

RESEARCH ARTICLE

Effect of upscaling nature-based coastal protection on estuarine biodiversity using foreshores and transitional polders

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Abstract

1. Nature-based solutions (NbS), integrating ecosystems and natural processes, offer a promising approach to deliver benefits to both ecosystems and human society. In estuarine and coastal regions, highly vulnerable to storm surges and large wave exposures, NbS schemes are often primarily evaluated for flood risk. Comprehensive assessments of their broader impacts on biodiversity are frequently overlooked.
2. This study presents an integrated modelling approach to compare the long-term estuarine biodiversity outcomes of two nature-based coastal protection schemes: (i) a seaward foreshore and (ii) a landward transitional polder (i.e. a temporary de-embankment). These schemes involve the creation of coastal wetlands, each subjected to different environmental and landscape settings. We also assess the influence of sea-level rise (SLR), sediment availability (i.e. suspended sediment concentration; SSC) and initial elevation on the temporal development of intertidal biodiversity, focusing on macrozoobenthos and tidal marsh vegetation.
3. The findings demonstrate that the effectiveness of different NbS schemes in enhancing biodiversity is strongly dependent on the initial environmental conditions and, consequently, on how the NbS is integrated into the landscape. In accreting environments, existing sloped foreshores facilitate rapid vegetation establishment and development, while initially flatter, lower-elevation transitional polders better support benthic biodiversity. However, flat transitional polders initiated at elevations above mean sea level rapidly become dominated by vegetation, reducing their benefits to benthos.
4. Over time, biodiversity outcomes in two schemes gradually converge as accretion progresses. SLR and SSC are key factors influencing the temporal development of

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biodiversity and scheme comparison. Higher SSC levels accelerate convergence, while SLR decelerates it.

5. *Synthesis and applications.* Our study provides a critical toolset for designing, comparing and planning nature-based solutions with respect to biodiversity effects, supporting coastal management strategies that integrate flood safety with optimal biodiversity outcomes. By considering the distinct biodiversity trajectories of different nature-based solutions schemes—shaped by sea-level rise and suspended sediment concentration—we highlight time-sensitive trade-offs and long-term ecosystem developments. These insights are particularly relevant given practical constraints, such as hydrodynamic challenges for seaward foreshores and societal resistance to land-use changes for transitional polders. This study facilitates informed decision-making for sustainable and adaptive coastal management.

KEYWORDS

biodiversity, coastal management, coastal protection, estuary, modelling, nature-based solution, sea-level rise, sediment availability

1 | INTRODUCTION

Nature-based solution (NbS), which involves leveraging natural processes, has gained widespread recognition as a strategy to adapt to climate change, protect biodiversity and ensure human well-being synergistically (Seddon et al., 2020). In estuarine and coastal regions, which are highly exposed to storm surges and large waves, integrating NbS into coastal protection is widely advocated (Temmerman et al., 2013; Temmerman & Kirwan, 2015). Coastal wetlands, such as tidal flats, saltmarshes and mangroves, can complement conventional flood-defence structures by reducing wave impact on seawalls (Duarte et al., 2013), even during extreme storms (Möller et al., 2014; Zhu et al., 2020). Furthermore, their flood-safety functions persist under sea-level rise (SLR) if sufficient sediment supply is available (Zhu et al., 2020).

Typically, NbS in estuarine and coastal systems focus on flood-safety function, with much less explicit consideration given to biodiversity benefits. However, estuarine and coastal ecosystems are among the most productive natural ecosystems (Barbier et al., 2011). Tidal ecosystems, consisting of both benthic communities and vegetation, play a significant role in carbon sequestration (Barbier et al., 2011; McMahon et al., 2023; Temmink et al., 2022), biogeochemical cycles (Lohrer et al., 2004; Tobias & Neubauer, 2019) and sediment transport processes (Cozzoli et al., 2021; Xu et al., 2022). Unfortunately, these valuable systems are globally threatened by coastal development, climate change and rising sea levels (Barbier et al., 2011). Implementing NbS provides a unique opportunity to reverse the substantial biodiversity and ecosystem loss that many estuaries have suffered over the past centuries. To maximize the benefits of this approach, NbS design should focus on both optimizing coastal protection and ensuring the preservation and enhancement of biodiversity.

Many studies have demonstrated the effectiveness of developing wetlands seaward of seawalls (or dike) as a nature-based coastal protection strategy (Möller et al., 2014; Zhu et al., 2020). This approach, referred to here as the *seaward foreshore* (Figure 1a), is widely recognized for its potential to enhance coastal resilience. However, constrained space and steep hydrodynamic gradients characteristic of these ecosystems often pose challenges to establishing such wetlands along many coastlines, particularly for the development of vegetated marshes, which frequently support limited biodiversity (Figure 1c) (Bouma et al., 2016; Marin-Diaz et al., 2023). As an alternative to seaward foreshore schemes, landward NbS offers a viable approach. These include conventional managed realignment, where the existing dike is moved landward to restore wetlands (French, 2006), and the 'double dike' strategy focused on in this study. Since the 12th century, many polders in the Netherlands have been created by reclaiming arable land by embanking silted-up tidal marshes. The double dike approach (Figure 1b) involves creating a *landward transitional polder* by reinforcing or constructing a second dike landward and opening the seaward dike to enable tidal exchange (van Belzen et al., 2021; Weisscher et al., 2022; Zhu et al., 2020). This innovative approach is not only intended to promote elevation gain and ecosystem development within the polder between two dikes but also to incorporate a rotational and regenerative land-use approach. The transitional polder can serve multiple purposes over time, including aquaculture or wetland restoration when opened to tides, and later being converted to agricultural land as elevation stabilizes through closure from tides. When SLR and subsidence cause significant divergence between land and sea levels, the polder can be opened again to gain elevation (Figure S1; van Belzen et al., 2021; Weisscher et al., 2022; Zhu et al., 2020).

In seaward foreshore areas exposed to strong longshore flows, which may be intensified by waves, relatively steep slopes (Fujii &

