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Vegetation traits and biogeomorphic complexity shape the resilience of salt marshes to sea-level rise

Loreta Cornacchia [1,2] ✉, Roeland C. van de Vijsel [3], Daphne van der Wal [1,4], Tom Ysebaert[1,5,9], Jianwei Sun [6], Bram van Prooijen[6], Paul Lodewijk Maria de Vet [2,6], Quan-Xing Liu [7] & Johan van de Koppel [1,8]

The adaptive capacity of ecosystems, or their ability to function despite altered environmental conditions, is crucial for resilience to climate change. However, the role of landscape complexity or species traits on adaptive capacity remains unclear. Here, we combine field experiments and morphodynamic modelling to investigate how ecosystem complexity shapes the adaptive capacity of intertidal salt marshes. We focus on the importance of tidal channel network complexity for sediment accumulation, allowing vertical accretion to keep pace with sea-level rise. The model showed that landscape-scale ecosystem complexity, more than species traits, explained higher sediment accumulation rates, despite complexity arising from these traits. Landscape complexity, reflected in creek network morphology, also improved resilience to rising water levels. Comparing model outcomes with real-world tidal networks confirmed that flow concentration, sediment transport and deposition increase with drainage complexity. These findings emphasize that natural pattern development and persistence are crucial to preserve resilience to climate change.

Ecosystems are clear examples of complex systems. Here, higher-level patterns emerge from interactions among species rather than being imposed by external forces, a process called spatial self-organization[1,2]. At the individual level, organisms can improve their habitat, such as plants increasing water infiltration in deserts[3] and seagrass improving sediment stability and reducing hydrodynamic stress[4,5]. These processes can lead to the emergence of ecosystem-level complexity, in the form of large-scale patterns at multiple spatial scales, as in mussel beds and desert fairy circles[6,7]. Self-organized patterns have been found to improve ecosystem resilience, in terms of faster recovery after a disturbance[6–9].

Self-organization theory has helped understand the mechanisms behind the adaptive capacity of ecosystems, in terms of the ability to maintain their functions in the face of environmental change. Previous studies pointed to the importance of landscape-level complexity, as in the case of multi-scale self-organization increasing resilience in mussel beds[6]. Similarly, it has been found that even when not driven by a species, purely physical forms of self-organization, like soil cracking in coastal salt marshes, can amplify ecosystem resilience to droughts[10]. However, ecosystem adaptability can be shaped by the traits of individual species. A single species may directly affect how the ecosystem reacts to changing environmental conditions[11]. For example, in landscapes with Namibian fairy circles, the presence of termites, an ecosystem engineer, enhances resilience against climate perturbations[7]. Zardi et al.[12] highlighted how species-specific behaviors affect self-organization in mussel beds and modulate their resistance to wave stress. Thus, it remains unclear to what extent ecosystem adaptability is ultimately determined by system-level complexity, or directly by the traits of the dominant species. Here, we address this question by considering the emergence of creek network complexity in coastal salt marshes, that develop through biogeomorphic feedbacks with plant species, which can provide a unique opportunity to explore the drivers of ecosystem adaptability.

Salt marshes are a striking example of a complex adaptive system, where patterns both emerge from and influence local interactions between

[1]Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research, Yerseke, The Netherlands. [2]Marine and Coastal Systems, Deltares, Delft, The Netherlands. [3]Hydrology and Environmental Hydraulics Group, Wageningen University, Wageningen, The Netherlands. [4]Faculty of Geo-Information Science and Earth Observation, University of Twente, Enschede, The Netherlands. [5]Wageningen University & Research, Wageningen Marine Research, Yerseke, The Netherlands. [6]Delft University of Technology, Faculty of Civil Engineering and Geosciences, Delft, The Netherlands. [7]School of Mathematical Sciences, Shanghai Jiao Tong University, Shanghai, 200240, China. [8]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands. [9]Deceased: Tom Ysebaert: June 2023. Initiated the project, contributed to the conception and design of the work, and critically revised the manuscript. ✉e-mail: loreta.cornacchia@deltares.nl

organisms and their environment. Salt marsh vegetation can have both a direct, local-scale effect of promoting sediment accretion to compensate for sea-level rise (SLR), and an indirect, landscape-scale effect by affecting channel network complexity. Certain vegetation traits such as height, stiffness, and density, play a direct role for ecosystem adaptability by increasing vegetation roughness. This attenuates wave energy, decreases tidal flow, and lowers bed shear stress, leading to reduced erosion rates[13–16]. Such conditions promote the sedimentation of suspended particles[17,18], increasing surface elevation. This creates a positive feedback to plant growth[9], because of the reduced inundation time. However, the adaptability of salt marshes is also influenced by tidal channels. Their geometry largely governs water and sediment supply into the marsh, with clear implications for adaptability to SLR[19]. Proximity to the creeks affects sediment deposition rates, with areas closer to creek banks experiencing higher deposition[20,21]. During higher tides, enhanced flow velocities in creeks also increase resuspension within the creek and sediment supply to the marsh surface[21]. Plant morphological and life-history traits can increase creek complexity by altering flow, erosion and sedimentation patterns around vegetation patches[22–24]. Vegetation patterns and channel complexity are strongly related, and tend to occupy two alternative stable biogeomorphic states, with either complex vegetation-and-channel configurations or simple vegetation-and-channel configurations[25]. Marshes with complex configurations exhibit sinuous, highly branched creeks and substantial vegetation patchiness, whereas simple configurations display relatively straight channels (or meandering channels with little branching) and more uniform vegetation patterns. While vegetation can enhance sedimentation both through local trapping and by affecting tidal channel complexity, the balance and relative importance of these processes for the adaptive capacity of salt marshes is unclear.

In this study we investigate how the emergence of creek network complexity during the initial stages of salt marsh development is influenced by different vegetation traits, how this interplay affects the ability of marsh ecosystems to accumulate sediment and, on the long term, their resilience to increased water levels. While the role of creek geometry on sediment transport and the impacts of sea-level rise have been studied in one-dimensional settings[26] and unvegetated tidal basins[27], the effect of the two-dimensional development of creek networks on sediment transport, and thereby marsh resilience, have remained understudied, and so are the effects of different vegetation species[28]. Our study aims to fill this gap by investigating how creek complexity and vegetation traits—with both their direct and indirect effects—interact to influence sediment accumulation and marsh resilience. This knowledge is also important for wetland restoration, indicating whether efforts should focus on promoting fast vegetation growth, or on ensuring the formation of complex creek networks within dense marsh platforms, to enhance salt marsh resilience. We focus on the following two aspects identified in the literature: a trait-based and a complexity approach, their relative importance and potential interactions. A trait-based approach suggests that specific plant traits (such as height and friction) have a direct effect on marsh accretion by locally enhancing sedimentation, rather than by influencing creek development. In this view, plant traits are considered the dominant contributors to marsh resilience. The complexity approach instead suggests that plant traits have an indirect effect on the ecosystem's adaptive capacity by influencing the complexity of the creek network. This network complexity, a system-level characteristic, promotes sediment transport and deposition in the marsh, thereby playing a dominant role in marsh resilience.

We use a numerical model of salt marsh development to separate the direct effects of plant traits on sediment deposition from their indirect effects of influencing creek structure. We then use field data from simple (parallel) and complex (highly branched) creek systems to support the model insights that flow concentration, sediment transport and deposition increase with drainage pattern complexity. Lastly, we evaluate the long-term resilience of simple and complex creek networks (emerging from different initial plants traits) by investigating critical rates of water level increase as a function of sediment availability, at which salt marshes can keep a constant elevation.

Results

Creek complexity promotes vertical accretion during salt marsh development

To gain insight into the relationship between channel network complexity and salt marsh accretion, we measured vertical accretion rates on the intertidal bar of Walsoorden (Western Scheldt estuary, The Netherlands). This site experienced recent salt marsh establishment and a rapid increase in creek network complexity, in constrast to an adjacent area that remained relatively unchanged in complexity (Fig. 1). Through remote sensing observations (see details in "Methods" section), we found that the area where creek complexity increased, as it transitioned from bare mudflat to salt marsh vegetation, accreted faster than the unvegetated area where complexity remained almost constant (both areas were initially at a comparable elevation). Along the vegetated transect T3, the area had a mean accretion rate of 2.3 cm year^{-1} between 2006 and 2017, compared to 0.3 cm year^{-1} in the unvegetated transect T1. During the transition to a salt marsh, the area directly around the creeks accreted at a much higher rate than the areas far from creeks, resulting in the formation of levees (Fig. 1). There, creek depth, length and branching order sharply increased since the start of vegetation colonization. In comparison, the unvegetated area showed only limited changes in creek network structure and had a relatively low and constant elevation at all distances from the creeks (within the margin of error of the DTM data), up to and including 2017. Thus, vegetation establishment co-occurred with strong vertical accretion and with an increase in creek complexity, as the area transitioned from a mudflat to a salt marsh. The observed differences in the development of the two sites could be linked to the local effect of vegetation on sedimentation, leading to higher accretion rates and more complex creek network development in the vegetated area.

