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## LETTER

# Mangrove diversity loss under sea-level rise triggered by bio-morphodynamic feedbacks and anthropogenic pressures

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## Abstract

Mangrove forests are valuable ecosystems, but their extent and diversity are increasingly threatened by sea-level rise and anthropogenic pressures. Here we develop a bio-morphodynamic model that captures the interaction between multiple mangrove species and hydro-sedimentary processes across a dynamic coastal profile. Numerical experiments are conducted to elucidate the response of mangrove assemblages under a range of sea-level rise and sediment supply conditions, both in the absence and presence of anthropogenic barriers impeding inland migration. We find that mangrove coverage can increase despite sea-level rise if sediment supply is sufficient and landward accommodation space is available. Tidal barriers are mainly detrimental to mangrove coverage and result in species loss. Importantly, we show that bio-morphodynamic feedbacks can cause spatio-temporal variations in sediment delivery across the forest, leading to upper-forest sediment starvation and reduced deposition despite extended inundation. As such, bio-morphodynamic feedbacks can decouple accretion rates from inundation time, altering mangrove habitat conditions and causing mangrove diversity loss even when total forest coverage remains constant or is increasing. A further examination of bio-morphodynamic feedback strength reveals that vegetation-induced flow resistance linked to mangrove root density is a major factor steering the inundation-accretion decoupling and as such species distribution. Our findings have important implications for ecosystem vulnerability assessments, which should account for the interactions between bio-morphodynamics and mangrove diversity when evaluating the impacts of sea-level rise on species assemblages.

## 1. Introduction

Mangrove forests are found along tropical and subtropical shorelines and typically show distinct zonation patterns, with each zone being characterized by a dominant mangrove species (Duke *et al* 1998, Tomlinson 2016). However, mangrove zonation not only implies changes in species but also in biophysical tree characteristics. Mangrove species along the intertidal gradient show great differences in both aerial root structure and density, which allows them to survive under specific inundation regimes (Chapman 1976, Duke *et al* 1998). Sea-level rise may modify

the inundation time along mangrove habitats thereby potentially altering forest width, zonation and thus species diversity (Duke *et al* 2007). Shrinking mangrove forests have raised concern on the loss of individual mangrove species, especially as even pristine mangrove forests are species-poor compared with other tropical ecosystems and because these systems are subject to 'coastal squeeze' (Alongi 2002, Gilman *et al* 2008). Mangroves provide valuable ecosystem services, including carbon sequestration, coastal protection and habitat provision for a plethora of organisms in some, or all life stages (Kathiresan and Rajendran 2005, Aburto-Oropeza *et al* 2008,

Alongi 2014). As the provision of ecosystem services is highly dependent on the composition of mangrove species assemblages, the loss of species diversity can have dramatic economic and environmental consequences for coastal communities (Duke *et al* 2007, Polidoro *et al* 2010). Improving our ability to predict the response of mangrove assemblages and zonation to external pressures is thus urgently needed (Jennerjahn *et al* 2017).

Predicting the fate of mangrove forests is hampered by a limited representation of bio-morphodynamic feedbacks in numerical models, especially in the case of multiple co-existing mangrove species (Fagherazzi *et al* 2017). Here, bio-morphodynamic feedbacks are considered as the physical effects of mangrove trees on tidal currents, sedimentation/erosion patterns and hydroperiods, which in turn affect tree growth and species distribution. So far, models evaluating wetland resilience to sea-level rise have primarily focused on parameterized processes controlling vertical accretion and the ability of wetlands to counteract rising water levels through enhanced sediment deposition (Kirwan *et al* 2010, Fagherazzi *et al* 2012, Mogensen and Rogers 2018, Schuerch *et al* 2018). Other recent approaches include a more comprehensive treatment of sediment transport and morphological processes but focus on single-species dominated saltmarsh systems (Zhou *et al* 2016, Mariotti and Canestrelli 2017). Developing reliable projections for mangrove assemblages requires capturing the interaction between hydro-sedimentary processes across the mangrove forest, multi-species vegetation growth and coastal profile change. Such bio-morphodynamic feedbacks depend on vegetation properties and the coastal setting but may also be greatly affected by sea-level rise and anthropogenic interventions including changes in sediment supply and lateral accommodation space, the latter describing the upland space available for vegetation colonization (Schuerch *et al* 2018).