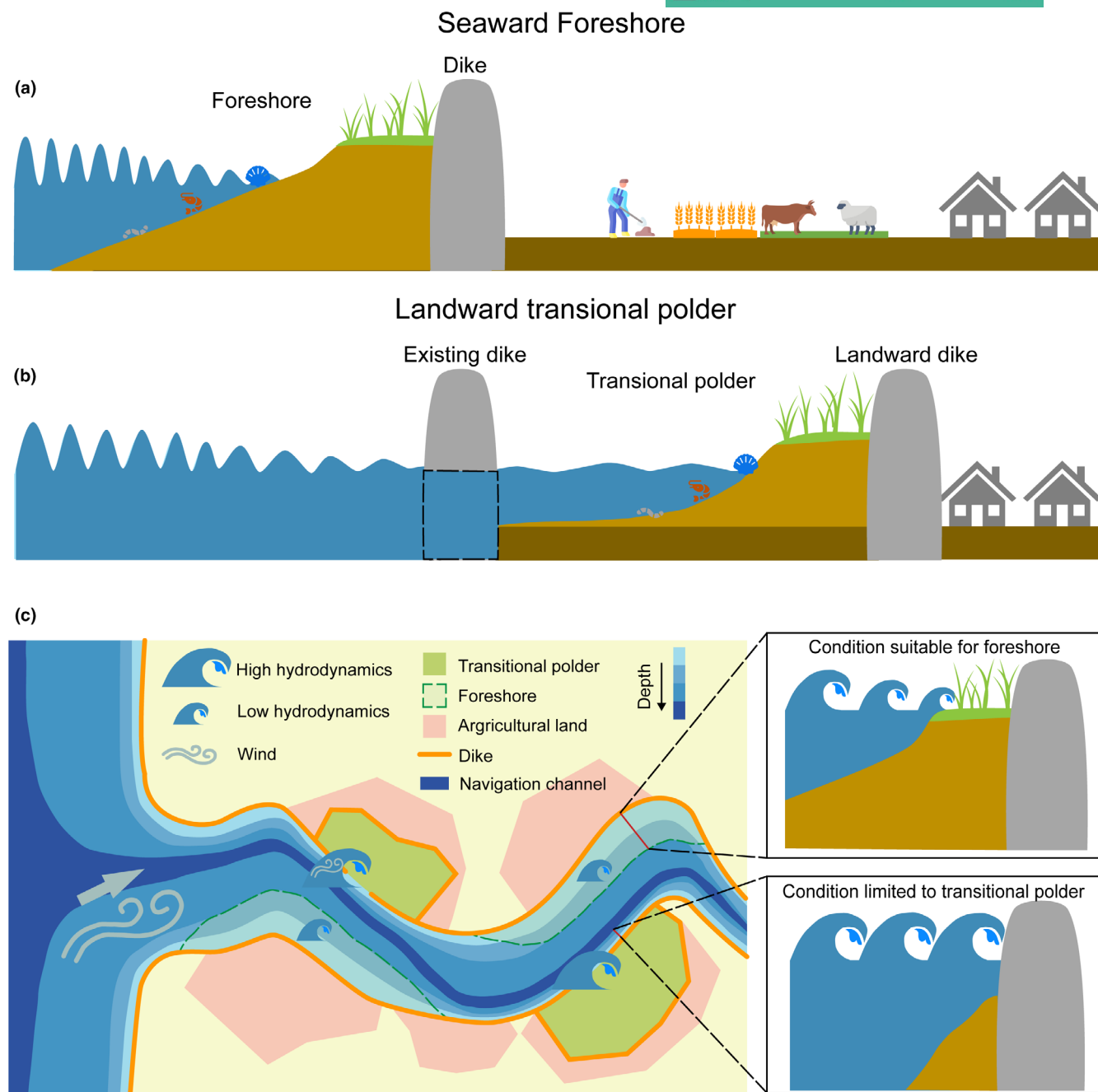


FIGURE 1 A conceptual illustration of two nature-based coastal protection schemes. (a) The seaward foreshore involves developing a saltmarsh in front of existing dikes to enhance coastal protection. (b) The landward transitional polder scheme involves creating a transitional polder between double dikes, which can act as a buffer and contribute to flood defence. (c) Feasibility of foreshore and transitional polder. In areas with gentle slope gradients and low-hydrodynamic forces, seaward schemes such as foreshores are more feasible as these conditions allow marshes to develop naturally and thrive (top right). Conversely, in regions near deep navigation channels with steep gradients and strong hydrodynamic forces, which may be further intensified by wind-induced waves (as depicted in the left high-hydrodynamics area), seaward marsh establishment is considerably more challenging or impossible (bottom right). In such high-energy environments, landward schemes, like transitional polders, are the only option for reliable nature-based coastal protection. Here, dikes can be (temporarily) breached by constructing a tidal inlet to convert agricultural land (temporarily) into tidal wetlands, offering a viable alternative for marsh creation in areas where direct seaward approaches are less effective or not effective.

Raffaelli, 2008) and coarser sediments (Herman et al., 2001) are typically formed. Conversely, landward transitional polders are characterized by shallow, gently sloped intertidal systems, which result from post-reclamation land management practices, such as filling tidal

creeks, ploughing and trampling (Lawrence et al., 2018). Moreover, transitional polders often exhibit varied elevations due to diverse pre-restoration practices (Janousek et al., 2021). The elevation differences within the tidal frame can lead to varying hydroperiods

after tide restoration, affecting land accretion processes and biodiversity development (Oosterlee et al., 2018). Biologically relevant environmental variables like inundation time and grain size are influenced by these initial morphological differences (i.e. slope, steepness, sediment type and elevation variations).

In addition to differences in initial conditions, the biogeomorphic development is affected by external driving factors like SLR and suspended sediment concentration (SSC). SLR can fast-track the submergence of coastal wetlands (Moorhead & Brinson, 1995). Reduction in sediment supply, caused by factors such as dam construction and storm-surge barriers (Ezcurra et al., 2019), can slow the rate of accretion, complicating the survival of coastal wetlands under SLR (Tognin et al., 2021). Understanding the impacts of these key external drivers, along with initial conditions, is crucial for guiding political decision-making on implementing NbS in diverse coastal environments.

In this paper, we investigated the effect of implementing contrasting nature-based coastal protection strategies (i.e. seaward foreshore and landward transitional polder) across different environmental contexts on biodiversity, specifically focusing on SLR and SSC. We developed a modelling approach that integrated biogeomorphodynamic and ecological models to compare the long-term biodiversity development of these NbS schemes, with a focus on macrozoobenthos (hereafter benthos) and vegetation. Biogeomorphodynamic models provide long-term environmental predictions, while species-specific Bayesian hierarchical models were constructed to predict species distribution based on environmental predictions. The species-specific results were then aggregated into two key biodiversity indices: geometric-mean biomass and richness. We used scenario simulations to compare biodiversity development between the seaward foreshore and landward transitional polder schemes and evaluate the impacts of SLR and SSC.

2 | MATERIALS AND METHODS

2.1 | Data collection

Our study focused on the Western Scheldt Estuary in southwestern Netherlands, where all data were collected (Figure 2). All fieldwork was carried out with the support of the local management agency and did not require any specific permits. We provide a full description of this area in Appendix S1. This dataset includes records of environmental factors and species. The environmental factors include median sediment grain size (D_{50} , μm) and inundation frequency, which are obtained through data collection in the field, while inundation time (% of time for which the site is submerged during a full tidal cycle) is derived from the validated hydrodynamic models. Vegetation data record species occurrence and coverage (%), while benthos data record species occurrence and biomass (g Ash Free Dry Weight m^{-2}). These data are used to model the relationships between species distribution and environmental variables.

2.1.1 | Environmental drivers to predict benthos and vegetation biodiversity

Environmental drivers included in the model to predict benthos and vegetation biodiversity and development were selected based on the following criteria: (1) known influence on species distribution, (2) data availability to enable us to derive relationships and (3) availability through our morphological model to forecast ecosystem development under different scenarios. These criteria led us to include salinity zone, inundation time and grain size as predictors for macrozoobenthic communities, while salinity zone and inundation time were employed as predictors for vegetation zonation (for a full description of environmental data collection see Appendix S2).

