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Pinpointing stage-specific causes of recruitment bottlenecks to optimize seed-based wetland restoration

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Abstract

1. Attaining the goals of 'The UN-Decade on Ecosystem Restoration' requires efficient methods for large-scale restoration of degraded ecosystems. Seed-based approaches may offer opportunities for massive recovery of native vegetation but are prone to failure when applied to highly valued coastal wetlands such as salt marshes. Pinpointing the impact of early life stage transitions on recruitment variation across species and contexts is a critical first step toward amplifying seed-based restoration efficiency.

2. Large-scale field experiments were conducted in 100 microhabitats across eight salt marshes to investigate root causes of variation in seed retention and seedling emergence, using four globally occurring salt marsh species as models. The resulting insights and dataset were then translated into predictors using machine learning, for targeted application in disentangling recruitment bottlenecks.

3. Seed retention, regardless of species, was identified as the principal bottleneck in recruitment with hydrodynamic intensity, bed-level dynamics, and burial depth as critical governing factors. Seedling emergence was discerned as the critical bottleneck driving cross-species recruitment variability and was pivotally influenced by soil salinity and burial depth.

4. Predictions using machine learning under different restoration scenarios indicated that simple management, such as seed burial or species selection, can create opportunities to bypass potential recruitment bottlenecks.

5. *Synthesis and applications.* Our results suggest that the failure of seed-based coastal wetland restoration should be attributed to multiple recruitment bottlenecks that arise from different life stage transitions and are context/species dependent. In planning future seed-based restoration practices, managers should assess the variability of life stage-specific dominant factors at target sites to identify site-specific recruitment bottleneck(s). Our work underscores the need for strategic management that buffers against recruitment bottlenecks to improve restoration efficiency and advances the application of data-driven techniques to make seed-based restoration predictive.

1 | INTRODUCTION

Coastal wetlands such as salt marshes, seagrasses and mangroves are both ecologically and economically highly valuable, given that they sustain many critical ecosystem functions and services, for example, in maintaining biodiversity (Schuerch et al., 2018), sequestering carbon (Temmink et al., 2022), attenuating waves (Gijsman et al., 2021) and stabilizing sediment (Silliman et al., 2019). Consequently, they are incorporated into nature-based solutions to reduce coastal flood risk and contribute to climate stability (Gijsman et al., 2021; Saunders et al., 2020). However, anthropogenic and climate change-related stressors have, over the last decades, caused a massive shrinkage of coastal wetlands world-wide, accompanied by the disintegration of their key functions and services (Schuerch et al., 2018; Zhu et al., 2020). Since natural recovery may take decades or may not even occur at all (O'Brien et al., 2018), significant global efforts are urgently needed for the large-scale restoration of these degraded coastal wetlands (Saunders et al., 2020; Silliman et al., 2019), in line with the United Nations' call to action in 'The UN Decade on Ecosystem Restoration' (Kettenring & Tarsa, 2020).

Significant potential exists to recover native vegetation through seed-based restoration approaches (Kettenring & Tarsa, 2020; Palma & Laurance, 2015). Relative to other revegetation strategies such as planting seedlings, transplanting rhizomes and installing vegetated patches, the seed-based approach is typically less expensive and logistically more feasible to achieve large-scale restoration (Balestri et al., 2021; van Katwijk et al., 2016). Additionally, the use of seeds allows the inclusion of high levels of genetic diversity, which may have far-reaching implications for enhancing long-term ecosystem resilience under changing climate (Balestri & Lardicci, 2012; Larios et al., 2017). However, demographic losses/mortality during the seed-seedling transition may strongly curtail the effectiveness of this approach (Kettenring & Tarsa, 2020; Larson et al., 2015). Particularly for coastal wetlands, in which highly dynamic disturbance regimes introduce more uncertainty to seed/seedling persistence (Hu et al., 2021; Zhu et al., 2020), results with success stories lag far behind those of their terrestrial counterparts (e.g. forests and drylands; Kildisheva et al., 2016; Palma & Laurance, 2015).

Uncovering recruitment bottlenecks driving demographic losses/mortality represents an important step towards amplifying restoration outcomes (Balestri et al., 2021; Saunders et al., 2020). Compared to terrestrial ecosystems, in coastal wetlands, seed fate postsowing might be more convoluted due to being subject to strong spatiotemporal heterogeneity of multiple disturbances (e.g. inundation and sheet erosion), with the relative importance of these disturbances varying with time as the seed transitions through its life course (Friess et al., 2012; Statton et al., 2017). Key life stage transitions include seed retention, seedling emergence and seedling establishment (Friess et al., 2012). It is well known that seedling establishment in coastal wetlands must be synchronized with the disturbance absent/low periods (i.e. windows of opportunity, WoO), which allow seedlings to root and build resistance while growing (Balke et al., 2011). Due to the stochastic nature of the occurrence of WoO, seedling establishment is failure-prone and hence widely recognized as a critical recruitment bottleneck in coastal wetland restoration (Hu et al., 2015, 2021). Increasingly, restoration practices have been dedicated to overcoming this bottleneck (e.g. Fivash et al., 2021; Temmink et al., 2020). However, recent evidence suggests that life stages before seedling establishment (i.e. seed retention and seedling emergence) appear to be even more vulnerable to dynamic disturbances (van Regteren et al., 2020; Zhu et al., 2021). Most experimental studies using seed addition have reported massive seed losses, while the remaining seeds may still fail to germinate due to unsuitable habitat conditions (Statton et al., 2017; van Regteren et al., 2019; Zhu et al., 2020). This suggests that seed-based restoration in coastal wetlands may encounter multiple recruitment bottlenecks nested in different life stages.