Plant traits steer creek formation, and creek structure alters sediment transport and deposition

To disentangle the direct impact of vegetation traits on marsh accretion from their indirect influence on creek landscape formation, we used a modeling approach with contrasting vegetation types. The model couples the dynamics of water flow, vegetation and morphology to describe channel network formation in salt marshes, and extends upon the one described in van de Vijsel et al.[29]. This study adds a sediment transport component to explore how the interplay of vegetation traits and creek complexity affects sediment transport, defining the salt marsh response to changes in water levels and sediment supply. Because of explicitly describing sediment transport, the model can provide a better understanding of marsh resilience. The model is fully explained in the "Methods" section and in the Supplementary Methods.

Model analyses using multiple combinations of vegetation traits revealed that the balance between vegetation aboveground and belowground effects shapes creek network geometries, which in turn strongly affect sediment transport (Supplementary Fig. 1). We illustrate this using two very contrasting combinations of vegetation traits to emphasize the importance of aboveground versus belowground effects (explained further in the "Methods" section). Specifically, we compare vegetation with high aboveground roughness but weaker effects on belowground sediment stabilization (the latter being representative of pioneer species with sparse root systems, such as *Salicornia* spp.), and vegetation with lower aboveground roughness but stronger belowground effects (typical of species with flexible stems but dense root systems, for instance *Puccinellia* spp.). Model simulations of these two contrasting plant types revealed that vegetation with higher roughness but weak belowground effects leads to the formation of many wide, first order creeks developing parallel to each other (Fig. 2). In contrast, vegetation with lower roughness but strong belowground effects has a highly branched structure, up to fifth Hack's order creeks. Strikingly, the higher network complexity results in faster sediment accretion and a higher slope of the landscape (Fig. 2A, D; Supplementary Fig. 1). This indicates that plant species traits have a strong influence on the development of creek network complexity, with belowground effects being the most

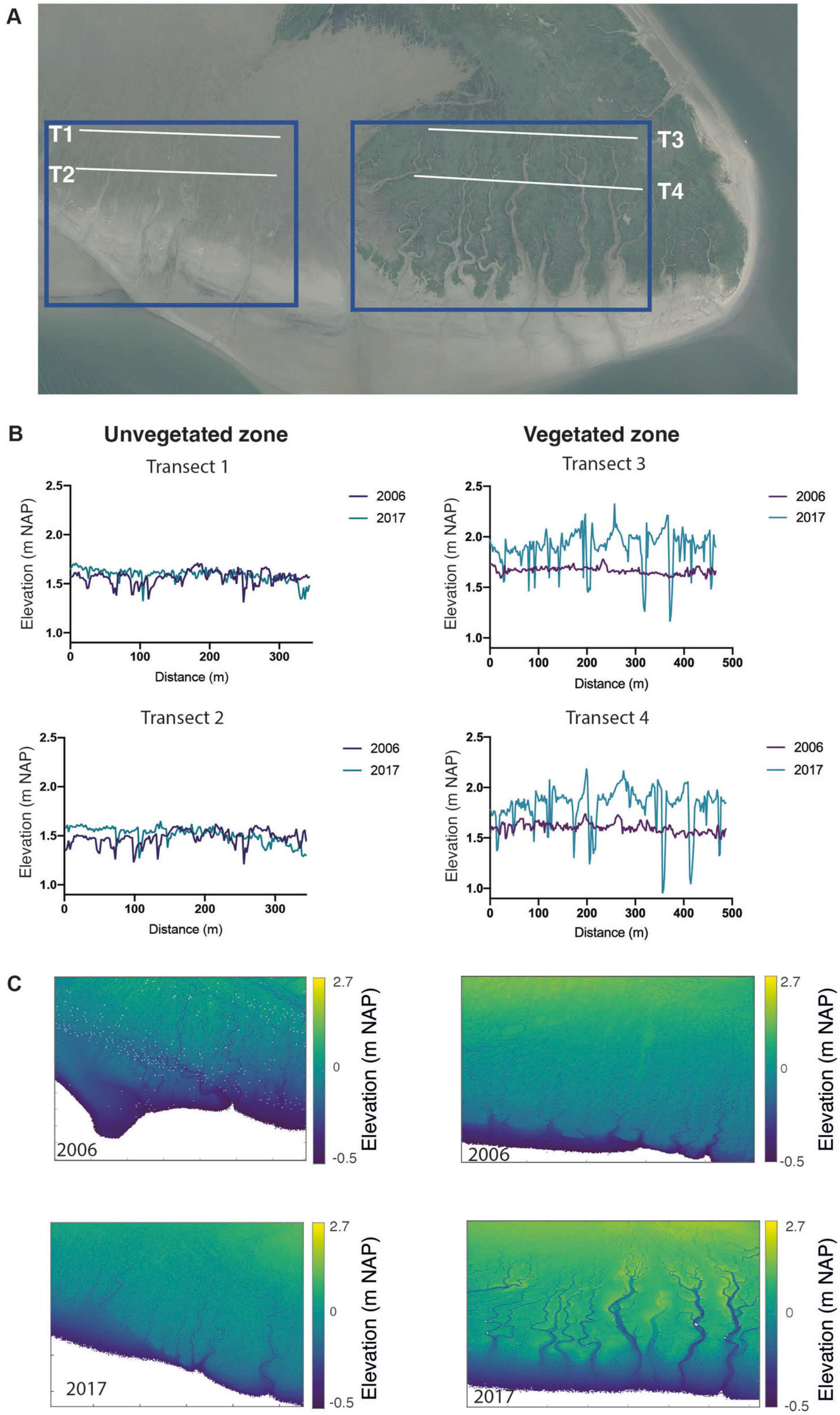

Fig. 1 | Temporal analysis on the intertidal bar of Walsoorden (Western Scheldt Estuary) from 2006 to 2017. A Location of transects in 2017, with green salt marsh vegetation. Aerial image dating from May 2017 and adapted from Google Earth Pro, © 2024 Google LLC. **B** Four horizontal transects taken across the DTM, derived from LIDAR. Two transects were in the unvegetated zone (T1, T2) and two in the vegetated zone (T3, T4). **C** DTM in 2006 and 2017; in the 'vegetated zone' that transitioned from a bare tidal flat to a salt marsh, the area directly around the creeks increased in elevation at a much higher rate than the areas far from creeks, leading to levee formation and increasing creek branching and complexity. In contrast, the 'unvegetated zone' showed minor changes in creek network structure and had a relatively low, constant elevation at all distances from the creeks. The DTMs are provided by Rijkswaterstaat and openly accessible under CC0 1.0 Universal license.

important in driving differences in creek formation, flow speeds and sediment transport.

Our results reveal that creek structure has a strong impact on salt marsh adaptability, by strongly affecting sediment transport and deposition, exceeding the direct effects of single plant traits (Fig. 3). To investigate the effect of creek complexity on sediment transport and deposition, we started with the final bathymetry obtained from simulations with each of the vegetation types and we used constant plant traits in both the 'low complexity' and 'high complexity' creek networks, while keeping the bed level unchanged. Our results show that, under the same plant characteristics, higher creek complexity leads to larger sediment transport distance (Fig. 2C, F; Supplementary Fig. 2) and a three-fold higher sediment retention in the marsh (Fig. 3). Sediment retention and transport are higher in complex creeks because flow concentration is stronger (as illustrated by the

