, bed-level change, and soil moisture, all factors that can vary daily with abiotic conditions and especially related to wind events, but it seems they were only collecting data at inconsistent month or month+ long intervals and not associated with events so that the drivers being tested are not actually being linked to the changes in vegetation in a real way that does not rely on an assumption that correlation means causation. This would have been a great application for the use of iLoggers.

Reply: Our study focused primarily on capturing spatial differences in environmental factors across sites rather than the short-term temporal variability. The primary goal was to assess how these spatial gradients influence vegetation over longer periods. We acknowledge that processes such as wind-driven bed-level changes or moisture fluctuations can impact results on shorter timescales, but we believe that the spatial heterogeneity we captured (with 750 plot replicates across diverse environmental conditions) offers a robust foundation for identifying patterns. We focused on capturing spatial rather than temporal variation given the strong spatial zonation of vegetation patterns on the beach.

To address potential limitations from lower temporal resolution, we averaged key variables (such as moisture and salinity) over time, which helps capturing broader trends. In the revised discussion, we emphasized that this study was designed to reflect spatial variability and that further research may be needed to address short-term temporal dynamics linked to specific weather events.

Change: We emphasized that the study was designed for a large spatial scale (*see: §1 Introduction, p. 3,* ***line 72;*** *§4. Discussion, p. 16,* ***line 325****),* which is reflected in the choice of our experimental design (*see: §2.2.2 Design establishment experiment, p. 6,* ***line 125****)* and we highlighted this further in the subsequent methods sections *(see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***line 176*** *and §2.4.2 Establishment success, p. 9,* ***lines 204 – 205****).* We also explained the reasons for averaging variables *(see: §2.4.2 Establishment success, p. 9,* ***lines 203 - 207****).* In the results we highlighted the range in abiotic variables as well as the spatial dependencies captured by the study (*see: §3.2 Establishment success, p. 12,* ***lines 275 - 279****).*

Moreover, we highlighted study limitations of using a spatial rather than temporal approach, discussing that at the current temporal resolution different ecological processes (germination, survival, growth) cannot be separated (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***lines 176 -178*** *and §4.2 Establishment success in response to environmental drivers, p. 20,* ***lines 442-443****),* that a higher temporal resolution combined with a larger time frame may be needed in future studies to better separate growth responses and deposition ("chicken and egg" problem) (*see: §4.3 Conditions for dune initiation, p. 22, **lines 520-521)*** and highlighted that the description of bed level change may not be very accurate for plots with large fluctuations in bed level over time (*see: §4.2 Establishment success in response to environmental drivers, p. 20, **lines 456 - 458**).*

- Line 135 - this section/paragraph on seedling mapping is not clear in a way that can be replicated. As worded, it appears that the plant densities were estimated as opposed to quantified

Reply: We encountered some mistakes in the description of the methods in this section. The interpolation was only carried out for seedlings and seedling presence/absence was only considered for plots with introduced seeds. This may have caused some confusion.

Change: We rephrased the section to better separate interpolation (used for visualization) and the calculation (estimate of seedling numbers close to adults) (*see*: *§2.4.1 Arrival limitations*, pp. 8-9, **lines 192 - 201**). We also removed "adult occurrence" (*see: §2.4.1 Arrival limitations*, p. 7, lines 192 - 193) and "rhizomes" (*see: §3.1* Arrival limitations, p. 12, Figure 2)

Results

- I do not see that the results are compared across sites. It seems like all the data are lumped together across 4 areas from 2 sites, but I am not convinced this is appropriate based on the info provided in the methods to justify it. Site differences can confound these results so that the significance being ascribed many just be inter-are or inter-site as opposed to a function of a real overarching pattern observed consistently relevant to all three hypotheses.

Reply: We appreciate the reviewers concern regarding site differences potentially confounding the results. While we did include all areas in one statistical model, we corrected statistically for the site effect by including site as random effects. This approach allows us to account for variability across the different sites and helps to ensure that the significances we observe are not merely due to inter-site differences but reflect a more consistent overarching pattern relevant to our hypotheses. We hope this clarifies our analytical strategy.

Change: We included an explanation of random effects as commonly used in mixed effects modelling and explained how they could account for within and across site specific differences in abiotic conditions in the statistical models (*see: §2.4.2 Establishment success, p. 9, **lines 218 – 225**).*

- Line 199- What are "extreme conditions" I do not see that these are defined in the methods or supplementary.