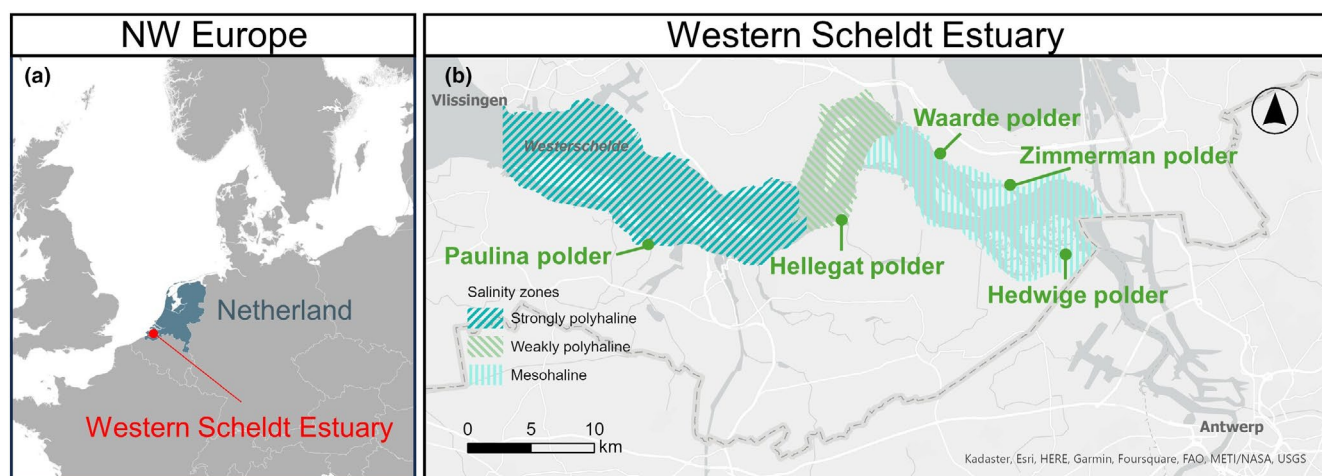


FIGURE 2 (a) Overview of study area location within northwestern Europe (b) Map of Western Scheldt Estuary and three salinity zones (strongly polyhaline, weakly polyhaline, mesohaline) according to OMES compartments (Maris & Meire, 2017). The vegetation sampling points are marked with green dots.

2.1.2 | Benthos

The data utilized in the current study was based on data from Cozzoli et al. (2017), which were sourced from the Benthic Information System (BIS version 2.01.0) hosted by the NIOZ in Yerseke, the Netherlands. Data collection occurred across depths ranging from 0 to 44m with respect to the Dutch Ordnance Level (NAP), with nearly 60% of the data recorded at depths not surpassing 5m. This extensive dataset was employed to encompass a wide range of environmental conditions and biological responses, providing a robust foundation for model development. A subset of 1362 records has been chosen based on the availability of abiotic data. The data contain about 28 species of major benthic classes that were collected from 2006 to 2010 in the Western Scheldt Estuary. We included in the distribution model only species that had more than 20 recorded observations.

2.1.3 | Vegetation

The data originated from surveys of marshes conducted along the salinity gradient of the Western Scheldt Estuary (names and locations in Figure 2) during the summers between 1990 and 1993. One or two line transects were established per marsh, crossing vegetation along the elevational gradient from the dike to the unvegetated mud flat. Each line transect consisted of a row of 1m×1m blocks, where the percentage coverage of vegetation species was visually assessed. Elevational heights (cm) were measured for each 1×1m² with respect to NAP, using a theodolite.

2.2 | Modelling approach

To assess the biodiversity outcomes of various NbS schemes, we developed an integrated modelling approach that dynamically links a biogeomorphodynamic model, a species distribution model and a logistic growth model (Figure 3). This structure allows us to capture the complex feedbacks between physical and biological processes. The biogeomorphodynamic model provides predictions of elevation changes that are fed into the species distribution model to estimate vegetation development. For benthos, these outputs from the species distribution model are further used by the logistic growth model to estimate biomass development. While this approach enables us to track the successive stages of tidal flat and salt marsh development, it introduces certain trade-offs.

On the one hand, linking multiple sub-models allows us to simulate realistic system-wide responses across environmental gradients, but on the other hand, the modular approach increases the potential for error propagation across scales. However, given the exploratory nature of this study, some degree of uncertainty is acceptable for the sake of understanding general trends in species distribution under varying environmental conditions. Our assumption is that species distributions are primarily shaped by abiotic drivers such as elevation, which act as a key environmental filter in intertidal systems (Lawrence et al., 2022).

To reduce model complexity and computational demand, we implemented a one-dimensional biogeomorphodynamic model based on cross-shore profiles, drawing from the work of van Belzen et al. (2021) and Mariotti and Fagherazzi (2010). This decision balances the need for tractability with the need to represent

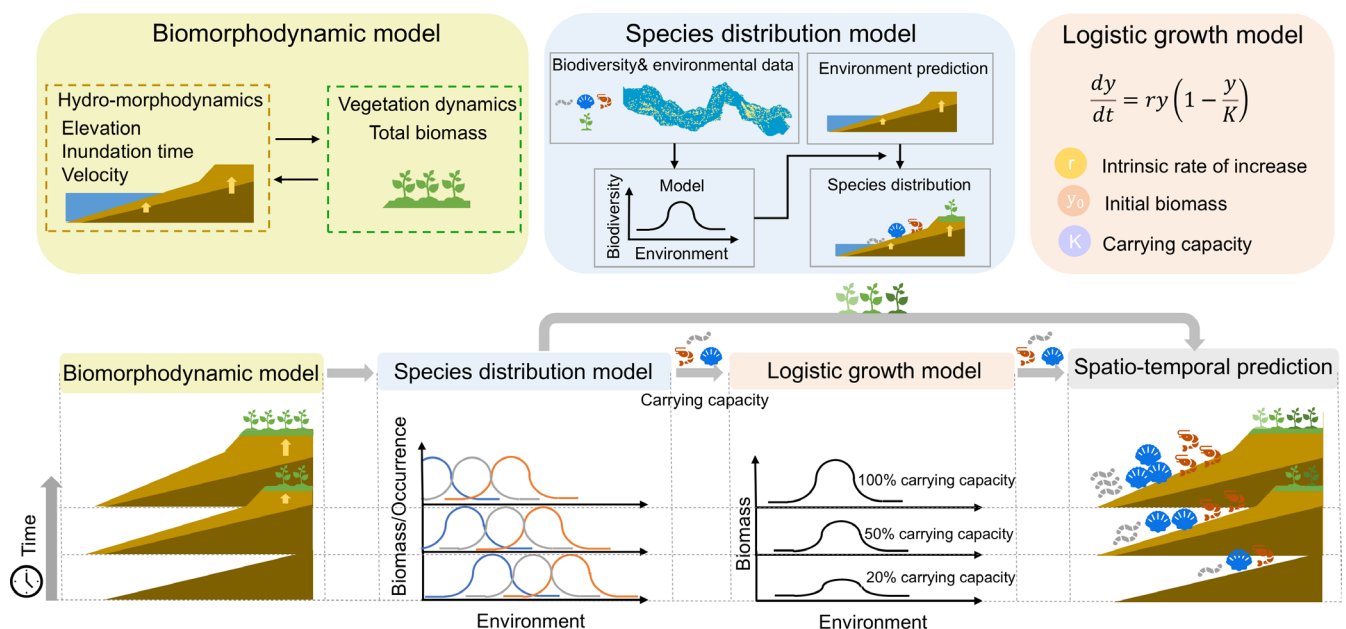


FIGURE 3 Framework of model approach. The model contains 3 components: A biogeomorphodynamic model, a species distribution model and a logistic growth model. The biogeomorphodynamic model tracks temporal dynamics of biologically relevant environmental factors, which are subsequently utilized in the species distribution model to generate predictions of species. Logistic growth equation used to simulate temporal dynamics of benthos biomass growth.

essential processes like sediment transport, tidal currents, vegetation dynamics and their interactions with erosion and deposition. The model spans a standardized 1000 m from sea to land and runs for 100 years (details in Appendix S3, with specific parameters listed in Table S1).