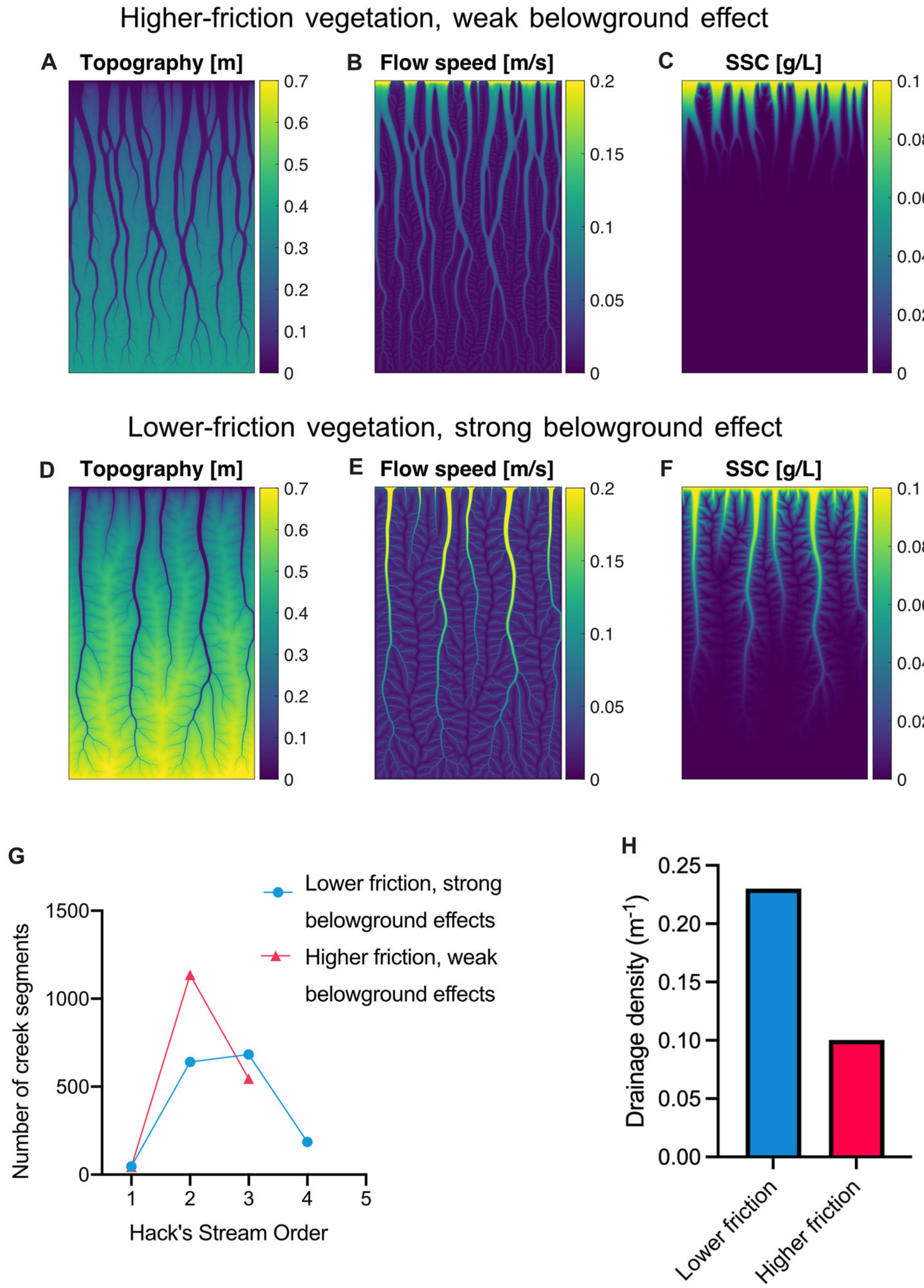

Fig. 2 | The influence of vegetation traits on creek network formation. Top view of the simulated channel network topography (m), flow speeds (m/s) and suspended sediment concentration (SSC, g/L) for vegetation with higher aboveground friction but weak belowground effects (**A**–**C**) and lower aboveground friction but strong belowground effects (**D**–**F**). The simulated dimensions are 100 by 150 m. A full overview of the combinations of aboveground and belowground effects is provided in Supplementary Fig. 1. The bottom plot (**G**) shows the difference in drainage complexity in terms of creek branching (n. of segments per Hack's stream order, where the main channel is given an order of 1 and the terminal channels have the highest order) between the two networks. The drainage density is 0.23 m^{-1} in the lower-friction simulation and 0.10 m^{-1} in the higher-friction simulation (**H**).

creek averaged flow velocities in Supplementary Fig. 1), and any point in the marsh is closer to a creek due to the higher drainage density and number of branches (i.e., the mean unchanneled path length is lower). In contrast, sediment deposition is comparable in simulations where plant traits were exchanged, but keeping the same creek systems. These findings demonstrate that ecosystem adaptability is determined by the spatial complexity emerging from local interactions between organisms and their environment, rather than simply being a direct effect of species traits.

Further model analyses revealed the counterintuitive result that higher aboveground roughness does not necessarily increase sediment deposition. Vegetation height and plant drag both shape vegetation roughness which reduced sediment deposition, while vegetation-induced erosion protection increased sedimentation (Fig. 4; Supplementary Fig. 2). A dense vegetation with high roughness leads to a strong sediment retention at the marsh front, preventing it from being transported further inland, whereas vegetation with an intermediate roughness fosters more complex channel networks and higher sedimentation next to the channels (Supplementary Figs. 1, 2). This further emphasizes the importance of the creek network in transporting sediment throughout the marsh.

The model provides several estimates of the emergent effects of complexity on salt marsh functioning. It shows that sediment deposition rates, flow concentration and suspended sediment transport in the creeks increase with channel network complexity (Fig. 5A, D, G). To validate this insight, we measured hydrodynamics and sedimentation processes in two field sites (Baarland and Hoofdplaat, located in the Western Scheldt estuary) that both comprise a zone with simple creeks and a zone with complex branched creeks (Supplementary Fig. 3), where Baarland represents simple and complex branched creeks at similar elevation, called ‘equally elevated’ sites, and Hoofdplaat represents a characteristic marsh where the complex, old network is at higher elevation than the simple, young one, called ‘differently elevated’ sites (see the “Methods” section for details on the site selection). This comparison aims to capture the qualitative trends (rather than exact numerical outputs) and assess the qualitative alignment between simulations and field observations. Our model is a simplified representation of the

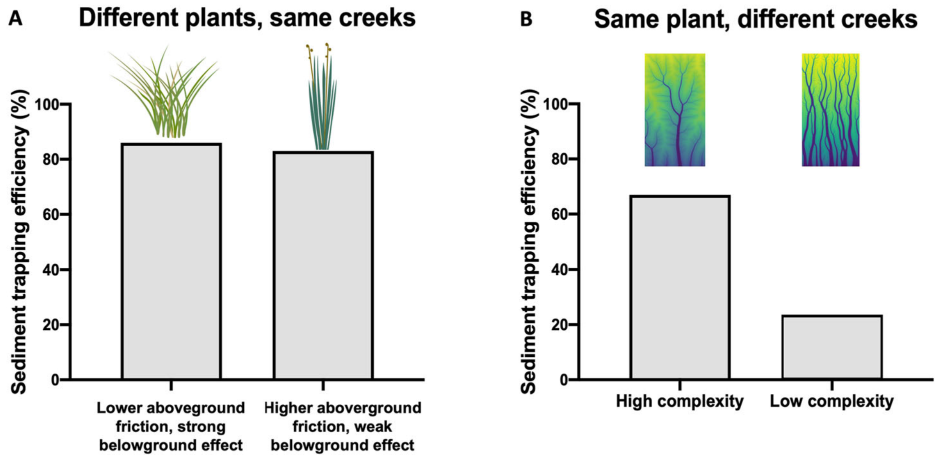

Fig. 3 | Disentangling the effect of vegetation traits and channel network complexity on sediment deposition. Differences in sediment trapping efficiency (total sediment deposited on the marsh platform divided by total sediment input in percentage) between model simulation with vegetation traits representing either higher friction but weak belowground effects, or lower friction but strong belowground effects, in the same given creek network (**A**), and in simulations with the same vegetation traits placed in either a branched (high complexity) or parallel (low complexity) creek network (**B**). Note that on the right graph, 'same plant' refers to average properties of the two vegetation types, leading to lower sediment trapping efficiency compared to the left graph.

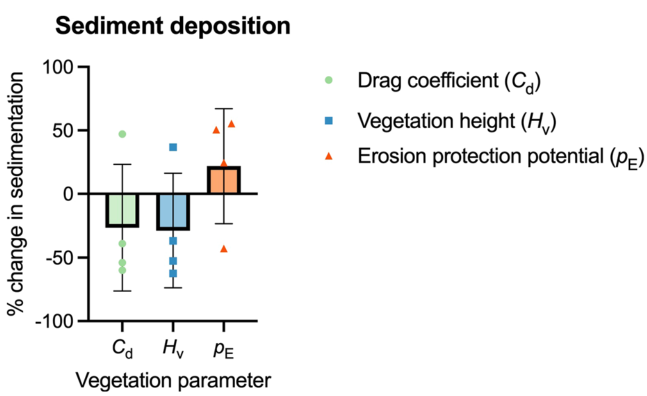

Fig. 4 | The impact of different vegetation traits on the deposition of transported sediment, represented as percentage change in sedimentation when each vegetation parameter is increased. The traits include drag coefficient (C_d), vegetation height (H_v), and erosion protection potential (p_E). Error bars indicate standard deviation. The data points indicate each model simulation; the interactive effects of simultaneous changes in multiple parameters are shown in Supplementary Fig. 1.

complex processes involved in salt marsh development. Its purpose is not to provide precise predictions, but rather to improve understanding.

Effects of creek complexity on early-development ecosystems

In the 'equally elevated' sites, we found support for all three model insights. First, sedimentation rate (g/m^2/tide) is significantly higher in the location with complex creeks, compared to the young marsh with simple creek patterns (two-way ANOVA, $F_{1,33} = 9.04$, $p < 0.01$) (Fig. 5B). Second, flow velocities in the creeks (defined as the absolute peaks in flood and ebb velocities), were significantly higher in second-order complex creeks than in simple creeks ($t_{827} = -2.01$, $p < 0.05$), but not in the first-order (main) creeks ($t_{328} = -1.09$, $p = 0.3$) (Fig. 5E). Finally, suspended sediment concentration (g/L), based on continuous in situ measurements (Supplementary Figs. 4–11), also increased in complex creeks compared to simple ones, both in the main channels ($t_{1175} = 15.95$, $p < 0.001$) and in the side channels ($t_{7789} = 10.07$, $p < 0.001$) (Fig. 5H).