Differences in environmental settings may drive recruitment bottlenecks formed in varied life stage transitions, causing the outcomes of similar restoration approaches to differ between sites (Larson et al., 2015; Statton et al., 2017). However, identifying specific bottleneck(s) that may occur at a targeted restoration site remains a formidable challenge (Brudvig et al., 2017), because we have a fragmented understanding of the underlying causes of variation in transitions across stages, particularly for stages before seedling establishment. Another critical recognition is that the success of life stage transitions is likely to vary between species even in homogeneous settings, given their contrasting seed and seedling traits or survival strategies (van Regteren et al., 2019; Zirbel et al., 2017). Resolving these context dependencies is integral to guiding restoration ecology towards a more predictive science, enabling restoration practitioners to ameliorate existing restoration strategies and thus overcome possible bottlenecks through forecasting based on site-specific conditions (Barnard et al., 2019; Brudvig et al., 2017). The latter would benefit from applying novel technologies such as machine learning, provided that sufficient large datasets are available for the application of such techniques (Hu et al., 2021).

In this study, our objective was to make seed-based wetland restoration predictive and inform management by (1) seeking integrated experimental evidence generalizing stage-specific causative factors for demographic loss/mortality and (2) developing predictors oriented towards site-specific bottlenecks. Specifically, this study is focused on seed retention and seedling emergence, as they represent the most vulnerable stages of life after sowing. First, by means of large-scale field experiments, we tested how seed retention and seedling emergence were affected by various management options and a wide range of physical settings. Variable screening was then implemented to identify stage-specific governing factors. Second, the resulting insights and dataset were used to develop stage-specific predictive models using machine learning. Model experiments were then conducted

under various scenarios to assess site-specific feasibility of potential seed-based restoration practices. Finally, we discuss the implications of our results in decision-making for restoring coastal wetlands.

2 | MATERIALS AND METHODS

2.1 | Experiments: Monitoring dynamics of seed retention and seedling emergence

2.1.1 | Study sites and species

We employed salt marsh as a model ecosystem. Eight salt marshes (Figure 1) in the Scheldt estuary in NW Europe were selected to encompass a spectrum of environmental settings comparable to those of areas that are potentially targeted for marsh restoration (details in Table S1 and Appendix S1). The pioneer area in two chosen marshes (i.e. Baar and Kete) is characterized by hummocks and hollows (Figure S1), which are two distinct microhabitats and may have a significant impact on seed-seedling transition. We conducted experiments in both microhabitats separately to include environmental differences due to microtopography. A total of 10 locations (i.e. eight sites, with hummocks and hollows sub-habitat at two of these sites) were used in this study.

Four dominant landscape-forming pioneer species in NW Europe salt marshes were considered as models: *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus* and *Spartina anglica* (see Table S2 for an overview of traits). Mature seeds were collected from field locations where the corresponding species formed monospecific meadows in autumn 2020. Seeds of *S. anglica* and *S. maritimus* were soaked in water in a 4°C fridge to simultaneously break dormancy; seeds of *S.*

europaea and *A. tripolium* were nondormant and stored dry in breathable paper bags in the same fridge. Seed storage was maintained for approximately 5 months until the commencement of this study.

2.1.2 | Manipulated experiment concerning seed retention

To establish the response of seed retention to varied environmental settings, a seed addition and recovery experiment was conducted across all locations in 2021. This experiment was repeated twice, before (mid-March to mid-April) and during (mid-April to mid-May) the period of seed germination, to expand the available environmental gradients. Before the experiment, seeds of the four species were repeatedly freeze-thawed until inactive to avoid germination during the experiment. Layered seed/sediment cores were created in transparent PVC pipes ($\Phi = 36$ mm, $h = 50$ mm; bottom sealed) with homogenized sediment and the pretreated seeds. Pretests showed that *S. europaea* seeds cannot be discerned from sediment/plant debris due to their small size ($\Phi < 1$ mm) and dark colour. Considering the contrast of *S. europaea* seeds with other species seeds (Table S2) and that seed retention may vary with seed size, we employed *S. europaea* seed mimics as a substitute for using real seeds. *S. anglica* seed mimics were used as controls, whose retention dynamics were then compared to those of real *S. anglica* seeds to verify the surrogate effectiveness of mimic seeds relative to real seeds. Mimic seeds are plastic chips with red colour and of similar size to the real seeds of *S. europaea* or *S. anglica*. Each core contained five seed addition depths: 0, 5, 10, 20 and 30 mm. Seeds of the five types (i.e. real seeds of *A. tripolium*, *S. maritimus* and *S. anglica* and seed mimics of *S. europaea* and *S. anglica*) were placed at different depths according to
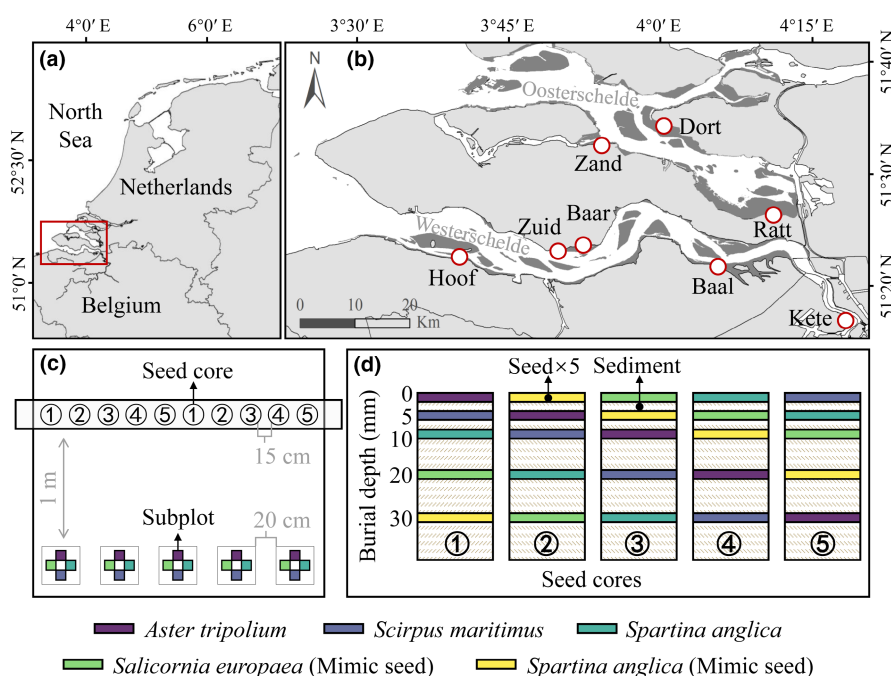