For species distribution predictions, we applied Bayesian hierarchical models for individual species using the *brms* package (version 2.18.0) in R v. 4.2.2., which leverages Stan (<https://mc-stan.org/>) for efficient computation (details in Appendix S4). Given the variability and challenges associated with real restoration, our Bayesian modelling approach explicitly incorporates uncertainty by generating probabilistic predictions. This approach can provide posterior distributions and confidence intervals, providing a robust framework for assessing the potential success of restoration efforts while accounting for parameter uncertainty and model limitations. It enables reliable forecasts of species occurrence and biomass, despite some limitations in predicting long-term dynamics for slower-growing macrozoobenthic species, which take time to reach their environmental carrying capacities (Hiddink et al., 2019). Vegetation, conversely, responds more quickly to favourable elevation conditions (Fivash et al., 2023). This contrast highlights the need for integrating a logistic growth model in benthos prediction to account for species-specific growth rates over time (details in Appendix S5).

2.3 | Benthos species prediction

Since our biogeomorphodynamic model did not directly simulate the dynamics of grain size, we used the inundation ratio, which can be directly derived from the biogeomorphodynamic model, to derive grain size predictions through linear regression. Median grain size often exhibits a shoreward fining trend along the tidal-flat inundation gradient (Wang et al., 2014). The transitional polder, frequently accomplished through regulated tidal exchange (Oosterlee et al., 2018), has comparatively lower and spatially uniform hydrodynamic energy compared to foreshores exposed directly to waves. Given that grain size serves as a recognized proxy for hydrodynamic conditions (Wang et al., 2014), it is noteworthy that grain size in the transitional polder exhibits less variability along the inundation gradient when contrasted with the foreshore. Therefore, we utilized separate linear models, developed from data in high-hydrodynamic areas and low-hydrodynamic areas separately, for sediment prediction in the foreshore and transitional polder (Figure S2).

Species distribution models generate predictions of biomass and occurrence. We further integrated logistic growth models to depict the temporal process of biomass niche filling. Predictions from the species distribution model, treated as time-varying carrying capacity, were input into the logistic growth model to generate forecasts of biomass over time. Further details on parameter determination of the logistic growth model are described in Appendix S5, with specific values presented in Tables S6 and S7.

2.4 | Vegetation species prediction

We converted elevation predictions generated by the biogeomorphodynamic model into inundation frequency predictions using empirical models (Oloff et al., 1997) (see Appendix S6). These predicted inundation frequencies were then input into the species distribution model to forecast the cover of each plant, which is regarded as a proxy for its aboveground biomass (Ónodi et al., 2017). The cover proportion of each plant species represents its proportion of the total biomass. The biogeomorphodynamic model predicts total biomass, assuming vegetation biomass varies parabolically along inundation time (Morris, 2006). The biomass of each plant species is obtained by multiplying the total biomass by the biomass proportion of each species. We realise that our biomass estimates are conservative for the more brackish part of the estuary, as highly salt-tolerant species typically grow larger under lower salt stress levels, and poorly salt-tolerant species typically grow smaller under higher salt stress levels.

2.5 | Community prediction

We conducted community-level predictions by aggregating species-specific results into two biodiversity indices: geometric-mean biomass and richness. The geometric-mean biomass, capturing trends in both biomass and evenness, was utilised to represent community-level biomass (Santini et al., 2017). The binary component in the species distribution model estimated species occurrence probability and shared the same covariates as the amount component. Species richness predictions were generated using probabilistic stacking, which involves summing the mean probabilities (Dubuis et al., 2011).

2.6 | Model scenarios

To represent the initial profiles of foreshore and transitional polder, we used for simplicity a slope with elevation increasing with distance from the sea versus a flat with constant elevation, respectively. Grain size distribution for foreshore and transitional polder was generated by two linear regression models developed from data in high- and low-hydrodynamic areas, respectively.

We incorporate the impacts of SLR in our model, specifically using the scenario (1 m, absolute SLR in 100 years compared to 1995) developed by Delta Program (Haasnoot et al., 2018) at a constant SLR rate of 10 mm yr⁻¹ over 100 years. The scenario is based on the IPCC Fifth Assessment Report (AR5) and has been further customized at the local level by KNMI. We also simulated scenarios without SLR to explore the impacts of SLR.

Sediment availability effects were explored with three scenarios with varying SSC: low scenarios with SSC of 10 mg L⁻¹, median scenarios with 25 mg L⁻¹ and high scenarios with 50 mg L⁻¹, based on model settings from Willemsen et al. (2022).

TABLE 1 Model scenarios.

System	Suspended sediment concentration (mg L ⁻¹)	Sea-level rise rate (mm year ⁻¹)	Position within the tidal framework (m)
Seaward foreshore (slope, high hydrodynamic)	10	0	0
	25	10	
	50		
Landward transitional polder (flat, low hydrodynamic)	10	0	-1
	25	10	0
	50		1

To further investigate the influence of the initial elevation of transitional polder, we design three scenarios with different initial elevations relative to sea level (-1 m, 0 m, 1 m), reflecting typical ranges of polder elevations in the Western Scheldt Estuary (van Belzen et al., 2021; Weisscher et al., 2022) (Table 1).

3 | RESULTS

3.1 | Comparison between seaward foreshore and landward transitional polder

Although species distribution patterns along environmental gradients were broadly similar between the seaward foreshore and landward transitional polder, there were notable differences in favouring benthos at lower elevations in the landward transitional polders. In both schemes, most macrozoobenthic species and geometric-mean biomass of the overall macrozoobenthic community showed a unimodal distribution in response to variations in inundation and grain size, with geometric-mean biomass peaking at an inundation ratio of approximately 0.5. Vegetation species generally increased in geometric-mean biomass with decreasing inundation time, except for *Salicornia europaea* and *Spartina anglica* (Figure 4).

In the seaward foreshore, vegetation caused the landward marsh to accrete slightly faster than the seaward tidal flats, forming a marsh plateau. As the elevation approached the mean high tide water line, accretion critically slowed due to reduced sediment supply from decreased inundation (Figure 5a). In the landward transitional polder, sediment accretion was more rapid on the landward side, resulting in a concave (i.e. hollow) tidal-flat profile. A marsh plateau also formed as the landward area reached the high tide water line (Figure 5b). The different morphology developments in the two NbS schemes led to distinct distributions of inundation time and grain size, with the sloped profile of the seaward foreshore causing more pronounced changes in inundation time and grain size compared to the flatter profile of the transitional polder (Figure 5c,d). Notably, the two NbS schemes also differ in aspects beyond slope, such as exposure to hydrodynamics, which is reflected in grain size.