Effects of creek complexity on developed ecosystems

In the 'differently elevated' sites, the differences in elevation and inundation time largely confounded the effect of complexity; nonetheless, the prediction of higher flow concentration in complex creeks was supported. First, sedimentation rates were higher in the simple creek system than in the complex one (two-way ANOVA, $F_{1,43} = 41.94$, $p < 0.001$) (Fig. 5C). This was expected because the simple, young marsh was much lower in elevation. Second, flow velocities were significantly higher in both first- and second-order complex creeks, compared to simple creeks ($t_{4576} = 7.4$, $p < 0.001$; $t_{168} = 3.5$, $p < 0.001$) (Fig. 5F). Finally, suspended sediment concentration (g/L) also increased in complex creeks compared to simple ones, both in the main channels ($t_{1277} = 3.75$, $p < 0.001$) and in the side channels ($t_{8655} = 3.01$, $p < 0.01$) (Fig. 5I). Thus, although the complex network is located at higher elevation (thereby receiving a smaller water in- and out-flow), the absolute flow velocities in these creeks are higher than in the lower-elevated simple creek network. Overall, despite the confounding factors, these results show the emergent effects of complexity on salt marsh functioning, in terms of increasing flow velocities and sediment concentrations in the creeks.

Biogeomorphic complexity promotes resilience to increased water levels

To test the resilience of simple and complex creeks to different rates of increase in water levels, we ran simulations from the beginning of salt marsh development, starting with each vegetation type (high aboveground roughness but weak belowground effects, or lower roughness but strong belowground effects). We refer to the terms inundation period and water level increase interchangeably. We found that simple marshes are more impacted by increasing water level rates than complex ones. Simulations with lower vegetation roughness but strong belowground effects reach higher mean elevations across all water level increase rates (Fig. 6d–f), while the salt marsh with higher roughness but weak belowground effects retreats substantially with moderate to rapid water level increases (Fig. 6a–c). Hence, complex creeks, driven by lower-friction vegetation with strong belowground effects, show greater adaptability to higher water levels.

Further analyses highlighted that the ratio between inundation and sediment supply is a crucial determinant for maintaining a constant marsh elevation. This ratio, or slope, indicates the amount of sediment needed to retain marsh elevation for a given water level increase, and thus reflects marsh resilience. A steeper slope means greater resilience, as less sediment input is needed for a given inundation to maintain the same elevation (Fig. 7; Supplementary Fig. 12; see "Methods" section for details). We found that marsh resilience increases by 65% across all cases where the vegetation-induced erosion resistance is higher. However, resilience decreases with higher vegetation roughness: taller vegetation reduces resilience by 27%, and similarly an increase in the drag coefficient reduces it by 8% on average. The findings suggest that taller, denser vegetation with higher roughness is not necessarily beneficial for the adaptive capacity of the salt marsh.

Furthermore, our findings show that faster water level increases reduce salt marsh accretion for both vegetation types (Fig. 6g). The highest final marsh elevation is seen in the reference simulation with constant water level, followed by simulations with moderate and rapid water level increases. This implies that the increase in sediment input (due to the higher water input) is not sufficient to compensate for the higher erosion rates (also driven by

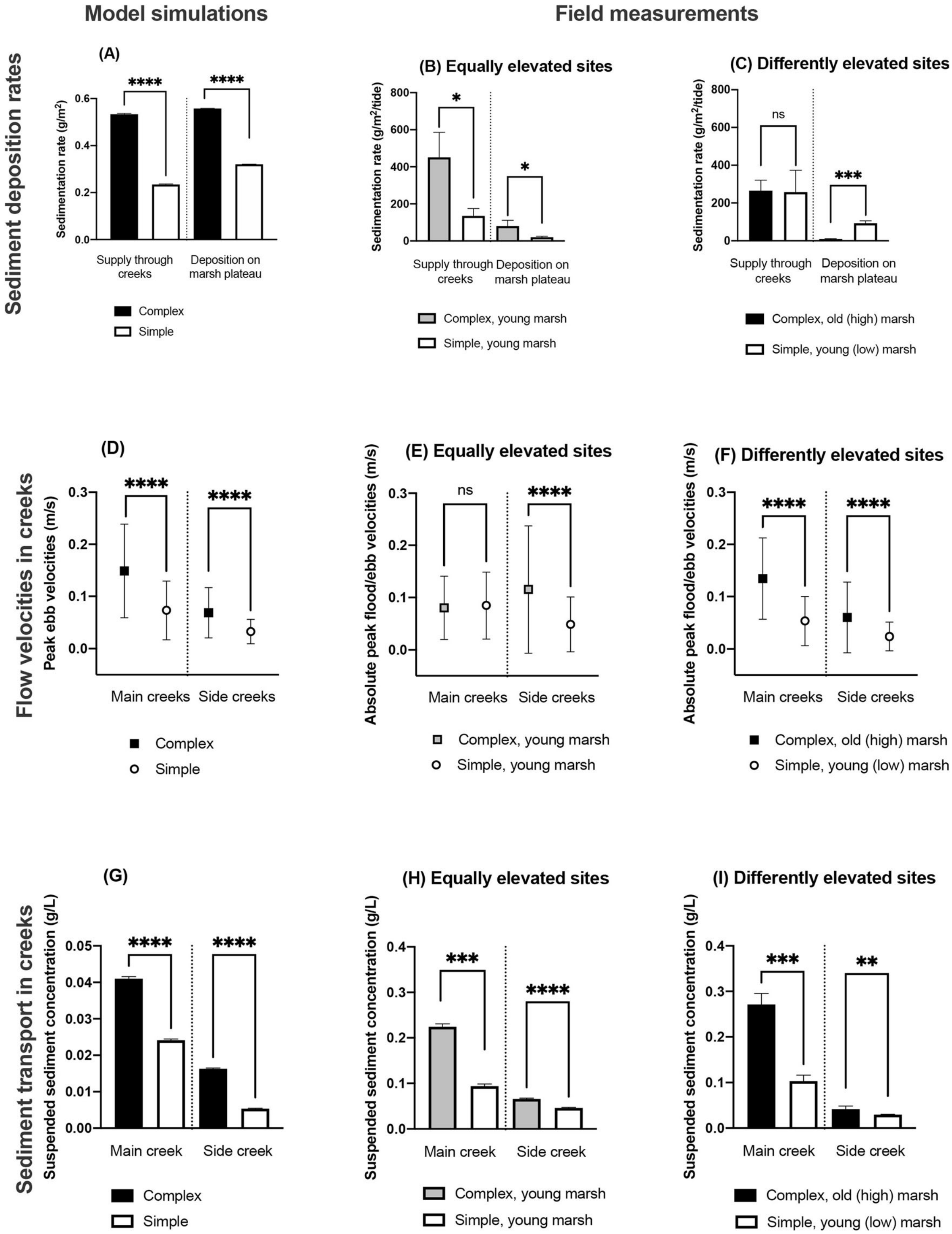

Fig. 5 | Comparison between model predictions and field measurements of sedimentation rates, flow velocities and sediment transport in simple and complex creek systems. **A**–**C** Sedimentation rates are higher in complex creeks. Model predictions and field measurements of sediment deposition rates (g/m^2/tide) supplied through the creeks and deposited on the marsh plateau, in simple creek networks (young marshes) and complex creek networks (in either young or old marshes) in the two study sites (Supplementary Fig. 3). Error bars indicate standard error of the mean. **D**–**F** Flow concentration is higher in complex creeks. Absolute values of peak flood and ebb velocities (mean ± SD, in m/s) between first- and second-order creeks in complex and simple creek networks in the model simulations, 'equally elevated' sites (Baarland), and 'differently elevated' sites (Hoofdplaat). **G**–**I** Sediment transport is higher in complex creeks. Differences in sediment transport (suspended sediment concentration in g/L in the creeks) between first- and second-order creeks in complex and simple creek networks, in the model simulations, 'equally elevated' sites (Baarland), 'differently elevated' sites (Hoofdplaat). Error bars indicate mean ± standard error of the mean. Non-significant differences ($p > 0.05$) are indicated with 'ns'.