FIGURE 1 (a) Location of the Scheldt estuary. (b) Geographical distribution of eight chosen salt marshes. See Table S1 for complete names of all sites. (c) Setup in each experiment plot. Circles with numbers indicate the order in which seed cores were deployed. Different numbers represent cores assembled with different rules shown in (d). Subplots were setup to conduct seedling emergence experiments and assigned with different sowing depths. In each subplot, seeds of the four species were deployed in a cross-shaped pattern to avoid mutual interference. (d) Protocol for making the layered seed cores. Each core was assembled from different types of seeds buried at specific depths. Different colours in (c) and (d) indicate different species or seed types.

the protocol shown in Figure 1d. Each depth contained five seeds of the same type. Each layer was freeze-set before adding a new layer of sediment and seeds to avoid mixing. The assembled cores were removed from the PVC pipes and stored in a frozen state to enable easier deployment in the field.

At each location, 10 fixed 1.5×1.5 m plots were established along two parallel transects located 5 and 35 m from the marsh edge. Each transect consisted of five plots with an interval of 20 m. Within each plot, 10 seed/sediment cores were deployed at 15 cm intervals with their surface flush with the sediment bed, using a prefabricated template (cf. Zhu et al., 2021) and following the protocol shown in Figure 1c. A total of 2000 cores were deployed in the two rounds of experiments ($n = 200$ for each seed type in each round). Each round of experiments lasted 4 weeks, after which all cores were positioned using the same template and completely retrieved using PVC pipes with a larger size ($\Phi = 100$ mm, $h = 150$ mm). Each seed type and their corresponding burial depth were determined using the deployment protocol and their retrieved location. After sieving through a 1 mm sieve, seed retention rate for each depth in each core was calculated as the proportion of seeds deployed that resulted in retrieved seeds.

At each plot during each round of experiments, elevation was determined using the differential global positioning system (DGPS) measuring five scattered points and expressed as an average. A dissolving plaster block wrapped in a net pocket (mesh size of 1 cm) was arranged above the sediment and fixed on a wooden pole inserted into the sediment. The plaster block was retrieved after 2 weeks. Relative mass (g; after hot-air drying at 60°C) loss of the plaster block was employed to quantify the integrated hydrodynamic intensity (%) from tidal currents and waves. Bed-level dynamics were determined using the sediment erosion bar (SEB) technique (cf., Hu et al., 2020). The initial height of SEB from the sediment surface was measured at 10 fixed and regularly spaced spots, and was set to zero as a reference elevation. Bed elevation change was calculated as the relative positive or negative change from the reference elevation. Data collected from the 10 spots were averaged to evaluate bed-level dynamics within the plot.

2.1.3 | Manipulated experiment concerning seedling emergence

Viable seeds were used for seedling emergence experiments. Germination pretests (detailed in Appendix S2) for all species showed that at least 80% of the seeds germinated under ideal culture conditions (Figure S2). Field experiments were implemented when seed germination requirements overlapped with field climatic conditions (i.e. from mid-April to mid-May 2021). Within each plot at each location, five subplots (20×20 cm) were established at 20 cm intervals (Figure 1c). These subplots were assigned to five different sowing depths: 0, 5, 10, 20 and 30 mm. At each subplot, four mesh bags each containing 20 seeds of one species were deployed in a 'cross-shaped' pattern to avoid mutual interference and fixed on a permanent wooden pole. Such deployment would prevent seeds

from being swept away by tidal motion. After 6 weeks, seedling emergence was determined by counting the shoots emerging from sediment surface. Emergence rate was calculated as the proportion of sowed seeds resulting in emerged seedlings.

During the experiment, five replicates of sediment cores ($\Phi = 8$ cm, $h = 5$ cm) were randomly collected in each plot within each location. These cores were cut in situ into separate sections: 0–5, 5–10, 10–20, 20–30 and 30–50 mm. One of the sediment core replicates ($n = 500$, covering five depth sections of 10 plots at 10 locations) was used in situ to measure soil salinity using a portable salinometer (EC1200-NIEUWKOOP). In laboratory, the other sediment core replicates were used to (i) analyse median grain size using a laser particle sizer (Malvern-Master-Sizer-2000); (ii) measure water content by calculating the difference of wet and dry weight (after oven-drying at 105°C for 48 h); (iii) measure pH using a pH metre (after air-drying; soil: water = 1:5); (iv) determine organic content using the loss on ignition method (after burning at 510°C for 3 h). In addition, elevation is closely related to the inundation period and was considered likely to affect seedling emergence, thus elevation at each plot was measured using the method described in Section 2.1.2.

2.2 | Exploration: Identifying stage-specific governing factors

2.2.1 | Regarding seed retention dataset

In a priori steps, the pairwise Wilcoxon rank sum test was used to determine the difference in retention rate between real and mimic *S. anglica* seeds. The resulting insignificant differences ($p = 0.26$) validate the surrogate effectiveness of mimic seeds relative to real seeds. Therefore, the retention rate of mimic *S. europaea* seeds was regarded as that of the real *S. europaea* seeds and compared with that of the other three species in subsequent analyses. The same method was also used to test the differences between the two rounds of experiments. The detected significant differences ($p < 0.001$) validated their independence and allowed us to treat the experiment as being conducted at 20 contrasting locations. Two-way analysis of variance (ANOVA) was used to test the effect of two fixed variables (i.e. species and burial depth) on retention rate. Since the variability in retention rate between species was negligible ($p = 0.96$; Table S3), pooled species data were used for subsequent analyses.

As a result, there were one fixed variable (i.e. burial depth) and three random variables (i.e. elevation, hydrodynamic intensity and bed-level dynamics) that could affect seed retention at the plot level. The following protocol was implemented to identify the critical factor(s) governing seed retention:

- *Screening random variables for potential associations using pairwise correlation analysis.* Random variables with correlation coefficients $|\rho| > 0.7$ were considered autocorrelated and filtered to retain one variable. To achieve this, seed retention was modelled with one of the autocorrelated variables using the function lme4::glmer()

specifying the 'binomial' family. The random variable corresponding to the candidate model with a smaller AIC (Akaike's information criterion) was delivered to the next step.