Our model predicts that the transitional polder supported higher macrozoobenthic biodiversity than the foreshore. This is because the gentle topography of the transitional polder creates more stable environmental conditions conducive to greater macrozoobenthic biodiversity. In contrast, the foreshore scheme allows for earlier

vegetation establishment, unlike the transitional polder. As a result, marsh plateaus form more quickly at higher elevations near the seawall, providing additional space for vegetation to establish and thrive (Figure 5e-h). Predictions and their corresponding confidence intervals for each species are presented in the Appendix, providing a representation of the uncertainty in the model outputs (Figures S4 and S5).

Although species composition and biomass vary among salinity zones, our analysis showed consistent patterns in comparison with the two schemes across these zones (Figure S6). This lack of a significant salinity effect underlined the essential role of biodiversity in maintaining ecosystem functions, which remained relatively stable across different salinity zones. For that reason, we only showed predictions for the strongly polyhaline situation (Figure 5).

In the early development stage, the transitional polder demonstrated a notable advantage in fostering greater macrozoobenthic biodiversity (Figure 6) and providing wider habitats (Figure S10), while the foreshore supported slightly higher biodiversity of vegetation (Figure 6) and broader vegetated habitats (Figure S10). However, these differences diminished over time as the profiles converged due to accretion. As development progressed, this trend reversed: the foreshore gradually caught up with the transitional polder in terms of benthos biodiversity (Figure 6) and habitats (Figure S10), while the transitional polder, in turn, caught up with the foreshore in terms of vegetation (Figure 6). Hence, the early-stage differences between the schemes became less pronounced or reversed as development progressed. We also calculated species richness as a biodiversity index, and the patterns in comparison of the two schemes were similar to that of geometric-mean biomass (Figure S8).

3.2 | Impact of SLR, SSC and initial elevation

Higher SSC led to faster accretion and extension of vegetated area at the expense of benthos area (Figure S10). This accelerated both the increase in geometric-mean biomass of vegetation and the decrease in geometric-mean biomass of benthos (Figure 6). In contrast, SLR increased inundation time, limiting vegetation expansion and preserving more space for benthos (Figure S10). This slowed the decline in geometric-mean biomass of benthos, as well as the increase in vegetation in the late development stage (Figure 6). Thus, higher sediment availability reduced the differences between the two schemes during development due to faster accretion, while SLR

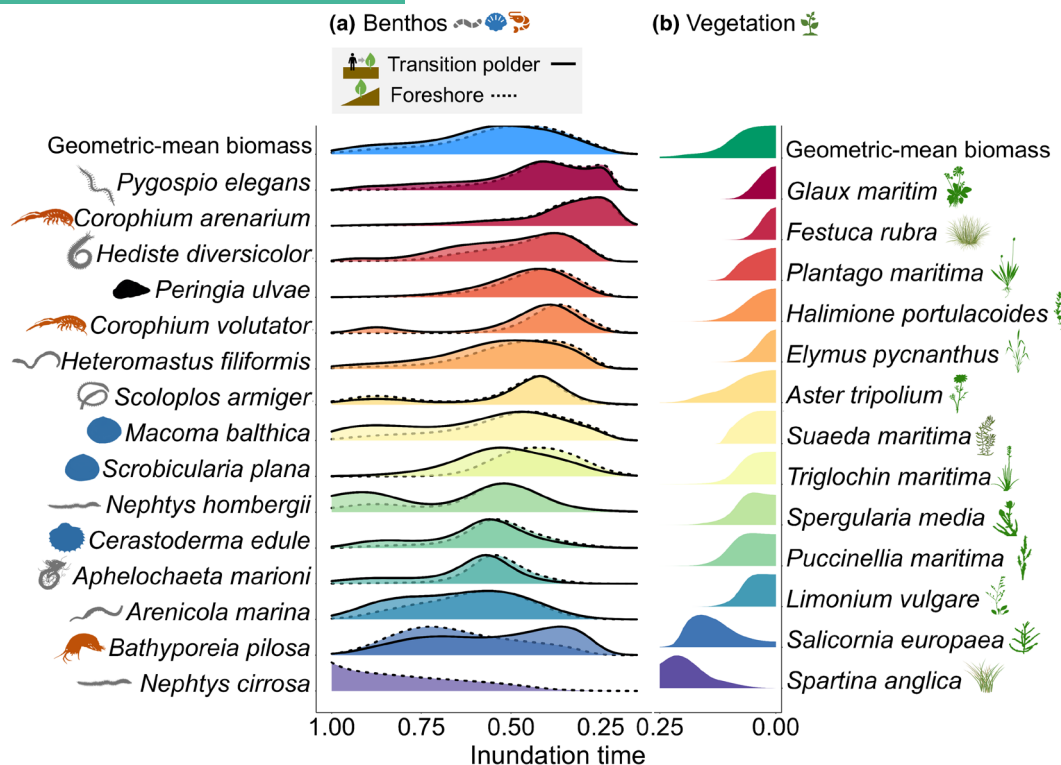


FIGURE 4 Species distribution along inundation gradients. Geometric-mean biomass and each species biomass along environmental gradient for (a) benthos and (b) vegetation. In (a), the foreshore is represented by dashed lines and the polders are represented by solid lines. Grain size is assumed to be linearly related to inundation time, which differs in foreshore and transitional polder. Since grain size is a predictor of benthos, this leads to different distribution patterns of benthos. Here distribution for strongly polyhaline are shown only. The colour of each species indicates the environmental location in gradient where its optimal ecological niches (maximal biomass) occur based on global prediction for all salinity zones (Figure S3). Blue (wet and low elevation) to red (dry and high elevation) represent the optimal ecological niches along the environmental gradient. Silhouettes for benthos and vegetation symbols are obtained from www.phylopic.org, <https://www.a-p-h-o-t-o.com/aphotomarine/> and <https://ian.umces.edu/media-library/>.

maintained the difference by slowing accretion relative to sea level. These effects were more pronounced on benthos than on vegetation (Figure 6). If transitional polders are at higher elevations (1 m), they would soon lose the initial advantage in benthos development compared to foreshore, but exhibited better vegetation development, especially under higher SSC (25 mg L^{-1} , 50 mg L^{-1}) or without SLR.

4 | DISCUSSION

Beyond their value for coastal protection (Temmerman et al., 2013; Temmerman & Kirwan, 2015), NbS provide a promising approach to mitigate the substantial biodiversity loss in estuarine and coastal ecosystems. Here we compared the biodiversity effects of two NbS schemes: seaward foreshore versus landward transitional polder. Initially, the foreshore promotes vegetation development, while the lower-elevation transitional polder favours benthos. However, with ongoing accretion, uprising transitional polders gradually become vegetation-dominated, losing their benefit to benthos. In contrast, foreshores due to their intrinsic gradient continue to provide benthic habitat between marsh vegetation and the water line, while

transitional polders often lack such intrinsic gradient. Nevertheless, our study suggests that the biodiversity effects converge over time due to accretion, making both solutions largely comparable in terms of long-term biodiversity outcomes. The choice of NbS is likely to be driven by environmental setting (Figure 1), as from a physical system perspective, seaward foreshore solutions are limited to specific locations, while landward transitional polders are applicable on a broader scale. As the biodiversity effects of both schemes are also strongly influenced by external drivers like SLR, sediment availability and initial elevation, locally adapted NbS schemes should carefully consider these factors through long-term modelling, using approaches like those introduced here.