Reply: We used the maximum or minimum measured environmental condition as a proxy for extremes. In line with a previous reply, this was not essential to the manuscript and we opted to remove it.

Change: Removed description of statistical analysis of min and max env. conditions (*see: §2.4. Data analysis*), removed section on extreme conditions from the results (see: §3.2

Establishment success) and removed Table S6 - S8 as well as Fig. S14 from the supplementary material.

What was the bed level change observed? This info does not appear to be reported in the results beyond what is in Fig 3 and from this figure average change appears to be only about 0.05 m reflecting the change one would expect to see if the collection interval is too low and missing the actual deposition events that might cause the emergence.

Reply: Figure 3c) illustrates the average bed level change as modeled in our statistical analysis (partial effects). In Figure 3a), the range of the underlying data is more clearly visible. Figure 3a) shows an average bed level change (averaged per plot over monitoring moments) ranging from -15 cm to +25 cm. When not averaged over time, the measured bed level change ranged from -52 cm to +84 cm. The range for which we observed shoots was lower ranging from -27 cm to +27 cm. Even though, the specific deposition events may not have been measured directly, the resulting bed level changes were considerable and it can be expected that the plant response was affected. Moreover, previous studies, such as Harris and Davy (1986) and Lammers et al. (2024), indicate that even minor bed level changes of just a few centimeters can impact plant establishment.

Change: We added the range in observed bed level change, salinity and soil moisture (*see: §3.2 Establishment success, p. 12, **lines 275 - 279***).

Pictures of the plots as a figure would be helpful to see and make it clear how different planted areas vary from the controls where seeds and rhizomes were not planted.

Reply: We added some pictures of blocks and plots to the supplementary material (see: §S2 Supplementary Material, p. 2, Figure S4)

Discussion

- The results are not surprising, which is not an issue, it's just that they are seem largely restated in the discussion as opposed to in context to explain them with the existing state of the science/literature, section 4.1 is an exception to this statement.

Reply: While there is considerable amount of literature on the growth response of adult dune building grasses, the amount of literature on the establishment of juvenile dune-building grasses is surprisingly limited. We expect the response of adult grasses to differ from the response of juvenile dune-building grasses which makes the comparison between literature values not straightforward. Having said that, we added some additional references to the discussion to give some more reference values.

Change: We added the following literature to the discussion to provide further context with respect to the following topics:

- ***Impacts of sea-level rise:***

Carter, R. W. G. 1991. Near-future sea level impacts on coastal dune landscapes. Landscape Ecology 6:29–39

Davidson-Arnott, R. G. D. 2005. Conceptual Model of the Effects of Sea Level Rise on

Sandy Coasts. Journal of Coastal Research 216:1166–1172.

Davidson-Arnott, R. G. D., and B. O. Bauer. 2021. Controls on the geomorphic response of beach-dune systems to water level rise. Journal of Great Lakes Research.

Garner, K. L., M. Y. Chang, M. T. Fulda, J. A. Berlin, R. E. Freed, M. M. Soo-Hoo, D. L. Revell, M. Ikegami, L. E. Flint, A. L. Flint, and B. E. Kendall. 2015. Impacts of sea level rise and climate change on coastal plant species in the central California coast. PeerJ 3:e958.

Gao, J., D. M. Kennedy, and T. M. Konlechner. 2020. Coastal dune mobility over the past century: A global review. Progress in Physical Geography 44:814–836.

van IJzendoorn, C. O., S. de Vries, C. Hallin, and P. A. Hesp. 2021. Sea level rise outpaced by vertical dune toe translation on prograding coasts. Scientific Reports 11:12792.

Keijsers, J. G. S., A. Giardino, A. Poortinga, J. P. M. Mulder, M. J. P. M. Riksen, and G. Santinelli. 2015. Adaptation strategies to maintain dunes as flexible coastal flood defense in The Netherlands. Mitigation and Adaptation Strategies for Global Change 20:913–928.

Lansu, E. M., V. C. Reijers, S. Höfer, A. Luijendijk, M. Rietkerk, M. J. Wassen, E. J. Lammerts, and T. van der Heide. 2024. A global analysis of how human infrastructure squeezes sandy coasts. Nature Communications 15:432.

Rijkswaterstaat. 2024. Kustlijnkaarten 2024.