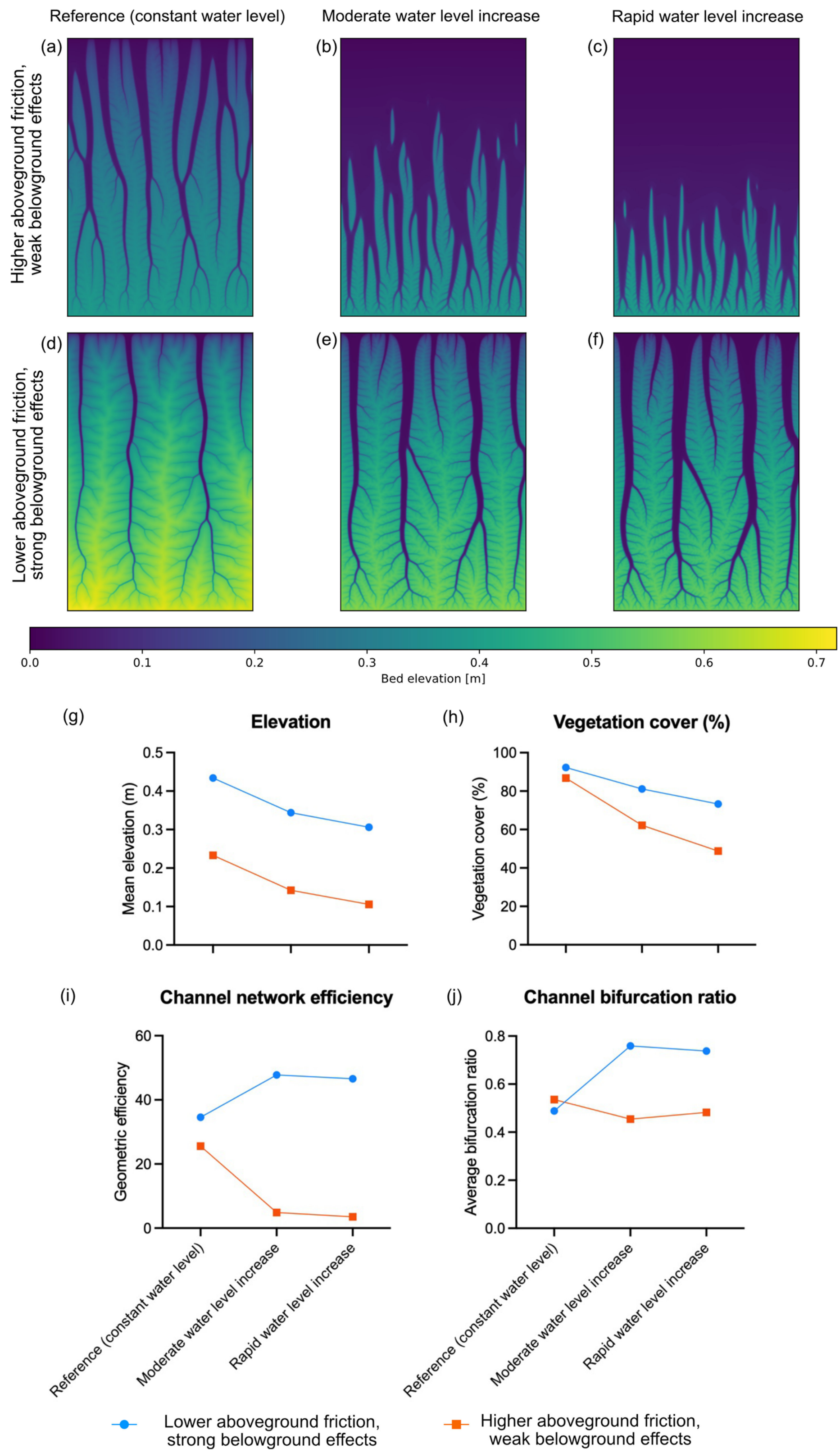

Fig. 6 | Salt marsh development and channel network morphology under increasing water levels and varying vegetation traits. Top view of the simulated channel network topography (m), for higher-friction vegetation but weak belowground effects (**a**–**c**) and lower-friction vegetation but strong belowground effects (**d**–**f**) for reference simulations and for two simulations with moderate and rapid water level increase. Results show the network after 21 years of development. The simulated dimensions are 100 by 150 m. **g**, **h** Mean elevation and vegetation cover at the end of the simulations under reference, moderate and rapid water level increase for each vegetation type. **i**–**j** Measures of channel network complexity (geometric efficiency and average bifurcation ratio) under reference, moderate and rapid water level increase.

increased water input and flow speeds), resulting in net erosion in our model. Additionally, inundation rates are simulated through an increased water input, meaning that more water accumulates in the domain. This results in an expansion of the channeled area in both vegetation models, and a further decrease in the domain-averaged vegetation cover and mean elevation. Both vegetation types show a decrease in vegetation cover with increased inundation rates, with the high-roughness vegetation but weak belowground effects showing larger differences between the two cases (Fig. 6h).

We further analyzed the impact of the rates of inundation increase on tidal network efficiency and the degree of channel branching, being indicators of improved water drainage and sediment supply through the channels, and thereby relating to salt marsh functioning and resilience. The

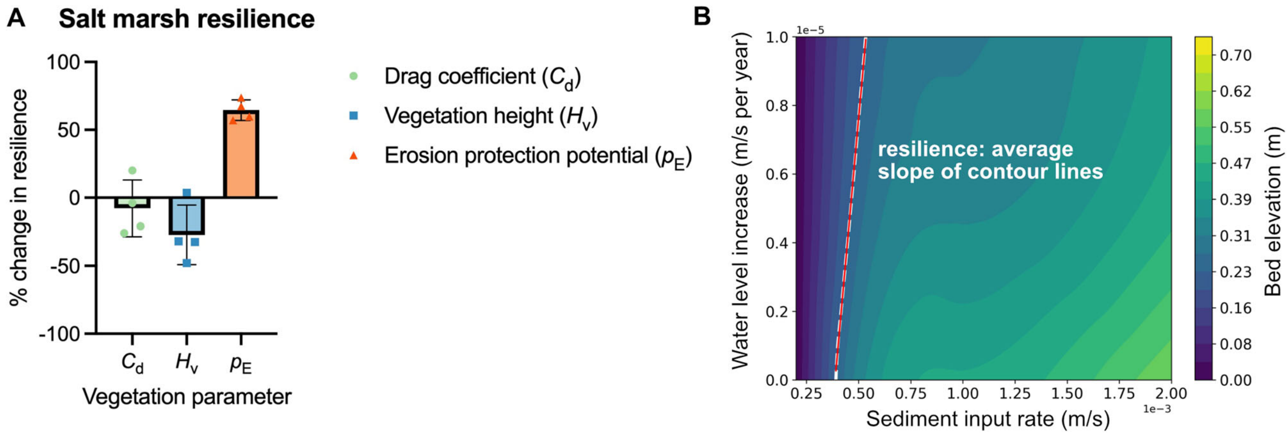

Fig. 7 | The impact of different vegetation traits on salt marsh resilience. **A** Percentage change in the average slope of water level increase over sediment input (H_{in} / S_{in}) when each vegetation parameter is increased. The slope H_{in} / S_{in} indicates the amount of sediment input needed to retain marsh elevation for a given water level increase, and thus reflects marsh resilience. The vegetation parameters include drag coefficient (C_d), vegetation height (H_v), and erosion protection potential (p_E). Error bars indicate standard deviation. The data points indicate the percent change in each model simulation; the interactive effects of simultaneous changes in multiple parameters are shown in Supplementary Fig. 12. **B** Example contour plot of final salt marsh elevation (m) in simulations with different annual rates of increase in water level and decreasing sediment input rates. Bed elevation corresponds to the final sediment layer thickness starting from a flat, horizontal bed. Salt marsh resilience was determined by averaging the slopes along the elevation contour lines (including only non-zero values). The dashed white line shows the contour whose slope matches the average slope of all contour lines most closely, and the red line shows the linear regression fit to that contour.

effect of inundation rates on channel network organization differs across the two modeled vegetation types. With lower-roughness vegetation and strong belowground effects, geometric efficiency increases, meaning that water travels a shorter distance to reach a channel, and the channel network drains the marsh platform more efficiently (Fig. 6i). However, geometric efficiency decreases for high-roughness vegetation but weak belowground effects (Fig. 6i). These changes are reflected in the observed branching patterns. For lower-roughness vegetation but strong belowground effects, the average bifurcation ratio increased (Fig. 6j). This indicates that there are more fine-scaled, higher-order channels branching off from each larger, lower-order channel. We expect that this improves ecosystem resilience, as networks with a higher number of channel branches are expected to be more resilient to perturbations[30]. In contrast, the bifurcation ratio decreased for the high-roughness vegetation. Overall, the results point to a higher adaptive capacity of complex creek systems when compared to simple ones, in terms of greater channel network efficiency and resilience in response to increased inundation.