4.1 | Temporal dynamics of scheme comparison on biodiversity

Our model results reveal that in the early stage, steep foreshore facilitates rapid vegetation establishment, while flat transitional polder exhibits advantages in benthos biodiversity. This aligns with research suggesting that profile shape may influence patterns of biodiversity (Fujii & Raffaelli, 2008). The differing trajectories of

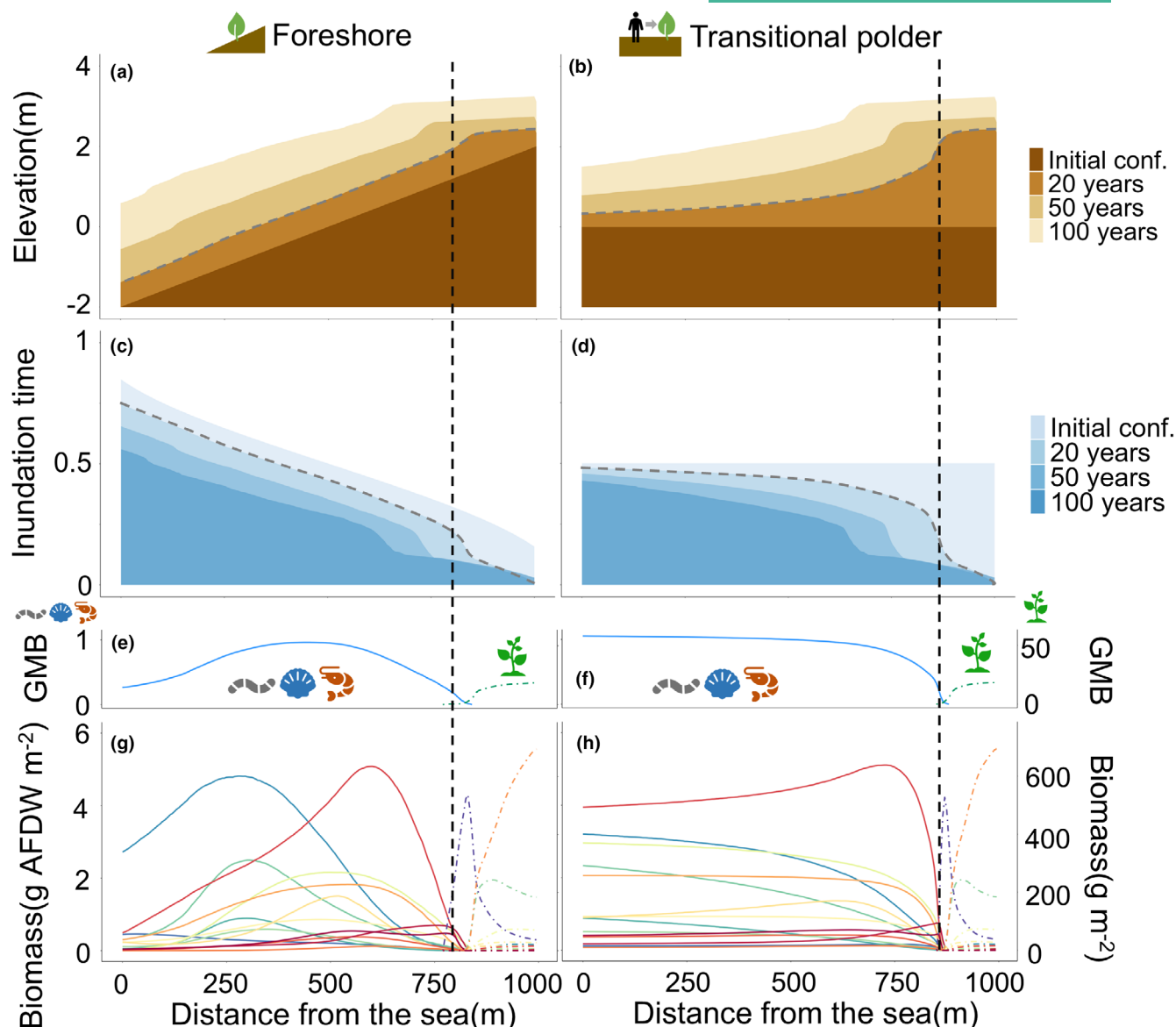


FIGURE 5 Comparison of seaward foreshore and landward transitional polder. This figure compares cross-shore distribution of elevation, inundation time, species biomass and geometric-mean biomass (GMB) between the seaward foreshore (panels a, c, e, g) and the landward transitional polder (panels b, d, f, h) under the median suspended sediment concentration (SSC) scenario ($SSC = 25 \text{ mg L}^{-1}$) with SLR rates of 10 mm yr^{-1} . Panels (a, b) show the evolution of elevation and (c, d) changes in inundation time over 100 years. The grey dash line in (a–d) marks the profile after 20 years, which corresponds to the panels (e–h). The geometric-mean biomass (e, f) and biomass of each species (g, h) along distance from sea after 20 years. The y-axis on the left is for benthos (solid lines), and the right one is for vegetation (dotted lines). The colour for each species is consistent with Figure 4. The black dash line is an approximate boundary between the benthos area and the vegetation area. Here, only results for strongly polyhaline are shown. Results for the other two salinity zones are provided in the Appendix (Figure S6).

biodiversity under the two schemes will result in varying preferences based on the specific goals. For biodiversity objectives, such as conservation of migratory shorebirds, maintaining bare tidal flats rich in benthos can be highly beneficial (Ysebaert et al., 2000), making transitional polder initially more advantageous. In contrast, vegetated marshes are most desirable from a flood-safety perspective (Bouma et al., 2014; Marin-Diaz et al., 2023; Morris et al., 2018), thus favouring vegetated foreshore. The prioritisation of different goals considerably influences the selection of NbS schemes, and it is

crucial to consider spatial and temporal nonlinearities in the delivery of various ecosystem functions (Barbier et al., 2008). For instance, effective flood mitigation can be achieved with relatively small marshes fringing a dike, as these are sufficient to stabilise the area and prevent dike breach growth (Zhu et al., 2020). However, from a long-term perspective, both options may ultimately converge in terms of biodiversity outcomes due to their comparable morphology relative to inundation time. This convergence influences decisions on scheme selection and duration, potentially shifting the focus of