Staudt, F., R. Gijsman, C. Ganal, F. Mielck, J. Wolbring, H. C. Hass, N. Goseberg, H. Schüttrumpf, T. Schlurmann, and S. Schimmels. 2021. The sustainability of beach nourishments: a review of nourishment and environmental monitoring practice. Journal of Coastal Conservation 25.

Vousdoukas, M. I., R. Ranasinghe, L. Mentaschi, T. A. Plomaritis, P. Athanasiou, A. Luijendijk, and L. Feyen. 2020. Sandy coastlines under threat of erosion. Nature Climate Change 10:260–263.

- ***Response to bed level change:***

Harris, D., and A. J. Davy. 1986a. Regenerative Potential of Elymus Farctus From Rhizome Fragments and Seed. The Journal of Ecology 74:1057.

Harris, D., and A. J. Davy. 1986b. Strandline Colonization by Elymus Farctus in Relation to Sand Mobility and Rabbit Grazing. The Journal of Ecology 74:1045.

Lim, D. 2011. Marram grass seed ecology: the nature of the seed bank and secondary dispersal.

Ievinsh, G., and U. Andersone-Ozola. 2020. Variation in Growth Response of Coastal Dune-Building Grass Species Ammophila Arenaria and Leymus Arenarius to Sand Burial. Botanica 26:116–125

Lammers, C., A. Schmidt, T. van der Heide, and V. C. Reijers. 2024. Habitat modification by marram grass negatively affects recruitment of conspecifics. Oecologia 204:705–715.

Del Vecchio, S., E. Fantinato, M. Roscini, A. T. R. Acosta, G. Bacchetta, and G. Buffa. 2020. The germination niche of coastal dune species as related to their occurrence along a sea–inland gradient. Journal of Vegetation Science 31:1112–1121

- ***Response to salinity***

Abdelhak, C., E. H. Latifa, and M. Mohammed. 2013. The effects of temperature, hydric & saline stress on the germination of marram grass seeds (Ammophila arenaria L.) of the SIBE of Moulouya embouchure (Mediterranean - North-eastern Morocco). Research Journal of Pharmaceutical, Biological and Chemical Sciences 4:1333–1339.

El-Katony, T. M., A.-H. A.-F. Khedr, and N. G. Soliman. 2015. Nutrients alleviate the deleterious effect of salinity on germination and early seedling growth of the psammophytic grass Elymus farctus. Botany 93:559–571.

van Puijenbroek, M. E. B., C. Teichmann, N. Meijdam, I. Oliveras, F. Berendse, and J. Limpens. 2017. Does salt stress constrain spatial distribution of dune building grasses Ammophila arenaria and Elytrichia juncea on the beach? Ecology and Evolution 7:7290–7303.

- ***Response to moisture***

Abdelhak, C., E. H. Latifa, and M. Mohammed. 2013. The effects of temperature, hydric & saline stress on the germination of marram grass seeds (Ammophila arenaria L.) of the SIBE of Moulouya embouchure (Mediterranean - North-eastern Morocco). Research Journal of Pharmaceutical, Biological and Chemical Sciences 4:1333–1339.

Schat, H., and K. Van Beckhoven. 1991. Water as a stress factor in the coastal dune system. Pages 76–91 Ecological responses to environmental stresses. Kluwer Academic Publishers, Dordrecht.

Konlechner, T. M., M. J. Hilton, and D. A. Orlovich. 2013. Accommodation space limits plant invasion: Ammophila arenaria survival on New Zealand beaches. Journal of Coastal Conservation 17:463–472.

Lammers, C., A. Schmidt, T. van der Heide, and V. C. Reijers. 2024. Habitat modification by marram grass negatively affects recruitment of conspecifics. Oecologia 204:705–715.

Lammers, C., P. M. J. Berghuis, A. G. Mayor, V. C. Reijers, M. Rietkerk, and T. van der Heide. 2024. Extreme heat and drought did not affect interspecific interactions between dune grasses. Estuarine, Coastal and Shelf Science:109020.

- Findings re-hypothesis #1 this is not surprising at all. Knowledge of seminal ecological works by Janzen and Connell in the 1970s would predict that seedlings emerge close to their parents. There is a whole body of literature around this not addressed or discussed, both in dunes and not in dunes.

Reply: We thank reviewer 2 for this insightful feedback. We agree that seedling emergence close to adult plants has been well established within ecological studies both at coastal dunes as well as in other ecosystems. This is precisely one of the reasons why we created this experiment: It is generally difficult to separate dispersal limitations from environmentally imposed establishment limitations. By introducing plant material across the study areas, we effectively removed dispersal limitations, allowing us to focus on the role of environmental constraints.