- *Assessing statistical evidence for the effect of remaining variable.* Using the function lme4::glmer() and stats::drop1(), we fitted a full model with all remaining variables and a series of reduced models in which one of the variables was dropped. The likelihood ratio tests were used to compare the full model with each of the reduced models. If the likelihood of a reduced model did not decrease significantly relative to the full model (with $p > 0.05$), its corresponding dropped variable was removed from the final model. To minimize the probability that a significant variable is actually spurious, two corrections to the p-value from multiple comparisons during drop-one model selection were applied using the Benjamini and Hochberg method and the Holm method (Tredennick et al., 2021).

2.2.2 | Regarding seedling emergence dataset

Two-way ANOVA was used in an a priori step to test the variability in emergence rate among two fixed variables (i.e. species and burial depth). The results indicated that both had a significant effect on emergence rate ($p < 0.001$; Table S3). Random variables that may affect emergence rate included soil salinity, pH, water content, organic content, grain size and elevation. The same protocol as above was applied but with emergence rate as the response variable, to identify the critical factor(s) that dominate seedling emergence. All analyses were performed using R (v4.1.0).

2.3 | Prediction: Assessing site-specific bottlenecks to inform restoration

2.3.1 | Developing machine learning predictors

The machine learning predictors were built based on the artificial neural network (ANN) using datasets obtained from field experiments. We qualified seed retention and seedling emergence as regression problems since both are continuous variables with a range from 0% to 100%. Retention rate and emergence rate were targeted as output variables of the ANN predictor, while their respective critical dominating factors were used as input variables. All variables were scaled to [−1, 1] in a preprocessing step using min–max normalization. Two-stage calibration was involved in the development of the ANN predictors, enabled by dividing the datasets into training, validation and testing subset. To simplify the ANN structure, we started training with one hidden layer. The maximum number of neurons in the hidden layer was set to be twice the number of input variables (cf. Oehler et al., 2012). Following this, the number of neurons was increased from one to the maximum to obtain the relative optimal performance of the predictor. Additional hidden layer(s) were added on the condition of drastically improving predictability. Performance of developed

predictors was evaluated based on 10-fold cross-validation and using the root mean square error (RMSE) criterion. The RMSE from 10 runs of validations was averaged to obtain the final RMSE for the predictor's performance.

2.3.2 | Identifying site-specific bottlenecks using predictors

To identify potential bottleneck effects at restoration sites with specific environmental settings, the constructed ANN predictors were used to carry out model experiments in which various restoration scenarios were compared. Burial depths and species were regarded as controllable management options and modelled as grouping factors. To reveal potential bottlenecks that originated from seed retention, in each prediction group, hydrodynamic intensity varied from 0% to 100% and bed-level dynamics varied from −20 to 20 mm (see Section 3.1 for the determination of critical factors). Regarding seedling emergence, the critical factor was identified as soil salinity (see Section 3.2), which was set from 0 to 15. All of the environmental setting ranges above were chosen to represent typical marsh habitats in NW Europe. The threshold criterion for identifying bottlenecks was set at 20% (cf. Stagg et al., 2020), that is, seed retention or seedling emergence tends to irreversibly fail when their probability of success falls below this 20% tipping point, thus forming a bottleneck for potential restoration practice.

3 | RESULTS

3.1 | Critical factors governing seed retention

In the variable screening procedure, elevation was excluded due to its significant correlation with hydrodynamic intensity ($|\rho| = 0.73$, Table S4) and relatively weak explanatory potential for seed retention variability (Table S5). The final model revealed that the critical factors dominating seed retention were burial depth, hydrodynamic intensity and bed-level dynamics (Table S6). Overall, the higher seed retention rates could be predominantly explained by (i) deeper burial depth (Figure 2a) and/or (ii) weaker hydrodynamic intensity (Figure 2b) and/or (iii) stable or accreting sediment regimes (Figure 2c).

3.2 | Critical factors governing seedling emergence

Regarding factors affecting seedling emergence, the grain size was excluded first due to its significant correlation with organic content ($|\rho| = 0.77$; Table S7) and relatively weak explanatory potential for seedling emergence variability (Table S8). The likelihood ratio tests showed that dropping pH, water content, organic content and elevation individually from the full model did not significantly degrade the model performance, they were thus excluded during the drop-one model selection (Table S9). The final model revealed that the