Here we present a novel modelling approach by coupling a detailed hydro-morphodynamic model that computes the deposition, erosion and transport of sediment across the coastal profile with a newly developed vegetation model that captures the dynamics of mangrove species occupying the lower, middle and upper intertidal area (figure 1). As such, we account for sediment transport between different vegetation zones and potential spatio-temporal variations in sediment availability. We conduct numerical experiments to systematically explore changes in mangrove forest extent and diversity under a broad range of sea-level rise rates and sediment supply conditions, both in the absence and presence of a tidal barrier (e.g. dike or seawall) that obstructs inland migration. This enables us to investigate for the first time shifts in mangrove species zonation linked to a dynamic coastal profile, differences in lateral accommodation space (i.e. possibility of coastal

progradation and landward migration) and mangrove properties (i.e. root density).
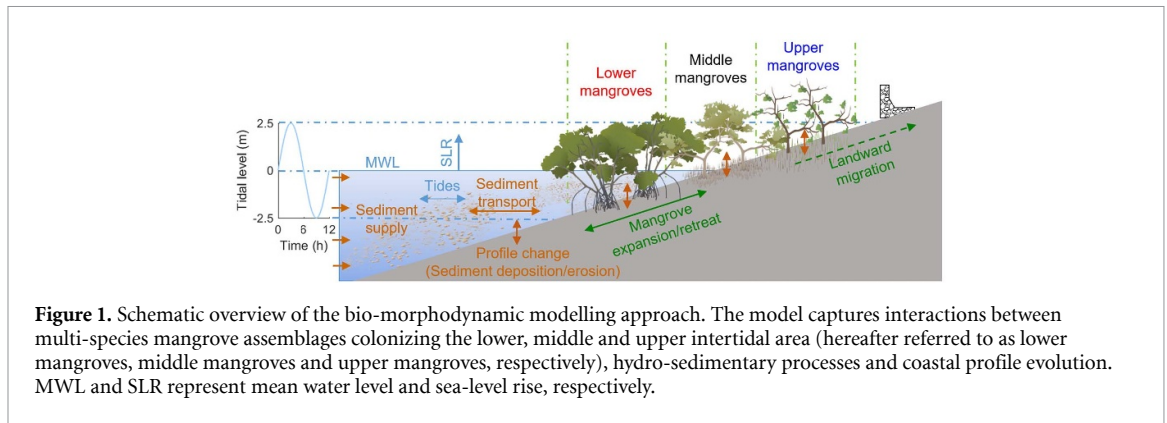
## 2. Methods

Mangrove and coastal profile dynamics are simulated by coupling an open-source hydro-morphodynamic model (Delft3D) (Lesser *et al* 2004, Brückner *et al* 2019) to a new dynamic vegetation model that considers multiple mangrove species thriving at specific inundation regimes. Information on local hydroperiod generated by the hydro-morphodynamic model is provided to the vegetation model controlling colonization, growth and mortality of mangrove trees. In turn, the vegetation model provides information on the dimensions and densities of vegetation objects to the hydro-morphodynamic model so that the effect of mangroves on tidal flow and consequently sediment transport is accounted for (figure S1 available online at https://stacks.iop.org/ERL/15/114033/mmedia). Although organic matter accretion within mangrove forests is known to increase resilience to sea-level rise (Krauss *et al* 2014, Woodroffe *et al* 2016), this process is not included here as we focus on the role of above-ground bio-morphodynamic feedbacks, thus providing conservative estimates on mangrove survival. Also, rather than simulating particular mangrove sites, we use simplified forcing conditions and parameterizations to describe forest characteristics, in order to explore distinct mangrove behaviours and identify the driving processes behind changes in mangrove extent, zonation and thus diversity under a broad range of environmental conditions.

### 2.1. Model description

To effectively capture mangrove lateral movement and changes in mangrove zonation, a one-dimensional cross-shore profile modelling strategy is used, assuming alongshore uniformity and absence of tidal channels (Roberts *et al* 2000, Zhou *et al* 2016). A detailed overview of the governing equations is provided in the supporting information (texts S1-S2). Tidal flow, sediment transport and bathymetric changes are calculated by the Delft3D model suite (Lesser *et al* 2004). Delft3D has been successfully applied in the past to investigate the evolution of vegetated muddy coasts (Zhou *et al* 2016). The presence of mangrove vegetation is incorporated by increasing flow resistance (Baptist *et al* 2007). We consider pure cohesive sediment as mangroves commonly thrive in muddy environments (Woodroffe *et al* 2016).

Based on earlier work on single-species mangrove modelling (van Maanen *et al* 2015), we developed a dynamic vegetation model considering mangrove assemblages growing along intertidal gradients and interacting with morphological change. We selected three species, namely *Rhizophora mangle, Avicennia*

**Figure 1.** Schematic overview of the bio-morphodynamic modelling approach. The model captures interactions between multi-species mangrove assemblages colonizing the lower, middle and upper intertidal area (hereafter referred to as lower mangroves, middle mangroves and upper mangroves, respectively), hydro-sedimentary processes and coastal profile evolution. MWL and SLR represent mean water level and sea-level rise, respectively.