Change: We modified the last paragraph of the introduction, putting the reasoning for creating the experiment in a better context (*see: §1 Introduction, p. 3,* ***lines 63 - 67***) while highlighting that dispersal limitations can be expected based on previous literature (*see: §1 Introduction, p. 3,* ***line 65)*** *and* (*§4. Discussion, p. 16,* ***lines 324 - 325***).

Specifically in dunes, Konlechner is cited, but then this work is not put in context with it or other similar works other than saying vaguely that the results are "in line with other studies." Reijers et al. 2021 is also cited in the intro, and this work is very relevant here, but never discussed in the discussion;

Reply: The study by Reijers et al. 2021 focuses on how the clonal expansion strategy of dune-building grasses can be influenced by burial from sediment. Clonal expansion is one of the main mechanisms for colonization of new areas on the beach. In our study we found that establishment from seeds does not seem to be a main factor for marram grass, but for sand couch. This may mean that marram grass dominantly colonizes by clonal strategies. We highlighted this better in our discussion section. Furthermore, we expanded our discussion about the study by Konlechner et al. 2013 giving reference values for rhizomes of *Ammophila arenaria* buried in glasshouse experiments (under static conditions).

Change: We included more context to the studies of Reijers et al. (see: *§4.1 Arrival and success of plant material*, p. 16, ***lines 369 - 370***), highlighting what we discussed above and included further context to the Konlechner study (see: §*4.2 Establishment success in response to environmental drivers*, pp. 18-19, ***lines: 386 – 387; 393 – 394; 414 – 415 and 425 - 426***)

how is this work or finding novel relative to that and other works? How are the findings around this hypothesis pushing the science so that we know something new?

Change: We revised the discussion to more clearly highlight the novelty of our study. Specifically, we emphasized the following key points:

1. Separation of arrival limitations and environmental constraints: Our study uniquely isolates these factors by introducing plant material on a large scale, allowing us to assess establishment success without the confounding influence of seed dispersal limitations while contrasting this with natural spatial emergence patterns. *(see: §1 Discussion, p. 16, line* ***323 - 327***)

2. Species-specific establishment differences: We identified significant differences in establishment success between the two species, which may be attributed to either arrival dynamics or varying resilience to environmental conditions. These differences provide insight into the species' niche differentiation within dune systems (*see: §4.1 Arrival and success of plant material, p. 18,* ***line 371 - 374***)
3. Plant density dependence in dune initiation: We found that dune initiation occurs only when environmental conditions favoring establishment promote sufficient shoot development.
(see: §4.3 *Conditions for dune initiation*, pp. 21-22, ***lines 500 - 502***)

By distinguishing arrival from environmental constraints and exploring these species-specific patterns, we believe our findings contribute novel insights to the field, particularly in terms of understanding the factors limiting dune initiation.

Findings re-hypothesis #2: I would suggest that the authors remove this hypothesis and element of work from the paper as the methods and data presented are not adequate to test this in a meaningful way as presented.

Reply: We disagree with this assessment. While daily or event-driven fluctuations could indeed provide additional insight into certain abiotic drivers, we believe the spatial heterogeneity captured in our study provides a robust method for identifying meaningful long-term patterns in vegetation response. To address any potential limitations, we averaged key variables (e.g., moisture, salinity) across time to reflect overarching trends rather than short-term variability.

Change: We made changes to highlight the scope of the study and discussed some limitations of the approach with respect to temporal resolution (point by point response see earlier responses).

Findings re-hypothesis #3: this is very interesting and holds implications for management and modeling of these environments. However, the few recent works on dune initiation (examples of main ones include Hesp et al. 2021, Hesp et al. 2019, Charbonneau et al. 2021, Costas et al. 2024) are lacking from the paper. Here a bit of a chicken or egg first style discussion would be interesting and relevant.

Reply: We thank the reviewer for the suggestions. Based on the comment we expanded the discussion on dune initiation while also taking a closer look at the recent study by Costas et al. 2024, cited on line 245, preprint.