FIGURE 2 (a) Seed retention rate at varying burial depths. (b) Response of seed retention rate to hydrodynamic intensity. (c) Response of seed retention rate to bed-level dynamics. Positive values on the *X*-axis indicate accretion while negative values indicate erosion. All figures were made using the pooled species data. In the legend, abbreviations indicate field locations while numbers represent experimental rounds at different periods. See Table S1 for complete names of all locations.
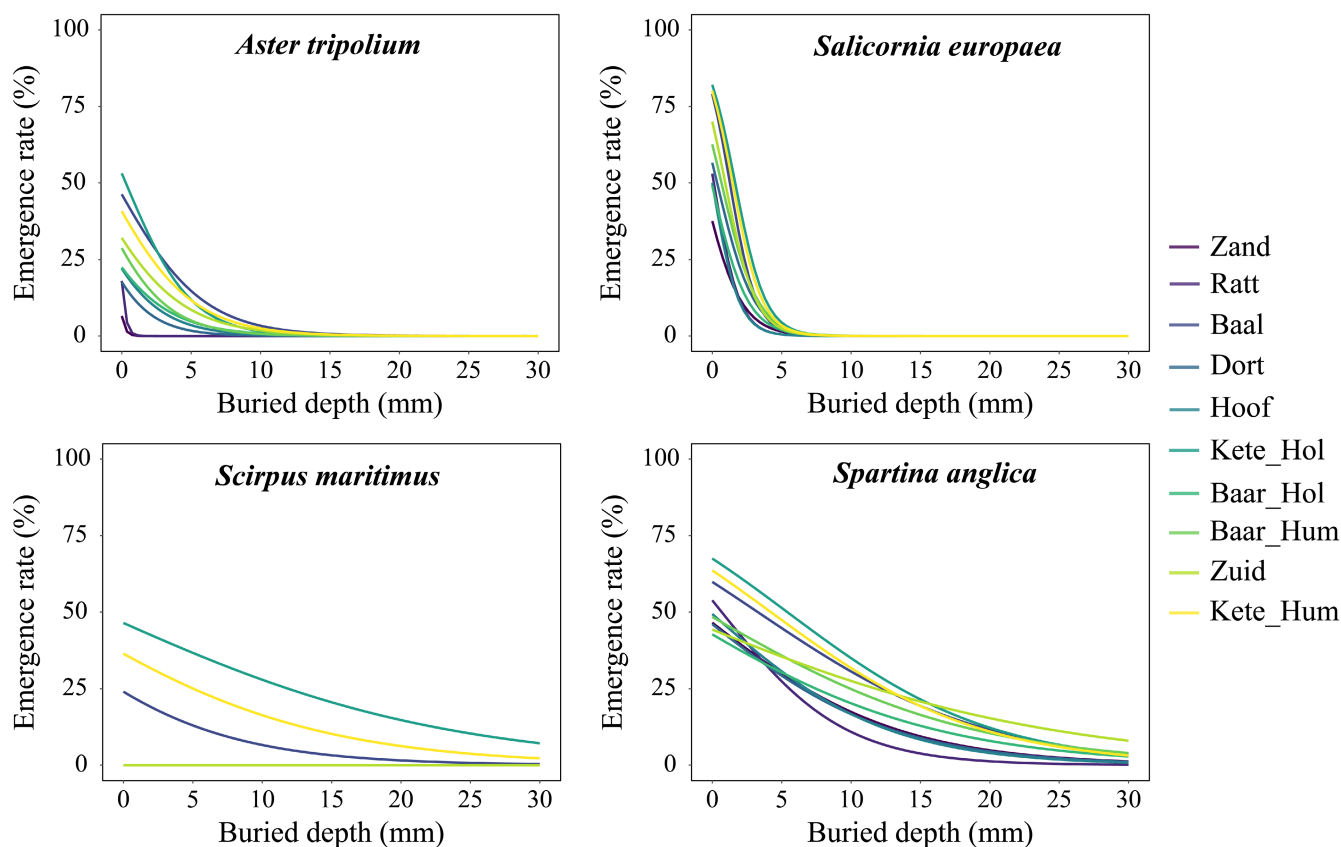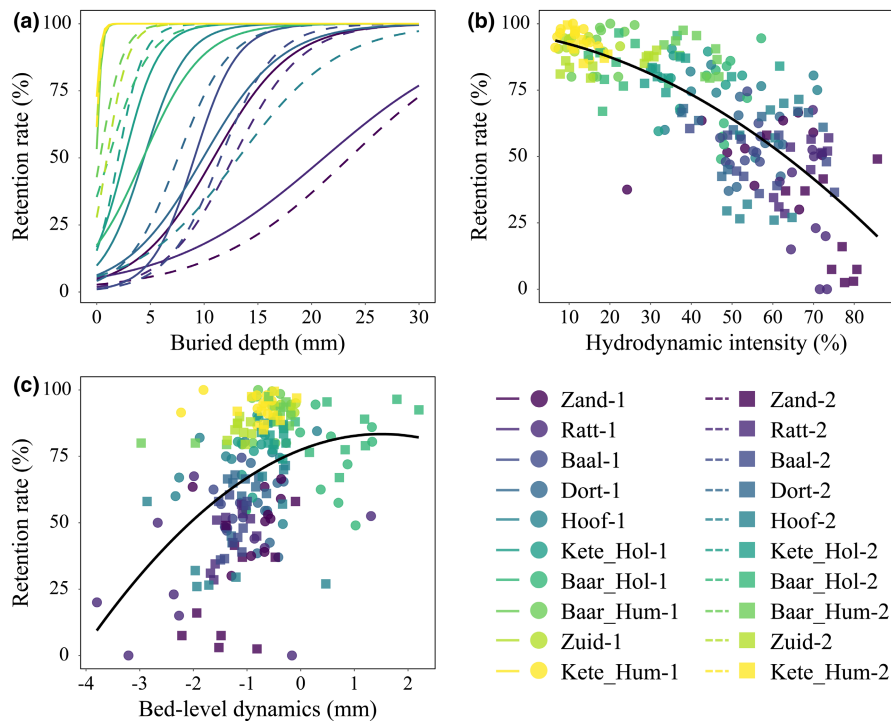

FIGURE 3 Seedling emergence rate at varying burial depths. The curves are the fitted response from logistic regression based on 10 replicate measurements for each species at each burial depth at each location. See Table S1 for complete names of all locations.