*germinans* and *Laguncularia racemosa*, to represent lower, middle and upper intertidal mangroves, respectively (figure 1). These species were chosen as they are known to thrive at different elevations (Lugo and Snedaker 1974, Chapman 1976, Duke *et al* 1998) and detailed information on their growth parameters is available (Chen and Twilley 1998, Berger and Hildenbrandt 2000, Komiyama *et al* 2008). Even though these specific species are adopted, our study also investigates the sensitivity to species characteristics (i.e. species distribution criteria and root densities) and therefore provides general insights on bio-morphodynamic interactions within mangrove assemblages.

Mangrove tree growth is represented by increasing stem diameter ($D_i$; cm) (Chen and Twilley 1998, Berger and Hildenbrandt 2000, van Maanen *et al* 2015):

$$\frac{dD_i}{dt} = \frac{G_i D_i \left(1 - \frac{D_i H_i}{D_{\max,i} H_{\max,i}}\right)}{\left(274 + 3b_{2i} D_i - 4b_{3i} D_i^2\right)} \cdot f_i \cdot C \qquad (1)$$

where $t$ is time (years), $D_{\max,i}$ and $H_{\max,i}$ are the species-specific maximum stem diameter and tree height, respectively. $G_i$, $b_{2i}$ and $b_{3i}$ are growth parameters. As such, the first term on the right-hand side of equation (1) describes optimal tree growth rates based on the actual stem diameter and tree height. Tree growth rates may be reduced under sub-optimal inundation conditions or because of limited resources through vegetation competition effects. This is incorporated through species-specific fitness functions ($f_i$) and a competition stress factor ($C$) which are included as additional terms in equation (1) (van Maanen *et al* 2015, D'Alpaos and Marani 2016). $f_i$ is dependent on inundation conditions (computed by Delft3D) and specifies that each species has an optimal hydroperiod for growth, while $C$ is dependent on mangrove biomass (figure S2). Thus, if $f_i = 1$ and $C = 1$ then tree growth is optimal; while lower values mean that tree growth is limited by inundation stress and competition. These two parameters also control mangrove colonization and mortality such

that the habitat of mangroves is restricted to intertidal areas and sea-level rise can cause mangrove dieback through extensive inundation. Finally, the model includes a description of mangrove root densities by relating the number of root elements to stem diameter and define a species-specific maximum number of elements per tree (figure S3 and text S2). The diameter, height and density of stems and aerial roots, both of which are simplified as cylindrical objects, are then used by Delft3D to compute additional flow resistance (equations S3 and S4). Since species-dominance and their accompanied root structures vary greatly across mangrove ecosystems, we also investigate the impact of root density on mangrove forest evolution and thus provide deeper insights into the role of bio-morphodynamic feedbacks in response to environmental factors.

To quantify mangrove diversity across the intertidal gradient, we developed a customized index, named the assemblage diversity index (ADI):

$$ADI = -\sum_{i=1}^{n} p_i \cdot \ln p_i \qquad (2)$$

The ADI is based on the Shannon's index (Hill 1973, Spellerberg and Fedor 2003), but here $p_i$ represents the cross-shore extent of species $i$ relative to the total forest extent. The above index uses the proportional extent of each species to provide a measure of diversity, accounting for both species richness and evenness along the cross-shore profile (Peet 1974). Thus, the value of ADI increases, and so does diversity, if the number of species present within the forest increases (increased species richness) and/or if their relative abundance becomes more similar (increased evenness). Accordingly, the maximum value of the ADI in our research is expected to reach ~1.1 (when $p_1 = p_2 = p_3 = 1/3$) while the minimum value is 0 when only one mangrove species is present. In our study we use the ADI as a post-processing step to effectively capture diversity changes in a single number that can be easily evaluated over time.

## 2.2. Design of model simulations

Mangrove environments are highly variable and although we do not simulate specific sites, we design our model simulations based on existing literature describing mangrove growth conditions. As such, an initial bed slope of 1/1000 is adopted based on field observations (Lovelock *et al* 2010, Phan *et al* 2015, Bryan *et al* 2017). This slope is also close to the equilibrium profile under current model settings, according to preliminary tests. The model is forced by semidiurnal tides of 2.5 m amplitude. Such settings provide a greater mangrove extent, thus helping to study the changes in mangrove zonation as well as in the coastal profile (Ellison 2015). We adopted a 50 m by 50 m grid size as such a resolution is commonly used in morphodynamic modelling and captures coastal profile and vegetation dynamics (Zhou *et al* 2016), while at the same time guaranteeing a reasonable simulation efficiency so that a large number of scenarios can be evaluated. An overview of the model settings is presented in the tables S1-S2.