Change: We extended the discussion on dune initiation while also taking some considerations regarding mutual influences between vegetation and sediment accumulation (see: *§4.3 Conditions for dune initiation, p. 22,* ***lines 509 - 513***). We also added the following works on dune initiation:

- Hesp, P. A., Hernández-Calvento, L., Hernández-Cordero, A. I., Gallego-Fernández, J. B., Romero, L. G., da Silva, G. M., & Ruz, M. H. (2021). Nebkha development and sediment supply. Science of the Total Environment, 773, 144815.
- Charbonneau, B. R., S. M. Dohner, J. P. Wnek, D. Barber, P. Zarnetske, and B. B. Casper. 2021. Vegetation effects on coastal foredune initiation: Wind tunnel experiments and field validation for three dune-building plants. Geomorphology 378:107594.
- Hesp, P. A., Y. Dong, H. Cheng, and J. L. Booth. 2019. Wind flow and sedimentation in artificial vegetation: Field and wind tunnel experiments. Geomorphology 337:165–182.

- What are next steps? How could the experiment be improved? What don't we know still and as a result of this study what do we now know around this?

Change: The following points were discussed to address this comment:

- While our seedling mapping and establishment experiment provided insights into plant response to environmental drivers, neither method could identify the arrival pathways of plant material, highlighting the need for future studies to investigate how seeds and propagules reach dune sites (see: *§4.1 Arrival and success of plant material, p. 15, **lines 342 – 344** and **lines 359 - 360***).

- Separating plant life stages more distinctly in future experiments could help clarify species-specific tolerances to environmental factors, giving a clearer picture of how seedlings, juveniles, and mature plants respond under varying conditions (see: *§4.2 Establishment success in response to environmental drivers, p. 20, **lines 450 - 454***).

- Increasing temporal resolution of environmental monitoring could offer better insights into highly fluctuating conditions, helping distinguish short-term environmental shifts from lasting impacts, and may aid in unraveling the "chicken and egg" problem (see: *§4.2 Establishment success in response to environmental drivers*, p. 20, ***lines 460 – 462*** and *§4.3 Conditions for dune initiation, p. 22*; ***lines 521 - 522***).

- Additionally, a plot design that considers facilitative effects among plants would enable exploration of facilitation across different life stages, providing insight into whether the presence of vegetation can benefit early plant establishment (see: §4.2 *Establishment success in response to environmental drivers, p. 21, **lines 473 - 475***).

- Future studies that incorporate additional abiotic and biotic factors, such as nutrient availability and biotic interactions, and focus on how these interact could further refine our understanding of successful establishment under natural dune dynamics (see: §4.2 *Establishment success in response to environmental drivers*, p. 21, ***lines* 476 - 486**).

- Humans may have a specially strong impact on establishment but more studies are needed on this (see: §4.2 *Establishment success in response to environmental drivers, p. 21, **lines 478 - 479***).

- Lastly, extending studies over a longer time scale could provide additional insights into recovery patterns after disturbances such as storms, contributing to a fuller picture of establishment dynamics which could be useful for coastal management strategies (see: *§5. Implications for coastal management, p. 23, **lines 554 -556***).

The differences in seedling and rhizome success are the most relevant and novel findings. I would suggest leaning into this more in how the work is presented/framed relative to Hyp 1 and 3.

- **Change:** In response to this comment we added average establishment success values per species and plant material (see: *§3.2 Establishment success, p. 12,* ***lines 293 - 296***) and the relative contribution of each treatment to observed dune initiation (*see: §3.3 Dune initiation, p. 14,* ***lines 301 - 303***). Moreover, we extended the discussion on treatment related establishment success highlighting that establishment success appeared to be related with plant material size (see: §4.1 *Arrival and success of plant material*, p. 17, ***lines 361 - 365***) and that *Elytrigia* may have some advantages over *Ammophila* due to high seed establishment success (see: *§4.1 Arrival and success of plant material, p. 18,* ***lines 371 - 374***)

Reviewer 3:

Homberger and colleagues collected an impressive dataset to understand environmental drivers of the establishment of two important ecological engineers from dunes: *Elytrigia juncea* and *Ammophila arenaria*. They combine censuses of plant emergence with supplementation experiments to understand how sand burial, erosion, but also how (average) conditions of humidity, salinity affect growth of the plants, and their subsequent impact on dune development. The strength of the work is clearly in the high spatial resolution at four beach sections in the Netherlands. I found the paper overall well written from a textual perspective, but especially in the methods section unclear to fully grasp what has been measured, let alone how the data were analysed. The work is clearly hypothesis driven (last paragraph of the introduction) but i am unsure (because of the very limited description of methods and results) whether the dispersal limitation can actually be tested. This is important as some strong conclusions are drawn from this (lines 295 and further). In conclusion, this seems to be a very good study, but it needs revision to reach its full potential with respect to impact and reproducability

Reply: We thank Reviewer 3 for this thoughtful feedback and the critical considerations. We especially appreciate the acknowledgement of the efforts regarding the dataset collection. In line with Reviewer 2, we understand that the method description could receive more attention to detail and we hope that we were able to address these concerns in the revised manuscript.