variability in seedling emergence can only be accurately accounted for when species, burial depth and soil salinity were considered. Overall, seedlings of all species were more likely to emerge at microsites with relatively lower soil salinity (Figure 4). Their emergence possibility would be further inhibited by increasing burial depth, while the response curve varied between species (Figure 3).
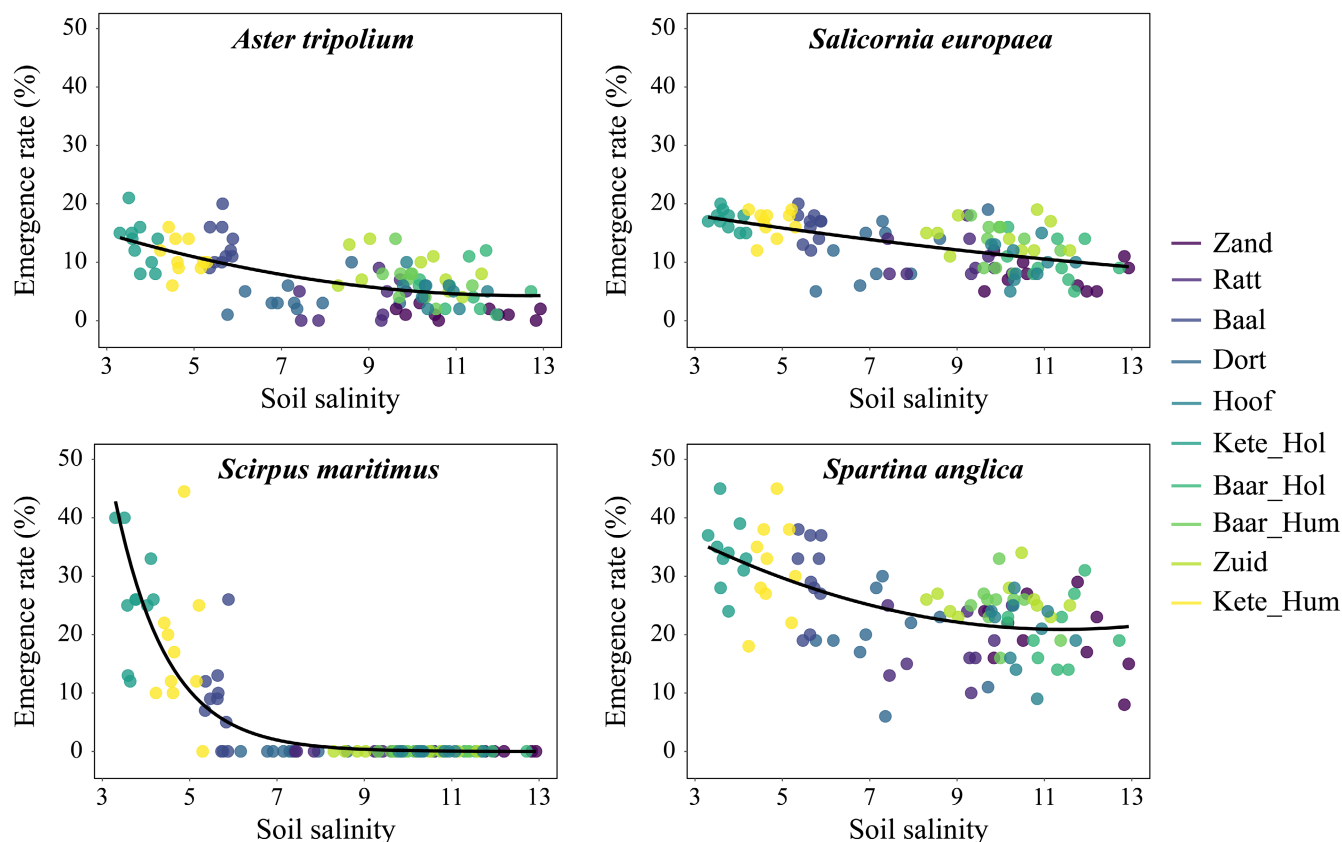
FIGURE 4 Response of seedling emergence to soil salinity. Emergence rate is the average of different depths at each plot. See Table S1 for complete names of all locations.

3.3 | Application of ANN predictors on seed retention

Burial depth, hydrodynamic intensity and bed-level dynamics were included as inputs to develop the ANN predictor for predicting seed retention dynamics, based on the results described in Section 3.1. The best predictor was obtained with a topology of two hidden layers, with four and one neurons respectively (Table S10; Appendix S3). This predictor showed a good capability to reproduce the retention of deployed seeds observed at field locations, with average RMSE of 0.22±0.03 and 0.23±0.04 for the validation and testing subset respectively (Table S10).

When the predictor was applied to assess seed retention variability in potential restoration practices, it turned out that the retention of seeds sown on the sediment surface (hereafter, surficial seeds) would invariably form a bottleneck effect (i.e. seed retention rate below the tipping point of 20%) in erosion-prone sites (Figure 5). In sites with stable or accretion-prone sediment regimes, the surficial seeds would remain in place successfully while the possibilities (ranged from 20% to 100%) were negatively correlated by local hydrodynamic intensity (Figure 5). Increasing sowing depth was shown to alleviate the emergence of the bottleneck effect, that is, the deeper the seeds were buried,

the wider the rang of habitats that will enable the seeds to persist (Figure 5).

3.4 | Application of ANN predictors on seedling emergence

Driven by the results described in Section 3.2, we developed four ANN predictors of seedling emergence for the four species using burial depth and soil salinity as input variables. The final predictors consist of one hidden layer, embedded with three, five, three and three neurons for *A. tripolium*, *S. europaea*, *S. maritimus* and *S. anglica* respectively (Table S10; Appendix S4). These predictors showed consistent performance in reproducing the dynamics of seedling emergence observed at field locations, with average RMSE resulting from both the validation and testing subset was 0.08±0.02, 0.08±0.01, 0.10±0.03 and 0.12±0.02 for *A. tripolium*, *S. europaea*, *S. maritimus* and *S. anglica* respectively (Table S10).