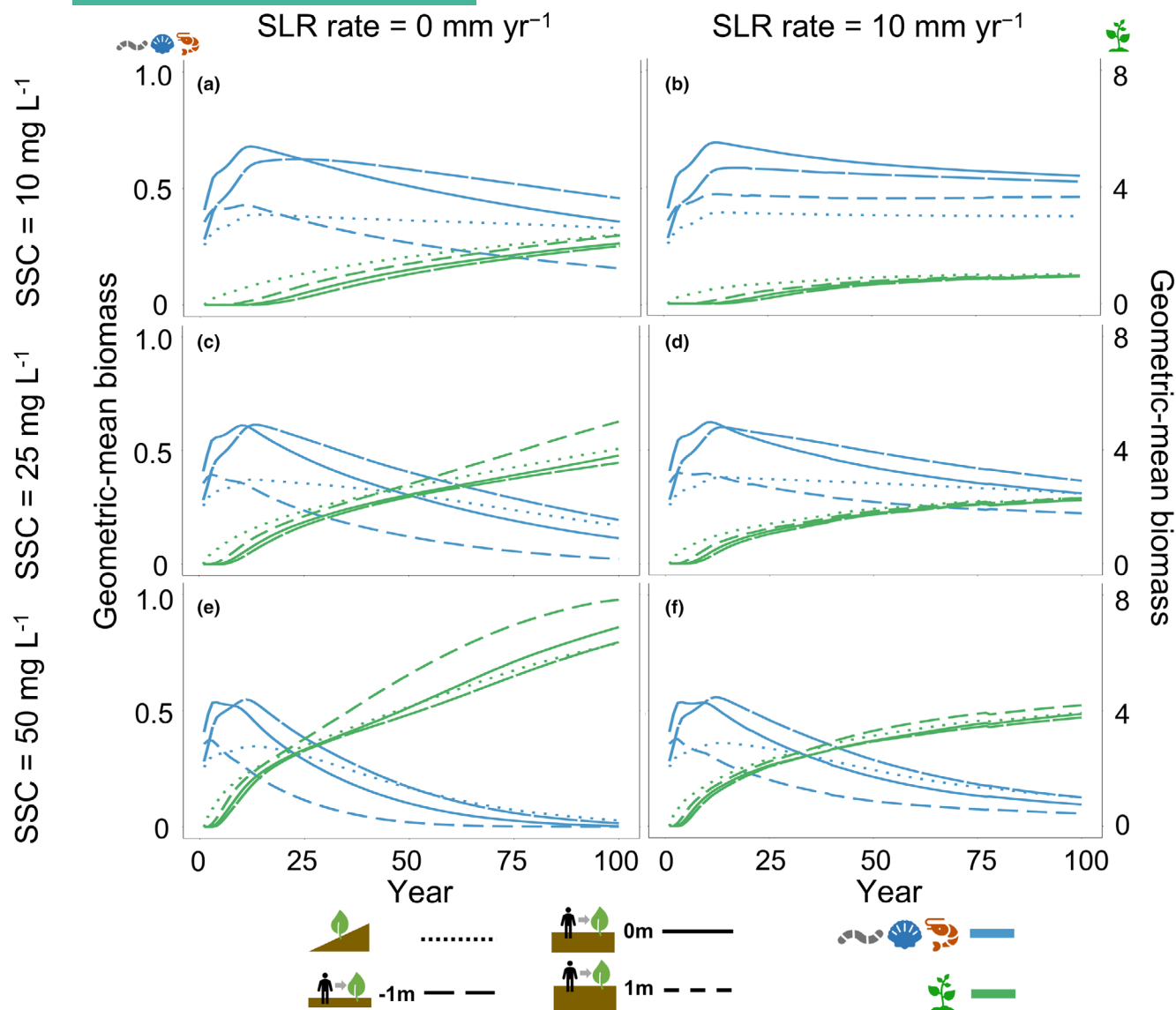


FIGURE 6 Comparison of seaward foreshore and landward transitional polder with different initial elevation on geometric-mean biomass. The seaward foreshore is represented by a dotted line, while landward transitional polder results are shown with solid lines for an initial elevation of 0m, dashed lines for an initial elevation of 1m, and long dashed lines for an initial elevation of -1m. The left column (panels a, c, e) and right column (panels b, d, f) present results for scenarios with sea level rise (SLR) rates of 0 mm yr⁻¹ and 10 mm yr⁻¹, respectively. The top (panels a, b), middle (panels c, d) and bottom (panels e, f) rows show results for scenarios with suspended sediment concentration (SSC) of 10, 25 and 50 mg L⁻¹, respectively. Blue lines indicate benthos, and green lines represent vegetation. This specific figure focuses on the strongly polyhaline zone of the Western Scheldt. Results for other salinity zones are provided in the [Appendix \(Figure S7\)](#).

decision-making to other factors, such as feasibility. It underscores the importance of considering the dynamic nature of ecosystems, which shapes biodiversity patterns and associated ecosystem services (Bouma et al., 2014; Rau et al., 2018).

4.2 | Balancing between habitat for benthos and marsh area

Benthos and vegetation often share habitats, with overlaps in suitable areas observed (Figure S10). Interactions between vegetation and benthos can further shape the distribution of both

groups (Van Wesenbeeck et al., 2007; Zhu et al., 2016). However, these interactions are not explicitly incorporated into our model, leading to uncertainty in predicting the boundaries between benthos and vegetation habitats. Despite this, our results indicate that most areas are spatially distinct (Figure S10), suggesting that the coexistence and interactions between vegetation and benthos are not prevalent across the majority of habitats. This highlights the need to carefully balance the expansion of marsh vegetation with the preservation of benthos habitats in the design and implementation of NbS. Typically, marsh development follows tidal-flat development as the elevation increases (Fivash et al., 2023), thereby enhancing flood protection. However, this

progression often reduces the area of low-lying tidal flats, compromising benthic biodiversity. Many NbS prioritise the establishment of marsh vegetation to enhance wave attenuation and minimise flooding risk (Macreadie et al., 2017; Morris et al., 2018) and stabilising dikes (Stoorvogel et al., 2025). Tidal flats with benthos, in contrast, have received much less attention when creating NbS (Solan et al., 2020). Despite contributing less to wave attenuation (Bouma et al., 2014; Marin-Diaz et al., 2023), these bare tidal flats are important for various reasons: (i) as foreshores ensuring stable width of vegetated zone (Bouma et al., 2016; Marin-Diaz et al., 2023); because a minimum tidal-flat width is needed for marshes to persist (Hu et al., 2021) (ii) as habitats that support a wide range of species serving as key trophic linkages in coastal ecosystems, including benthic algae and bacteria (Herman et al., 2000), macrozoobenthic communities, elasmobranchs (Leurs et al., 2023) and other flatfish species like plaice, sole and flounder (Van Der Veer et al., 2022), thereby attracting birds that utilise these areas as feeding grounds (Ysebaert et al., 2000) and (iii) a plethora of other essential estuarine biochemical processes (Rios-Yunes et al., 2023).

Prioritizing coastal protection may require intervention measures that accelerate marsh development, including thin-layer sediment placement, which promote elevation gain and wetland expansion (Croft et al., 2006), vegetation planting (Duarte et al., 2013) and actively creating windows of opportunity for vegetation establishment (van Belzen et al., 2022). Conversely, if biodiversity is prioritized, refraining from such interventions allows the natural evolution of tidal flats, extending the period during which benthos, fish and migratory shorebirds benefit from this habitat type. In this context, the initial advantages of transitional polders for benthic species offer a unique ecological development window. However, regardless of the priority, NbS designs must ultimately ensure long-term flood protection. Without this, the focus shifts from NbS for coastal protection towards ecosystem restoration.