Detailed comments:

Line 64: windows of opportunity typically refer to temporal windows where sudden environmental conditions are favourable and promote establishment. Here, it is more used from a realised niche perspective as i could not detect any proper analyses of the temporal effects. Only in S7 some data are provided, but they are clearly not central to the work as only rudimentary touched upon.

Reply: In line with reviewer 1, we agree with this assessment. Indeed, the aim was not to narrow down timing or phenology of the emergence data but rather to quantify environmental conditions that explain long term establishment success and subsequent dune initiation. While the window of opportunity term could potentially be defined in a broader sense, we removed it from the manuscript to avoid further confusion.

Change: We removed window of opportunity from the title with the new title being: "Narrowing down dune establishment drivers on the beach". We also made some further adjustments in the text removing "window of opportunity" and replacing it by "drivers" or "required conditions" (*see: § Abstract, p. 1,* ***line 17****, §1 Introduction, p. 3,* ***line 63*** *and §4. Discussion, p. 16,* ***line 323*** *and* ***line 332****).* We also removed a reference to a study by Balke et al. 2014, as this work emphasizes the window of opportunity concept (*see: §1 Introduction, p. 2,* ***line 42****).*

Line 120. Only plots where shoots were present the year before were visited to record dune development. How can you separate whether the shoots accumulated sand, or whether shoots were already shooting on elevated locations, so on embryonic dunes.

Reply: Dune initiation was measured relative to the surroundings of the plot. So it is indeed possible that some of the locations were already elevated. Moreover, it is possible that shoot emergence happened as a consequence of added sediments, or burial under optimum conditions. On the other hand, it may also be that more shoots emerged and therefore more sediment was trapped. Our experiment does not allow for a direct separation between the two aspects. We think it is likely that both play a role. To address this, we added to the discussion on the feedback between burial and emergence.

Change: We substantially increased the discussion around how plant density and sediment trapping may amplify each other creating a feedback loop (see: *§4.3 Conditions for dune initiation, p. 22,* ***lines* 509 - 515**) and which factors may have played a role for dune initiation (see: §4.3 *Conditions for dune initiation*, p. 21, ***lines 495 – 497*** and p. 22, ***lines 516 - 517***).

Line 135: it is not clear how you can separate dispersal limitation (false absences) from establishment limitations (true absences from environmental constraints).

Reply: In the case of spontaneous establishment, we acknowledge that it is difficult to separate dispersal limitations from establishment limitations. This limitation is one of the reasons why we designed the experiment. By introducing plant material across the study area, we effectively removed potential dispersal limitations, allowing us to focus on the role of environmental constraints.

While we cannot completely rule out that observed seedling patterns may still be influenced by environmental factors, our approach demonstrates that the space for establishment could potentially be broader if dispersal limitations were absent. This is for example illustrated in Figure xxx.

Change: We added in the discussion that results from the seedling mapping itself do not exclude the presence of environmental limitations (see: *§4.1 Arrival and success of plant material, p. 17,* ***line 342)*** but with the establishment experiment arrival limitations were removed which is reflected in the control plot having significantly lower establishment (see: §3.2 *Establishment success, p. 12,* ***lines 270 – 272*** and §4.1 *Arrival and success of plant material, p. 17,* ***lines 343 - 346***)

Line 138: this does not make so much sense to me. How can you infer changes in densities (so within plots to my opinion) from changes in frequencies of plots with relative to without existing mature vegetation.

Reply: We thank reviewer 3 for pointing this out. Density is a poor choice of wording here.

Change: We corrected seedling "density" to seedling "occurrence" (*see: §2.4.1, Arrival limitations, p. 8, **line 195***).