Species-specific bottleneck effects formed by seedling emergence were detected while applying predictors under a wide range of key physical settings (Figure 6). *S. anglica* was proven to have the widest habitat range suitable for seedling emergence. Only when *S. anglica* seeds were buried deeper than 10mm in
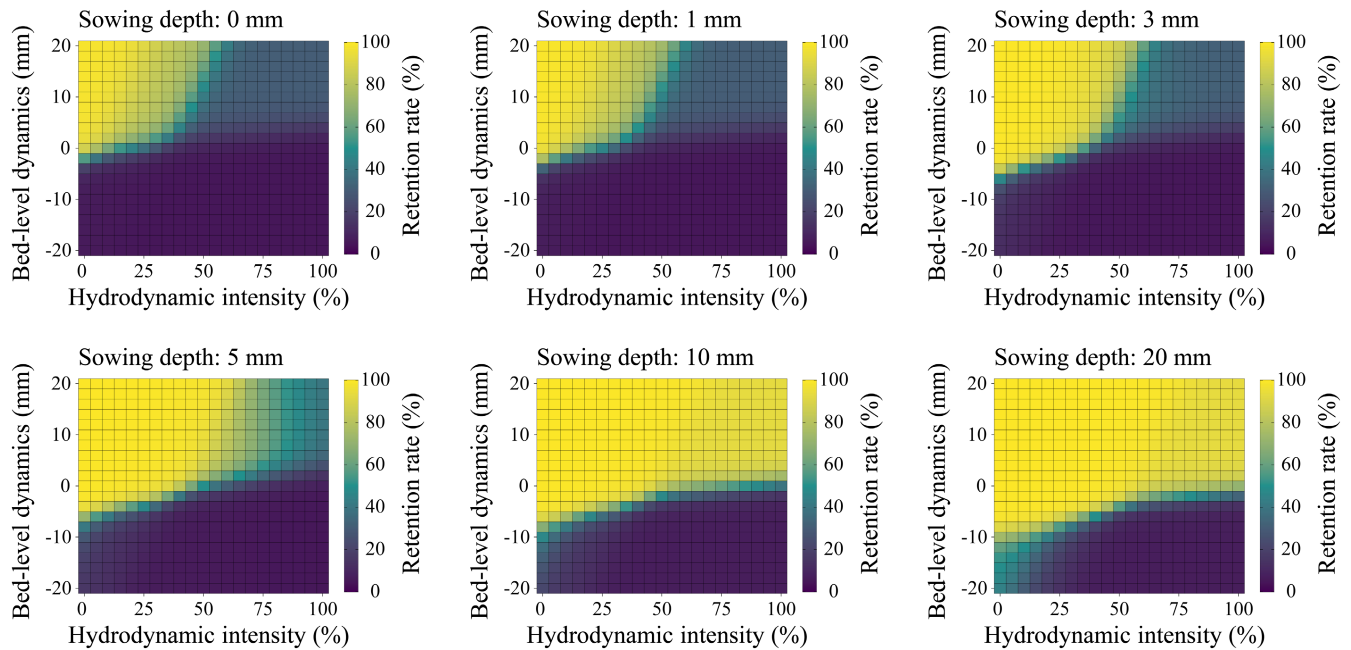
FIGURE 5 Modelling results of the developed machine learning predictors on retention variability for seeds buried at different depths, when placed in contrasting restoration scenarios. These scenarios were parametrically characterized with broad variation in critical site-level factors, that is, hydrodynamic intensities and bed-level dynamics.

FIGURE 6 Modelling results of the developed machine learning predictors on seedling emergence probability in potential restoration practices. These practices were parametrically characterized with broad variation in critical factors (i.e. burial depth and soil salinity) governing seedling emergence.
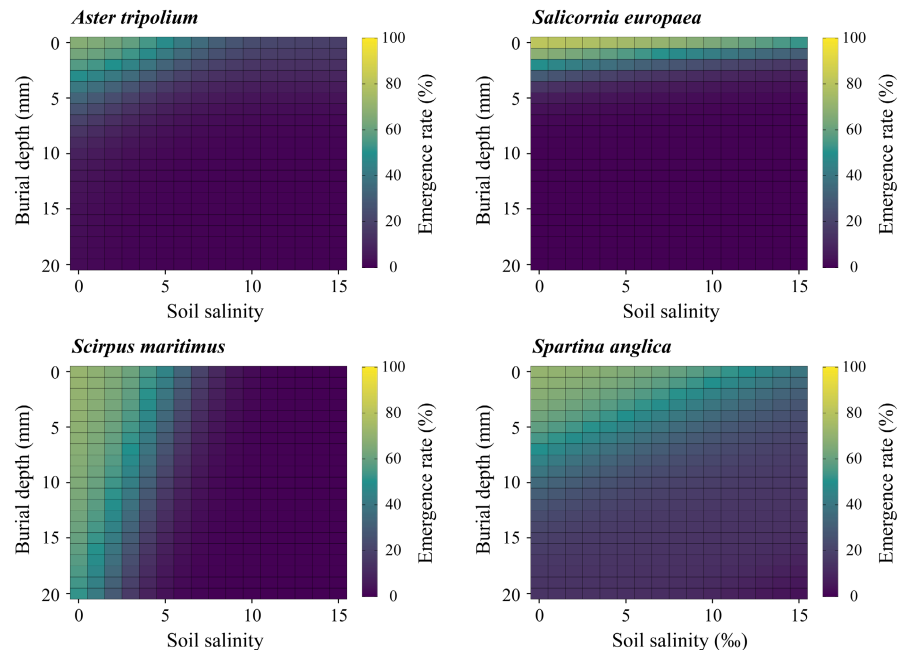
areas with higher soil salinity did their emergence rate drop below 20%. For *S. europaea*, emergence of surficial seeds did not form a bottleneck, while seeds failed to emerge once buried deeper than 5 mm. For *S. maritimus*, the emergence bottleneck always existed in areas with higher soil salinity. With increasing burial depth, the narrowness of the salinity range in which *S. maritimus* could emerge increased. *A. tripolium* showed the narrowest habitat range suitable for seedling emergence; their seeds hardly emerged once buried below 5 mm or deployed in areas with higher soil salinity.

4 | DISCUSSION

4.1 | Linking restoration failures to stage-specific bottlenecks

Quantifying demographic losses across all early life stages of establishing plants is an essential step in determining the stages that are most likely to inhibit recruitment and thus limit seed-based restoration (Kettenring & Tarsa, 2020; Statton et al., 2017). Major recruitment bottlenecks in coastal wetlands have been widely

attributed to individual loss/death during seedling establishment and survival (Balke et al., 2011; Hu et al., 2021). In contrast, this study focused on demographic processes prior to seedling establishment. Our broad-scale experiments showed that a substantial loss of superficial seeds (75%–100% in most locations) would occur routinely following sowing, suggesting that seed retention rather than seedling establishment was perhaps the principal bottleneck to recruitment in seed-based restoration. This finding supports earlier arguments (e.g. James et al., 2011; Larson et al., 2015) that high mortality later in life may be insignificant in determining plant abundance, when mortality early in life is also considered. This finding also corroborates the recently advocated view that seed availability is a nonnegligible recruitment limitation in coastal wetlands (van Regteren et al., 2019; Zhu et al., 2020). Unlike related studies that attribute low seed availability to naturally low seed yields or dispersal limitations (Broadhurst et al., 2016; Kettenring & Tarsa, 2020), our study revealed that hydrodynamic intensity and sediment erosion were the dominant drivers of low seed availability after sowing.