Discussion

There is growing interest in understanding how ecosystems can adapt to altered environmental conditions imposed by the changing global climate. In our study, we have found that vegetation traits determine landscape complexity which, in turn, is the relatively larger contributor to the ecosystem's adaptive capacity. In tidal marshes, we found that while different vegetation traits have similar direct effects on local sediment deposition, their largest impact is indirect, through the creation of creek networks of different complexity. Once a certain creek network has formed through plant-flow interactions, its planform geometry determines the distance that sediment travels into the marsh and the amount of sediment deposited. Field data from different salt marshes supported these predictions, showing that flow velocities and sediment transport in creeks, and deposition on the surrounding marsh platform, are higher in complex networks compared to simple ones. Vegetation traits associated with lower vegetation roughness but higher erosion protection potential, leading to complex creek systems, showed greater adaptability to increased water levels and reduced sediment supply, due to changes in channel network organization towards geometries that have higher drainage efficiency. Our findings emphasize the importance of spatial complexity in improving resilience to future conditions.

Our study contributes to a better understanding of how species effects and system-level complexity interact to determine an ecosystem's adaptive capacity. The channel patterns we observed are nested within one another, forming multi-scale regular patterns[29]. We found that higher pattern complexity was linked to increased ecosystem resilience, consistent with findings on multi-scale self-organization in mussel beds[6] and arid systems[7]. Similar bio-physical feedbacks increase the adaptive capacity of vegetated rivers, where interactions between plant growth and water flow redistribution create spatial patchiness that can buffer freshwater ecosystems against changes in discharge[31]. These findings emphasize the importance of spatial patterns, patches, and other forms of spatial complexity in creating climate resilience[32]. Several other ecosystems, like coral reefs or mangroves, rely on maintaining surface elevation to adjust to rising sea level and persist under climate change[33,34]. Investigating both direct biological influences and their indirect, emergent effects can help identify the drivers of resilience in other ecosystems.

Tidal marshes can be considered ideal systems to investigate how the interplay between species traits and system-level complexity contributes to ecological resilience. This is linked to the dual role of vegetation traits, exerting a direct, local-scale effect on sediment accretion, and an indirect, landscape-scale effect by influencing channel formation. The coupling between the two processes leads to biogeomorphic complexity, which, in turn, enhances the adaptive capacity of the salt marsh. Belowground traits were more important than aboveground friction in determining the development of complex creek patterns, confirming the role of root systems in decreasing topographic diffusion and strengthening biogeomorphic feedbacks[29]. Similarly, Schwarz et al.[35] indicated that vegetation traits reflecting a high capability for lateral expansion through root systems are more important for landscape development than stem height or density, supporting our results. Moreover, we found that under taller, denser vegetation (higher vegetation height and plant drag), most of the sediment is trapped in front of the marsh, reducing the amount being delivered to the inner area. Geng et al.[36] observed a similar effect, suggesting that higher vegetation density may not per se be favorable for the marsh as a whole. Indeed, our simulations showed that marsh resilience was generally higher with stronger belowground effects and low to intermediate vegetation roughness. Nonetheless, although variations in single species traits can affect resilience, it is their coupling with biogeomorphic complexity that ultimately shapes the salt marsh and its resilience.

Our findings support previous work pointing to the existence of alternative, stable biogeomorphic states of either complex channel and vegetation configurations *or* simple channel and vegetation configurations[25]. The complexity of creek networks, which arises from interactions between vegetation traits and geomorphology, appears to increase sediment deposition and transport rates in two main ways. First, we found that a highly branched network reduces the mean unchanneled path length, ensuring that sediment can reach a larger portion of the marsh. This effect is further amplified in vegetated creek networks, compared to unvegetated ones[37]. Second, side creeks in a highly branched network become narrower as their branching order increases. Although channels naturally narrow landward due to reduced water discharge, vegetation enhances flow confinement. This flow confinement allows flow velocities and suspended sediment concentrations in the channels to remain higher than if creeks maintained the same width across all orders (high-order creeks would be relatively overdimensioned). This finding is consistent with previous work showing that vegetation-induced channel confinement leads to stronger flow concentration within the channel and between the vegetation patches, resulting in higher flow speeds and therefore increased sediment transport[23,38]. Our field measurements, showing higher flow velocities and sediment concentrations in more complex creeks, align with conventional theories. This supports the broader applicability of the findings from our field sites towards a more general understanding of marsh resilience in various settings and conditions.

While our modeling study is meant to provide broadly applicable insights, the processes and trends identified should be evaluated across a wider range of salt marsh sites and settings. In salt marshes with other plant communities, we can expect vegetation to have a different impact on sedimentation, which may influence the balance between direct and indirect vegetation effects. Also, organogenic salt marshes such as those found in North America, which are dominated by organic material derived from salt marsh vegetation, may be less dependent on sediment supply from tidal creeks. Moreover, the effect of creek network morphology on storm-driven sediment transport, a major sediment transport pathway[39], should be considered. However, despite of expected variability, our findings provide a basis for further detailed field and modeling studies to investigate these processes.

Our findings indicate that in more complex systems, both drainage and flooding of the marsh platform tend to be more efficient, accompanied by more uniform sedimentation across the marsh, compared to simple systems (Fig. 5A). In more complex systems, the creek network is also longer, which leads to more extensive areas for deposition since sedimentation primarily occurs directly next to the channels (Supplementary Fig. 1). However, as salt marshes evolve and increase in elevation, they get inundated less often[9,19,40,41]. The overall gross sediment supply is therefore higher at lower marsh elevations (Fig. 5B). In addition to sediment supply, these results suggest that the interaction between vegetation traits and channel complexity can be highly important for wetlands to be more resilient to increased rates of sea-level rise, to enhance storm surge attenuation (as predicted by previous model results[29]), and to dissipate perturbations through their high number of channel branches[30].

Our study contributes to the growing body of literature on the role of spatial self-organization in determining ecosystem resilience[8,10], countering or preventing tipping points and irreversible transitions[32,42,43]. The insights from our study on disentangling the direct and indirect effects of vegetation are relevant for designing marsh restoration projects. Most projects still focus on achieving the optimal growth conditions for vegetation and its faster development into a dense marsh platform, rather than allowing enough time to develop the optimal channel configuration to allow drainage and sediment transport, which are crucial factors for long-term marsh resilience. Hence, it is crucial not only to facilitate vegetation growth, but also to allow sufficient time for this vegetation to develop an extensive network. These findings also further emphasize the importance of well-designed artificial creek networks in wetland restoration projects to maximize sediment import, encouraging fast vertical accretion and potentially vegetation establishment. In restoration of salt marshes[44] or mangroves[45], oversized tidal channels tend to silt up over time. A more appropriate creek geometry would involve narrowing creeks as they extend further inland into the marsh. Similarly, side creeks should progressively narrow compared to the main, first-order creeks. Hence, the development of a complex creek network, with smaller creeks nested within larger ones, can increase the rate at which marshes accumulate sediment. Conserving the natural patterns in ecosystems, and allowing them to develop naturally, is crucial to preserve and optimize the adaptive capacity of ecosystems to climate change.

Methods

Field site selection

We studied three salt marshes in the Western Scheldt Estuary, the Netherlands: Walsoorden (51.3780° N, 4.0827° E), Baarland (51.3948° N, 3.8792° E) and Hoofdplaat (51.3740° N, 3.6662° E). These sites experienced recent salt marsh establishment and creek formation. At Walsoorden, our aim was to test whether an increase in creek complexity was accompanied by faster vertical accretion, relative to an adjacent area that remained relatively unchanged in complexity. Complexity is defined here as the extent of channel network development, in terms of channel lengthening and branching at increasingly smaller scales. At Baarland and Hoofdplaat, we compared flow velocities, sediment transport, and deposition in simple, parallel creeks and complex, branched creeks, with other environmental conditions remaining consistent. The field sites were selected for the presence of creek networks with different levels of complexity and in close proximity with each other, to minimize the differences in other environmental conditions (e.g., tidal range, sediment availability). The salt marsh at Walsoorden is mainly colonized by *Spartina anglica*, while Baarland is dominated by *Salicornia procumbens*, *Suaeda maritima*, *Spartina anglica* and *Puccinellia maritima*. In Hoofdplaat, the most common vegetation species include *Spartina anglica*, *Suaeda maritima*, *Elymus athericus*, and *Salicornia procumbens*. The Scheldt estuary has high sea-level rise rates of 6 mm/year on average[46,47], due to natural and human factors[48], but the marshes are keeping up with sedimentation[46].

Quantification of sediment deposition patterns from Digital Terrain Models

We used Digital Terrain Models (DTM) generated from airborne LiDAR data by Rijkswaterstaat (https://rijkswaterstaatdata.nl/) to quantify sediment accretion patterns in both a vegetated and unvegetated area in Walsoorden, from April 2006, February 2012, and April 2017 (before the start of the plant growing season, to minimize the potential error in marsh surface estimation from LiDAR data). The DTMs have a vertical accuracy of 0.1 m (as reported in the metadata). This site is an initially uncolonized intertidal bar with an area that transitioned from a tidal flat to a salt marsh over the course of 5 years (starting around 2010), and an area that remained unvegetated. Two transects were selected in the unvegetated area and two in the vegetated area (Fig. 1), to calculate the elevation difference between the DTMs from 2006 and 2017. The elevation difference was averaged per transect to obtain their accretion rate in cm/year. To ensure that the DTM elevations reflected the bottom topography, especially beneath the vegetation, we used RTK GPS data collected by Rijkswaterstaat in 2005 and 2017 (with vertical accuracy of 2 cm) for validation. These data showed good agreement with the DTM elevations in both vegetated and bare areas (see details in Supplementary Fig. 13).