Line 140: unclear how you interpolate per block, and how to compare with the natural settlement. What spatial analyses were done? Some spatial correlations? This is interesting but not developed. What i understand is that you compare the spatial pattern in blocks with/without supplementation? Or comparing spatial patterns of natural emergence and experimental supplementations in the same block (but then how can you separate natural from assisted settling)

Reply: We thank the reviewer for their comment. For block interpolation, we converted the recorded shoot numbers of *Elytrigia* and *Ammophila* to presence/absence data per block and used a simple interpolation method primarily for visualization, as shown in Figure 2 (p. 11). We did not develop this further because a formal spatial analysis would be complex: In the mapping approach, we used a higher plot density and larger plots compared to the introduction experiment, which makes direct comparisons challenging. Moreover, we did not quantify the seed or plant material bank for natural establishment, whereas in the establishment experiment, we precisely controlled the amount of introduced plant material. While this difference allowed us to examine environmental constraints by removing dispersal limitations in the experimental blocks, the presence of environmental constraints cannot be excluded from the spontaneous establishment.

Change: We further clarified the methods used for interpolation (see: *§2.4.1 Arrival limitations, pp. 8-9, **lines 192 - 198***), while explaining the reason for not doing a more in depth spatial analysis of the resulting patterns (see: *§2.4.1 Arrival limitations, p. 9, **lines 199 - 201***). Furthermore, we also added limitations of the seedling mapping approach to the discussion (see: *§4.1 Arrival and success of plant material, p. 17, **lines 342-343**)*

Line 142: so you also are able to test seedling mortality? I overall don't understand how the first approach (absence/presence after one growing season, and linked to max or min changes) is different than its correlation to average environmental conditions. I assume these are the same abiotic factors? Is plant establishment success then different that presence/absence after one season (not to me), or is the difference in the average versus min/max conditions? Also in stats, you mention absence/presence but never disappearance or conversely survival.

Reply: Indeed the difference is minor and we expect a correlation between average and maximum measured conditions. This was a minor analysis point in the main manuscript and we decided to remove it. Plant establishment success measured includes, survival, mortality, germination and growth, without explicitly separating the phases.

Change: Removed description of statistical analysis of min and max env. conditions (see: §*2.4.1 Establishment success*), removed section on extreme conditions from the results (see: §*3.2 Establishment success*) and removed Tables (formerly S6 - S8) as well as Fig. S14 from the supplementary material.

To clarify what was meant with establishment success we made the following changes: Removed "(shoot emergence, survival and shoot density)" from the Abstract (***line 9***); replaced "shoot emergence, survival and growth" with "establishment success (i.e., the net effect of germination, shoot emergence, survivorship and growth)" (*see: §1 Introduction, p. 3,* ***line 68****;*, removed "long-term survival" (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***line 168****)*, removed the sentence "We defined plant survival as shoot presence at the last monitoring moment." (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***line 174****)* and adjusted our definition of establishment success highlighting that several ecological processes are included: "Therefore, our definition of establishment success includes the net result of several ecological processes such as the germination from seeds, emergence from rhizome fragments as well as subsequent shoot emergence from the soil, survivorship and growth." (*see: §2.3.1 Shoot numbers and dune initiation, p. 8,* ***lines 177-178****)*. We also added that we consider the net effect of establishment to the discussion "In this study we did not separate the life stages of the species, but rather described establishment success as a result of patterns observed over a longer time in the field" (*see: §4.2 Establishment success in response to environmental drivers, p. 20,* ***lines 442 - 443****).*

Line 153: the k-clustering is used to identify plant establishment and dune development. I read further that it is used to identify or locate blocks?

Reply: k-means clustering was used in the experimental design to identify areas with similar env. conditions (or strata). As covariates we used the Topographical Wetness Index, elevation, and change in elevation. The blocks were allocated using doubly spaced sampling algorithm, spreading locations in coordinate and covariate space (same covariates). Both approaches were used seeking to capture a wide range in environmental conditions. A lot of this description was moved to the supplementary material.

Change: To further clarify we moved the experimental design description to the main manuscript and extended the explanations on how kmeans clustering was used to derive strata as part of the experimental design (*see: §2.2.2 Design establishment experiment, p. 6,* ***line 139***)

Line 156: which corners? The ones with strongest difference in height i presume?

Reply: The main wind direction in the Netherlands comes from the SW, therefore we opted for measuring the elevation at the SE & NW corners. We always measured the same corners during repeated data collections.