Once seeds are retained, for example, due to burial by benthos or due to high sediment accretion (Friess et al., 2012; Marion et al., 2021), our large-scale seedling emergence experiments suggest that unequal emergence probability is a key driver of recruitment variation across species. Furthermore, surficial seeds of species such as *S. europaea* and *S. anglica* were shown to be able to emerge under a wide range of environmental conditions. This implies that such emergence limitations could be circumvented through management such as species selection during the early planning stages of restoration. Although salinity was shown to be tied to seed germination (Rand, 2000; van Regteren et al., 2020), our results revealed its lingering implications for subsequent seedling emergence. Unlike hydrodynamic intensity and bed-level dynamics which dominate seed retention and are highly spatiotemporally heterogeneous, soil salinity typically has little within-site variability (van Regteren et al., 2020), suggesting the feasibility of avoiding emergence limitations further by site suitability assessment.

4.2 | Burying seeds to amplify restoration output

Broadcast sowing to the soil surface has been widely adopted to achieve rapid and large-scale restoration (Kettenring & Tarsa, 2020; Marion & Orth, 2010). However, our findings imply that this approach tends to fail in coastal wetlands due to substantial seed loss after sowing. Restoration efforts typically compensate for high seed losses with bet-hedging strategies such as a large seed supply (Marion & Orth, 2010; Statton et al., 2017) or multi-year sowing (Groves & Brudvig, 2019), ignoring the possibility that excessive seed collection may risk damage to donor populations, which in turn counteract the intended effects of restoration (Balestri & Lardicci, 2012; Kettenring & Tarsa, 2020). This study suggests that proper seed burial as an alternative may yield greater returns in improving seed retention,

leading to more efficient restoration with limited seed supply. The suitability of this alternative varies by species as a consequence of differences in emergence probability. Species-specific burial depth thresholds below which seedlings cannot emerge should thus be identified to practice this alternative in restoration.

Sowing seeds to the depths ideal for species involved are common with restoration practices in terrestrial systems (Kildisheva et al., 2016; Palma & Laurance, 2015), but very few efforts have been made in coastal wetlands due to the technical difficulties involved in quickly burying large quantities of seeds (Marion et al., 2021; Marion & Orth, 2010). Potential seed-planting approaches that have been attempted in coastal wetlands include drill seeding (Zilverberg et al., 2014) and dispenser injection seeding (Tan et al., 2020). However, their labour-intensive nature renders them impractical for large-scale restoration efforts. Hydroseeding with a slurry as part of dredging projects may offer opportunities for this purpose and has been attempted in salt marshes (Saunders et al., 2020; Thorne et al., 2019), although it cannot precisely control the seed-planting depths. Furthermore, this approach may be limited in its application in coastal wetlands that require 'clear' water, such as in seagrass habitats (Thorne et al., 2019). Marion et al. (2021) reported a machine that allows burying seeds into specific depths in hectare-sized plots at sandy sites; unfortunately, its applicability to muddy sites has not been robustly validated. Therefore, technological advancement in ecosystem-specific seed-planting methods/machinery is urgently needed to attain the goals of large-scale restoration in coastal wetlands.

4.3 | Hitting restoration targets based on a priori predictions

Experimental studies providing in-depth insight into recruitment bottlenecks, in tandem with modelling approaches, represent an important step contributing to cultivating predictive capabilities prior to restoration initiation (Barnard et al., 2019; Brudvig et al., 2017). This study given the first attempt to apply field data-driven machine learning to identify recruitment bottlenecks associated with seed-based restoration in coastal wetlands. The ANN exemplified here has a high overall prediction accuracy, reflecting the highlighted value of this and similar algorithms (e.g. classification and regression tree, random forest) in improving the predictability of restoration ecology (Barnard et al., 2019; Hu et al., 2021), although comparisons between multiple algorithms are pending in future research. It is important to note that the predicted retention and/or emergence probability in our study may not represent the long-term population trajectory in a restoration context. Constrained by a sequence of threshold effects related to windows of opportunity (cf., Balke et al., 2011), the number of seedlings eventually established appears to constitute a small fraction of available seeds/seedlings (Hu et al., 2015; Statton et al., 2017). However, it is possible that the few survivors could result in rapid population growth due to potentially

high reproductive output (Friess et al., 2012). This suggests that more information is required for predicting long-term restoration outcomes. Our study provides the underlying research framework needed for this purpose, which includes broad-scale experiments on outcome variability, model exploration of root causes and field data-driven predictions on site-specific bottleneck(s). Although such an approach requires significant investment, especially when focusing on broader demographic processes in restored populations (e.g. survival of seedlings and adults), it appears to be the next indispensable step towards a future of predictive restoration (Brudvig et al., 2017).

5 | CONCLUSIONS

Our results demonstrate that early life stage transitions significantly impact the outcomes of seed-based restoration in coastal wetlands, with seed retention as the principal bottleneck responsible for demographic plummets and seedling emergence being the critical bottleneck driving cross-species variability. To improve restoration efficiency, hydrodynamic intensity, bed-level dynamics and soil salinity should be included in assessment metrics for site suitability. Furthermore, small steps in strategic management were shown to drive giant leaps in restoration output. For example, species selection combined with species-specific seed burial would minimize seed loss while eluding the emergence limitation. In particular, this study exemplifies the value of data-driven techniques in predicting variability in restoration outcomes based on site conditions. The resulting a priori expectations can help practitioners position restoration in areas most likely to be successful and inform strategic management to overcome recruitment bottlenecks. Despite these advances, it remains difficult to determine the long-term demographic trajectory of restored populations. A logical next step would be to develop field data-driven predictors oriented towards life stage transitions after seedling emergence using the advocated integrative research approach.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via 4TU.Research Data https://doi.org/10.4121/21071089 (Zhao et al., 2022).

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