Comparison of simulated flow and sediment deposition patterns with field experiments

A field campaign was carried out in 2020 to measure flow velocities, sediment transport and deposition in creeks at different spatial scales (i.e., channel orders) and in sites with different creek complexity. The two field sites (Hoofdplaat and Baarland) presented a zone with parallel creeks (simple, young marsh) and a zone with complex branched creeks in both a young and an old marsh. In Baarland (hereafter referred to as the 'equally elevated' sites), the two zones were similarly elevated (2.28 ± 0.20 m in the complex, young marsh, 2.24 ± 0.16 m in the simple, young marsh). In

Hoofdplaat (hereafter referred to as the 'differently elevated' sites), the elevation of the complex, old marsh was 2.14 ± 0.41 m and that of the simple, young marsh was 1.68 ± 0.26 m. Although this elevation difference was not intended in the experimental design, creek complexity tends to increase with marsh age (time since vegetation establishment) and older marshes are higher elevated[22,25,35,49,50], and thus shows the difficulty of finding simple and complex creek networks of comparable age.

For each zone, we placed a set of instruments in two locations (Supplementary Fig. 3): (1) at the entrance of a main creek (first-order, following Hack's stream order) into the marsh, and (2) in the second-order side creek. Aquadopp HR ADCPs (Acoustic Doppler Current Profilers) were placed in locations B1, B3, H1 (corresponding to the creek entrances of three of the sites) to measure velocity profiles with 2 cm vertical resolution and with a sampling rate of 1 Hz, a burst interval of 10 min and 60 samples per burst. In the other locations (B2, B4, H2, H3, H4), Vector ADVs (Acoustic Doppler Velocimeter) were used to measure flow velocities with a sampling rate of 8 Hz, a burst interval of 10 min and 2400 samples per burst. Additionally, in each location, we measured the water level every 5 min using HOBO U20L Water Level Loggers and the suspended sediment concentration every 10 min with an OBS (Optical Backscatter Sensor) C3 Submersible Fluorometer (Turner Designs). The OBS was calibrated with water samples collected in the field. In the 'differently elevated' sites, the measurements were carried out for one month between June and July 2020 simultaneously at both locations (complex, old marsh and simple, young marsh). As not enough instruments were available to measure at the same time during the campaign in the 'equally elevated' sites, the measurements were carried out over two separate spring-neap tidal cycles (~15 days) between August – September in the complex, young marsh, and September – October in the simple, young marsh.

To estimate sediment deposition patterns at different spatial scales, we used circular plastic sediment traps (24 cm diameter) that were placed inside the creeks (distance: 0 m) and along transects at different distances from them (2 m, 15 m, and up to 30 m in the absence of other creeks in the surrounding), and at different distances from the marsh edge (0–140 m, at 20 m intervals). Each trap was attached to the marsh surface using tent pegs and its location was recorded with a DGPS Trimble ($n = 30$ traps in both the developing and mature marsh in the 'differently elevated' sites; $n = 33$ in the developing and $n = 30$ in the mature marsh in the 'equally elevated' sites; Supplementary Fig. 3). The sediment traps were retrieved after two tidal cycles to measure short-term sedimentation during spring tide. We carried out the experiment twice, for replication, in both locations for each field site (24–25 June and 22–23 July 2020 in 'differently elevated' sites; 04–05 August and 17–18 September 2020 in 'equally elevated' sites). In the laboratory, sediment plates were dried for 48 h in the freeze dryer, sieved at 1 mm to remove macroscopic plant material and/or shells, and weighed to determine the deposition rate of suspended sediment in g m^{-2}. To correct for differences in salt content in the sediment samples, salinity was estimated on subsamples of 0.5 grams of sediment using a refractometer.

Mathematical model of salt marsh development

We used a numerical model to investigate how the emergence of complex creek networks during early salt marsh development affects the ability of marsh ecosystems to accumulate sediment, thereby compensating for sea-level rise. While field observations provided insights into the relation between vegetation development, creek complexity and marsh accretion, we opted for a modeling approach to isolate and examine co-varying factors. This method allowed us to disentangle the direct effects of vegetation traits from their influence on the development of creek complexity. The model has idealized sediment transport and tidal dynamics, reducing the complexity of salt marsh dynamics compared to more physically realistic biogeomorphic models[35,36,51,52]. However, it has the advantage of being computationally less costly, allowing for simulations at a sufficiently high spatial resolution to capture the nested spatial patterns of highly branched channel networks.

The model couples the dynamics of water flow, vegetation and morphology to describe channel network formation in salt marshes, and extends upon the one described in van de Vijsel et al.[29,53]. In this model, the hydrodynamic component simulates the dynamics of water depth (h) and depth-averaged flow velocities (u, v); the morphodynamic component calculates the bed elevation (z) and the vegetation component is used to calculate changes in plant biomass (B). Compared to the original model (which included only local sedimentation, erosion and soil diffusion as morphodynamic processes), in this study we added a sediment transport component to be able to investigate the effects of creek network complexity on sediment transport. Aside from the inclusion of an additional process in the model, the novelty of our study resides, to the best of our knowledge, in using the model to explore the relation between creek complexity and vegetation traits, disentangling their direct and indirect effects. Moreover, the model is used to investigate the salt marsh response to varying rates of water level increase and sediment supply, processes which had not been considered in the original model, thereby providing insights on the impact of vegetation traits and creek complexity on marsh resilience. A complete description of the model components and equations is provided in the Supplementary Materials. Some parameter values have been changed or added compared to the default model[29] and are indicated in Supplementary Table 1. The code and data used in this study are publicly available online[54,55].

In the original model, the morphology evolves as function of local sedimentation, erosion and slope-driven sediment transport. The latter is topographic deformation or topographic diffusion, also known as slumping or soil creep[56]. This process has a smoothing effect on topographic relief. This form of sediment transport is related to the bed slope and inversely related to sediment cohesion, either abiotically or biotically (e.g., root binding[29]). However, the original model did not include the advective transport of sediment onto the marsh. For this paper, the model was extended to simulate sediment fluxes towards the marsh, since our aim was to describe how sediment transport and deposition onto the marsh platform are affected by creek network geometry and vegetation characteristics. Such an extension cannot simply be based on the sediment mass balance equation directly, as we only model the ebb flow period in this model approach. We built a sediment transport model based on an advection diffusion equation. The horizontal sediment fluxes in the model are represented by an advection and a diffusion term. In reality, the net advection flux during a tidal cycle is a complex non-linear interaction between time varying water depth, flow velocity and sediment concentration. Such a simulation would require simulation on short time scales. In our simulation, where the flow is defined as an ebb flow only, we use an advection velocity that is opposite of the continuous ebb-flow velocity to mimic the sediment flux. Flood flow is generally bringing in more sediment than the ebb flow exports, implying an import of sediment, justifying the advection velocity opposite of the ebb flow. The scaling with the ebb velocity is based on the observations that ebb and flood currents are correlated (Supplementary Fig. 14) and that sediment fluxes are generally higher for higher flow velocities. These relationships are consistent with relationships and observations previously described in the literature[57,58]. This expression results in import of sediment, scaling with the local flow velocity. In addition to the advection term, a diffusion term with a constant and uniform diffusion coefficient is applied. Finally, we added a term to denote the settling and erosion of transported sediment (assuming that higher flow speeds lead to more erosion and thereby less sediment is accreted at higher velocities). The distribution of sediment is then described by the following advection-diffusion equation:

$$\frac{\partial c}{\partial t} - u\frac{\partial c}{\partial x} - v\frac{\partial c}{\partial y} - D\left(\frac{\partial^2 c}{\partial x^2} + \frac{\partial^2 c}{\partial y^2}\right) = -\frac{1}{T_{\text{dep}}}\left(\frac{U_{\text{ss}}}{U_{\text{ss}} + \left(\sqrt{u^2 + v^2}\right)}\right)c \quad (1)$$

Here, c is the concentration of the transported sediment (g/L), $u\frac{\partial c}{\partial x}$ and $v\frac{\partial c}{\partial y}$ describe advective sediment transport, $\frac{1}{T_{dep}}\left(\frac{U_{ss}}{U_{ss}+(\sqrt{u^2+v^2})}\right)c$ represents the reduction of suspended sediment concentration due to deposition and $D\left(\frac{\partial^2 c}{\partial x^2}+\frac{\partial^2 c}{\partial y^2}\right)$ is the diffusion term. T_{dep} represents the deposition time scale of transported sediment (in seconds), i.e. a characteristic time scale over which sediment deposition occurs. U_{ss} (m/s) is the settling velocity of the transported sediment, or the speed at which sediment falls through the water. To ensure that sedimentation is reduced at higher flow velocities, sediment concentration c is multiplied by the term $\left(\frac{U_{ss}}{U_{ss}+(\sqrt{u^2+v^2})}\right)$. This ratio decreases as the net flow speed $\left(\sqrt{u^2+v^2}\right)$ increases, implying that sedimentation rate decreases with higher flow velocities. This flow speed-dependent sedimentation implicitly represents the effect of flow on erosion: higher flow velocities enhance the water's capacity to transport sediment, thereby reducing the rate at which sediment can deposit. This advection diffusion equation is not coupled to the morphological component of the model. The deposited material (right-hand-side of the equation) does therefore not induce a morphological update in the model: we aim to quantify and isolate the effect of creek geometry on sediment transport before including the effect on morphology. At the outflow boundary, there is a continuous source of SSC (0.1 g/L). Bed elevation in the model evolves assuming a spatially homogeneous sediment supply as in the original model version (Eq. 8, Supplementary Methods).