Change: We highlighted that we oriented plots with respect to geographic North to standardize wind exposure (*see: §2.2.3 Plant Material, p. 7,* ***line 159****)*. We clarified that we always measured the same SE & NW corners (*see: §2.3.2 Bed level change, moisture and salinity, p. 8,* ***lines 182 - 184****).*

Line 158-168: the statistical analyses are too rudimentary explained in the main body. It seems that you control for spatial correlation between blocks and study area to remove spatial variation at larger spatial scales.

I am still unclear how large blocks are so whether you have also within-block spatial variation that needs to be accounted for (for instance differences in shelter within blocks may promote dependency of responses in the plots). I would also suggest to document the error distributions for each model separately. From the supplements, i could first not understand which distributions were modelled, why some offsets for plant biomass were used. So this had to be better linked to different models (i.e. shoot establishment success is a proportion of the total added). In the model formulations, also explain what is s/ti is. Also, was model selection used or only full model considered.

I have the impression that analyses are done correctly but i remain unsure when linking the models to the different analyses, and how they are described.

Reply: We thank the reviewer for this suggestion.

Change: We extended the description of the statistics in the manuscript highlighting that random effects were used on the study area and block level to account for potential differences across and within sites (*see: §2.4.2 Establishment success, p. 9, **lines 218 - 225***). Offsets were used to account for differences in plant material introduced, to model the shoot number relative to the introduced plant material instead of the raw counts (*see: §2.4.2 Establishment Success, p. 9, **lines 215 - 217***). Thin plate regression spline smoothers (or s in the supplementary material) and tensor product interaction smoothers (ti in SM) were used to model non-linear relationships and interactions (*see: §2.4.2 Establishment Success, p. 9, **lines 226 - 228***). The error distributions were also documented (*see: §2.4.2 Establishment Success, p. 9, **lines 214 - 215** and §2.4.3 Dune initiation, p. 10, **lines 236 - 237***)

Line 175-178: where is this tested, why are these arrival limitations and not niche constraints?

Reply: In the case of spontaneous establishment, we acknowledge that it is difficult to separate dispersal limitations from establishment limitations.

While we cannot completely rule out that observed seedling patterns may still be influenced by environmental factors, our approach demonstrates that the space for establishment could potentially be broader if dispersal limitations were absent (see also a more detailed earlier point by point response).

Table 4: why full models and salinity models? I somewhere missed why two different models were used here

Reply: This was an oversight as this was previously only explained in the supplementary materials. The effect of salinity was tested on smaller dataset, since the WET-2 sensor which was available to us at the time is only able to record salinity once a soil moisture content of 15 % has been exceeded. We moved this to the main manuscript.

Change: We highlighted that the WET-2 sensor only measures salinity at a soil moisture content of 15 % (*see: §2.3.2 Bed level change, moisture and salinity, p. 8, **lines 187-188***) and explained how this resulted in a different statistical model (*see: §2.4.2 Establishment success, p. 9, **lines 209 - 213***)

Line 225: i need to be convinced of this. Is absence not a question of establishment limitation, or due to the fact that seeds are blown away, and accumulate close to sheltering adults plants?

Reply: Likely both play a role. We extended the discussion regarding this aspect (see also previous replies).

Line 253: this 2cm corresponds nicely with the depth the plants were buried. So this might be an artefact of the experimental treatment? I would assume, or learn from this that all seeds need some burial..

Reply: We thank the reviewer for pointing this out. The initial burial may have indeed played a role. Nevertheless, both figure 3a) and b) point towards a tolerance against erosion that goes beyond the initial burial depth of 2 cm.

Change: We pointed out that the positive effect on plant establishment success of erosion is probably related to the depth of initial burial (*see: §4.2 Establishment success in response to environmental drivers, p. 18,* ***lines 399-400****)*

Line 330-333. Restoration projects typically start from shoots, so is this relevant?

Reply: Our findings should be indeed relevant for long-term restoration projects, even if these typically start from shoots. Our results suggest that Elytrigia juncea may have distinct advantages for re-establishment after disturbance, given its ability to establish from both seeds and rhizome fragments. In contrast, Ammophila arenaria appears more reliant on rhizome fragments and clonal expansion for regeneration. Moreover, most dunes were initiated from Elytrigia seeds. By including Elytrigia in restoration projects, particularly in areas prone to frequent disturbance, it may contribute to greater resilience in response to future storms.

Change: We added the possible advantage of *Elytrigia* to establish from seeds and what this may mean for dune initiation and storm recovery (*§5 Implications for coastal management, p. 23,* ***lines 551 - 554***)