4.3 | Effects of SLR, SSC and initial elevation

In regions with limited sediment availability, particularly under high SLR conditions, implementing seaward foreshore becomes increasingly challenging (Reed et al., 2018), making transitional polders principally better suited. Transitional polder can reduce tidal range and consequently mitigate flood risk exacerbated by SLR, even during storm surges (Weisscher et al., 2022). Additionally, low-elevation polders can form intertidal mudflats that support productive macrozoobenthic communities, providing food and shelter for wading birds and juvenile marine fish (Ysebaert et al., 2000). Polders at higher elevations may be less effective in supporting benthos development but favour vegetation growth. With sufficiently high sediment supply, both NbS schemes exhibit rapid accretion of wetlands, enhancing their resilience to SLR (Grandjean et al., 2024; Kirwan et al., 2010) and facilitating marsh vegetation (Gourgue

et al., 2022) which provides significant coastal protection benefits (Möller et al., 2014; Zhu et al., 2020). Consequently, schemes converge quickly in terms of biodiversity outcomes and ecosystem functions, leading to comparable benefits across different NbS schemes. Therefore, a comprehensive consideration of these factors, alongside biodiversity goals, is crucial for developing suitable NbS.

4.4 | Feasibility and prospects

In addition to assessing the benefits of these NbS approaches, it is essential to evaluate their feasibility. Human activities such as channel deepening for navigation and land reclamation have led many estuaries to become narrower and deeper (Doody, 2004; Van Maren et al., 2015), creating steep hydrodynamic gradients (Van Dijk et al., 2021). These conditions—characterized by deeper water levels and higher wave energy—are where marsh protection is most needed but also where marshes are least likely to develop spontaneously (Marin-Diaz et al., 2023). Establishing a foreshore in such environments requires substantial human intervention to manage sediment supply, control erosion and adjust hydrodynamics to facilitate marsh formation (Hu et al., 2021; Marin-Diaz et al., 2023; Mariotti & Fagherazzi, 2013). However, these interventions can be costly, and in some cases, marsh development remains unachievable despite considerable efforts. Additionally, shifting marshes seaward through foreshore development can alter tidal dynamics, potentially leading to upstream tidal amplification and increased flood risks for communities located further inland (Fivash et al., 2023; Weisscher et al., 2022).

Transitional polders offer a promising NbS and regenerative land-use alternative compared to foreshores (van Belzen et al., 2021; Weisscher et al., 2022; Zhu et al., 2020) but may face public resistance due to reduced agricultural land. However, coastal agriculture is increasingly challenged by subsidence and salinization, which degrade soil and crop productivity over time (Hoogland et al., 2012; Kirwan et al., 2024; Mondal et al., 2023). Restoring such lands as wetlands provides a sustainable alternative, offering benefits like sediment trapping, reduced salt intrusion (Tarolli et al., 2024), carbon sequestration, flood protection and biodiversity support (Barbier et al., 2011). As wetland elevations stabilize with SLR, the land can temporarily return to agriculture after salts are leached from the soil, though productivity again declines over time due to subsidence and salinization. This rotational strategy—alternating tidal wetlands with agriculture—links wetland development to the agricultural boom–bust cycle, addressing salinization while supporting ecosystems (Velilla et al., 2025). Scaling transitional polders across estuaries using spatial planning and phased tidal exposure can better align regional agricultural and ecological objectives but requires further study to optimize trade-offs and ensure social acceptance. While this model focuses on the Western Scheldt Estuary, its principles are broadly applicable and can inform NbS assessments in other regions, with site-specific data improving its relevance and sustainability.

5 | CONCLUSIONS

Vegetated marshes are crucial for Nature-based coastal flood protection, while tidal flats, rich in macrozoobenthic communities, hold high ecological value for migratory birds. Balancing a trade-off between enhancing coastal defence and conserving biodiversity requires balancing the area of both these habitats. The two NBS schemes—seaward foreshore and landward transitional polder—initially offer distinct benefits for biodiversity and ecosystem functions while converging over time. As the long-term biodiversity development is strongly influenced by SLR and SSC, these drivers may affect NbS selection and their objectives in the long term. The physical constraints of seaward foreshores and societal challenges related to land use for transitional polders necessitate careful consideration in determining the appropriate NbS for each location. Rotational strategies, applied both spatially and temporally, provide a promising approach to address this challenge. The present model provides a quantitative tool, offering ecological insights to optimize the design of future NbS, thereby aiding policymakers and conservation planners in achieving effective and sustainable coastal management.

AUTHOR CONTRIBUTIONS

Xuerong Wu, Tjeerd J. Bouma, Francesco Cozzoli and Jim van Belzen conceived the ideas and designed the methodology; Xuerong Wu and Jim van Belzen developed the simulation model and analysed the data; Xuerong Wu wrote the first draft manuscript, which was elaborated with help from Tjeerd J. Bouma, Francesco Cozzoli, Johan van de Koppel and Jim van Belzen. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the 4TU.Research Data Repository <https://doi.org/10.4121/fbcd9a70-92be-47aa-8c49-cb469188e9a2> (Wu et al., 2025).

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SUPPORTING INFORMATION

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

Figure S1. A conceptual illustration of rotational management in a transitional polder.

Figure S2. Linear regression between inundation time and grain size for foreshore and transitional polder.

Figure S3. Species distribution along inundation gradients based on global prediction for all salinity zones.

Figure S4. Posterior predictive distribution of cross-shore biomass for each species in the foreshore.

Figure S5. Posterior predictive distribution of cross-shore biomass for each species in the transitional polder.

Figure S6. Comparison of foreshore and transitional polder regarding cross-shore distribution of biomass under the median SSC scenario in three salinity zones.

Figure S7. Comparison of foreshore and transitional polder regarding temporal change in richness and geometric-mean biomass averaged over the entire profile in three salinity zones.

Figure S8. Comparison of seaward foreshore and landward transitional polder with different initial elevation on richness.

Figure S9. Comparison of scenarios without SLR and with SLR regarding cross-shore distribution of elevation, inundation time and biomass.

Figure S10. Comparison of foreshore and transitional polder regarding temporal change in the proportion of potential habitats for benthos and vegetation.

Table S1. Parameters of biomorphodynamic model.

Table S2. The parameters estimates of quadratic polynomial function describing the change in vegetation biomass with inundation ratio.

Table S3. Bayesian *p*-value of model of each species.

Table S4. WAIC-based model comparison for each benthos species.

Table S5. WAIC-based model comparison for each vegetation species.

Table S6. The mean-record longevity and intrinsic rate of increase for each benthos species.

Table S7. The initial biomass for each benthos species in logistic growth model.

Table S8. Parameters of calculating inundation frequency based on elevation.

Appendix S1. Detailed description of the study area.

Appendix S2. Detailed description of the environmental data collection.

Appendix S3. Detailed description of biomorphodynamic model.

Appendix S4. Detailed description of species distribution model.

Appendix S5. Detailed description of Logistic growth equation.

Appendix S6. The dependence of annual inundation frequency on elevation.

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