Model scenarios

To test the effect of different vegetation traits on creek landscape formation and sedimentation, we modeled different vegetation types with contrasting effects on above-ground friction and below-ground sediment stabilization. Different physical plant properties were modeled by adapting plant height H_v, drag coefficient C_d, and two parameters describing the potential of vegetation to reduce slope-driven sediment transport (with its root network) p_D, and the potential to reduce erosion p_E (see the Supplementary Methods for details on model parameters). We initially tested multiple combinations of vegetation traits to determine which were most influential for creek network development and sediment transport (Supplementary Fig. 1). A vegetation type with high aboveground roughness but weaker belowground effects ($H_v = 0.3$ m, $C_d = 12$, $p_D = 0.3$, $p_E = 0.3$), was compared to vegetation with 59% lower aboveground roughness, but strong belowground effects ($H_v = 0.5$ m, $C_d = 2$, $p_D = 1.0$, $p_E = 0.9$). Roughness was calculated as the Chezy coefficient resulting from the combined effects of H_v and C_d (Supplementary Methods, Eq. 6). The simulations were run for 21 years, after which no further changes in the domain-averaged plant biomass, sediment level and flow velocities were observed. At the end of the simulation, the final bathymetry and the total amount of suspended sediment retained within the marsh platform (sediment deposited, as calculated from the term $\frac{1}{T_{dep}}\left(\frac{U_{ss}}{U_{ss}+(\sqrt{u^2+v^2})}\right)c$ in Eq. 1, divided by total SSC input from the outflow boundary) were recorded to quantify the effect of vegetation traits on sediment deposition and channel network geometry.

Further, to disentangle the effect of physical plant properties and creek complexity on sediment deposition at the marsh platform, a set of simulations was conducted where the same bathymetry was kept (i.e., a fixed creek system) while varying the physical plant properties. Here, we tested the effect of creek network geometry on sediment transport, by comparing creek systems with varying degrees of complexity, while using the same physical plant properties (i.e., average parameter values of the two vegetation types).

We investigated the long-term resilience of simple and complex creek networks to water level increase rates, by increasing the water input H_{in} over 21 years for different combinations of vegetation parameters. Given the idealized nature of our model, these simulations are used to explore qualitative trends rather than realistic scenarios. Our model setup allows us to manipulate the water input rate (H_{in}), which reflects the mean water column that drains away over a tidal period. An increase in this parameter thus qualitatively relates to both inundation period and tidal range (see details in Supplementary Materials). While SLR directly results in longer inundation periods, it does not necessarily lead to increased tidal range[59], due to a non-linear and spatially variable relationship[60]. By manipulating H_{in}, we thus simulate the effect of increased inundation stress experienced by the tidal marsh, without distinguishing between the exact underlying processes (increase in mean sea level and/or tidal range). The rates of increase in H_{in} were chosen to qualitatively investigate the system's response to varying conditions, providing insights into trends without aligning with realistic SLR projections.

We used two hypothetical cases with different rates of increase in water input. In case 1 (moderate water level increase), H_{in} increased from $3.0\cdot10^{-5}$ m/s to $1.35\cdot10^{-4}$ m/s over 21 simulation years, with an annual increase of $0.5\cdot10^{-5}$ m/s. In case 2 (rapid water level increase), H_{in} increased from $3.0\cdot10^{-5}$ m/s to $2.4\cdot10^{-4}$ m/s over 21 simulation years, with an annual increase of $1.0\cdot10^{-5}$ m/s. To evaluate the effects of increased water input rate on resilience and salt marsh productivity, we compare the temporal changes in mean elevation and vegetation cover over the simulated domain. We chose a 21-year simulation period to have a balance between a sufficiently long time to reach a morphodynamic equilibrium, and to observe the effects of increasing H_{in} on salt marsh development. Additionally, this duration allows for faster computations and hence higher spatial resolution. Our model was not designed to handle very high water depths, which can result in higher flow speeds and potentially violate numerical stability criteria like the Courant–Friedrichs–Lewy condition. By selecting a relatively short simulation period, we ensured stable simulations that are still long enough to capture the effects of an increase in inundation and tidal range.

Additional simulations were carried out to quantify marsh resilience, by testing how different rates of water level increase and sediment supply affected salt marsh elevation, along with different combinations of vegetation characteristics. This allowed us to identify a critical ratio between sediment supply and water input rates, which is a measure of the marsh's sensitivity to increased water levels. We tested three rates of water level increase H_{in} (0 m/s, $0.5\cdot10^{-5}$ m/s and $1.0\cdot10^{-5}$ m/s per year), and four rates of sediment supply S_{in} (0.0002 m/s, 0.0005 m/s, 0.001 m/s and 0.002 m/s), interpolating the average salt marsh elevation at the end of each simulation in a contour plot. By analyzing the slopes in the contour plots of inundation rates vs. sediment input, we defined marsh resilience as the slope H_{in} / S_{in} needed to maintain a constant marsh elevation. This was determined by averaging the slopes observed along all elevation contour lines, including only non-zero slopes. Steeper slopes indicate higher resilience, meaning that the marsh needs less sediment input for a given inundation rate to maintain its elevation. Finally, we ran a systematic analysis of the combined effect of different vegetation trait parameters (p_E, C_d and H_v) to quantify their effect on resilience. We calculated the relative percent change in marsh resilience with an increase in each parameter value, to identify the effect of specific traits on resilience. The interactive effects of simultaneous changes in multiple parameters are shown in Supplementary Fig. 12.

Channel network characterization

To quantify the structure of creek networks, we analyzed the real-world DTMs and the simulated topographies predicted by the model in Python, using the Whitebox Toolbox and Rasterio package. Based on this DTM, the Whitebox Toolbox is used to delineate the stream skeleton, and the streams are numbered using Hack's stream ordering system[61]. This ordering system was chosen because of its nested nature, where the main channel always has an order of 1 and side channels are given increasingly higher orders, so that (nested) complexity could be readily compared between systems[29]. In contrast, other alternatives, such as the Strahler system, could lead to varying orders for the main channel as new, smaller channels develop, making it less suitable for comparisons. The drainage density is calculated as the total length of the channels divided by the total catchment area[62] (or simulated domain in the case of model results). Finally, the shortest distance to a channel from each point on the marsh platform is calculated using the Proximity (raster distance) tool in QGIS. The distance between each point on the marsh platform and a channel is also called unchanneled path length[63,64]. The inverse of drainage density divided by the mean distance to a channel is defined as geometric efficiency, and it indicates how well a channel network serves the marsh platform[37]. Channel bifurcation ratio is used as a measure of branching complexity and is calculated as the number of creeks of one order higher (more fine-scaled) relative to the current order (N_{i+1}/N_i)[65].

Data availability

The data that support the findings of this study are publicly available via https://doi.org/10.4121/9b2fb6d8-e2e7-4768-ad1a-bcf903c4eb20. Source data are provided for Figs. 1–7 and are available as a Source Data file at the link above. The Digital Terrain Models (DTM) generated with airborne laser altimetry and the RTK GPS transects are available from Rijkswaterstaat (https://rijkswaterstaatdata.nl/).

Code availability

The code that supports the findings of this study is publicly available via https://doi.org/10.4121/9b2fb6d8-e2e7-4768-ad1a-bcf903c4eb20. Version 1.1 of the model (SFERE – Scale-dependent Feedback Recursion) is available on Zenodo (https://doi.org/10.5281/zenodo.13895002).

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Author contributions
L.C., D.vd.W., J.vdK., T.Y. designed the study. L.C., R.C.vdV. and J.vdK. developed the model. L.C. performed model simulations and data analyses and led the writing of the paper, to which all co-authors contributed. L.C., B.vP., J.S. carried out the field experiments. T.Y., D.vdW., B.vP., L.dV.,J.vdK., Q.-X.L. helped in the development of model, data analyses and paper.

Competing interests
The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Loreta Cornacchia.

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