We investigate the response of mangrove assemblages to environmental change through a series of simulations with different combinations of sea-level rise rate and sediment supply, both in the absence and presence of a tidal barrier. For practical reasons we use two different domain sizes for scenarios with and without a barrier (figure S4). To focus on non-linear bio-morphodynamic feedbacks, sea-level rise rates are assumed constant through time varying from 0 to 10 mm/year covering the range of IPCC RCP2.6 to RCP8.5 sea-level rise estimates towards the end of this century (Oppenheimer *et al* 2019). Rising sea levels are incorporated by incrementally raising the water level ($\eta$ in equation S1) at the seaward boundary. Variations in sediment supply are imposed by varying suspended sediment concentrations at the offshore boundary from 0 to 50 mg L$^{-1}$ (Lovelock *et al* 2015). Simulations are conducted for a period of 330 years. The first 30 years are used as an adaptation period during which mangroves can settle, allowing the analysis of mangrove assemblage dynamics over the remaining 300 years. The model tracks key forest characteristics, including tree density, type of species, stem diameter, tree height and associated biomass. We here focus on changes in total forest coverage and species distribution (i.e. ADI).

## 3. Results

### 3.1. Mangrove coverage and diversity under environmental change

To explore distinct mangrove responses, we first considered extreme combinations in sea-level rise rate and sediment supply. A high sea-level rise rate (10 mm yr$^{-1}$) and low sediment supply (10 mg L$^{-1}$) led to retreat of the mangrove forest over time (figures 2(a)–(b)). In the absence of a tidal barrier all mangrove species could shift upland (ADI $\sim$ 1.1)

(figure 2(a)), whereas the presence of a tidal barrier led to a reduction in forest extent and loss of the middle and upper mangroves (ADI $\sim$ 0.6) (figure 2(b)). Under intermediate to high sea-level rise rates (4 mm yr$^{-1}$ for no barrier; 10 mm yr$^{-1}$ for barrier) and intermediate sediment supply (25 mg L$^{-1}$), sea-level rise was balanced by vertical accretion, keeping the forest seaward edge relatively stable (figures 2(c)–(d)). This led to an increased forest extent due to landward migration and stable ADI in the absence of a tidal barrier (figure 2(c)). When inland migration was restricted, forest extent remained constant through larger vertical accretion compared to the scenario without a barrier, but a redistribution in mangrove species resulted in a lower ADI (figure 2(d)). Under low sea-level rise (2 mm yr$^{-1}$) and high sediment supply (50 mg L$^{-1}$), coastal progradation was possible and this caused seaward mangrove expansion. Even though both scenarios with and without barrier showed an increasing forest extent, a reduction in ADI occurred because of the increased dominance of lower mangroves and a reduced extent of upper mangroves (figures 2(e)–(f)).

We then considered the full range of simulated sea-level rise (0–10 mm yr$^{-1}$) and sediment supply (0–50 mg L$^{-1}$) combinations to provide a clear overview of conditions that led to the above described mangrove behaviours (retreat, stable and expansion), and to identify when losses in diversity and mangrove extent were most significant (figure 3). In the presence of a tidal barrier (figure 3(b), (d), (f) and (h)), changes in the mangrove seaward edge, forest extent, and mangrove diversity (ADI) followed a similar pattern. High sea-level rise rates combined with reduced sediment supplies led to increased landward retreat and forest shrinkage (both up to 8 m yr$^{-1}$), and a strong decrease in ADI (up to 0.4 reduction) (figures 3(b), (f) and (h) B1). In contrast, low sea-level rise rates and high sediment supplies allowed for seaward expansion and an increase in mangrove forest extent (both up to 6 m yr$^{-1}$), with only minor changes in ADI (up to 0.08 reduction) (figures 3(b), (f) and (h) B3). In the absence of a tidal barrier, changes in the mangrove seaward edge did not show the same trend in response to sea-level rise and sediment supply as the mangrove forest extent and mangrove diversity (figures 3(a), (c), (e) and (g)). Although an increasing/decreasing sea-level rise rate and decreasing/increasing sediment supply resulted in increasing mangrove landward retreat/seaward expansion (figure 3(a) N1 and N3), forest extent was mainly increasing especially with higher sediment supplies (>6 m yr$^{-1}$) (figure 3(e)). Mangrove diversity remained mainly stable when there was no tidal barrier present and only exhibited a slight decrease for combinations of low sea-level rise rates and high sediment supplies (figure 3(g) N3). This particular ADI reduction, however, was independent from the presence of a tidal barrier (figures 3(g) N3
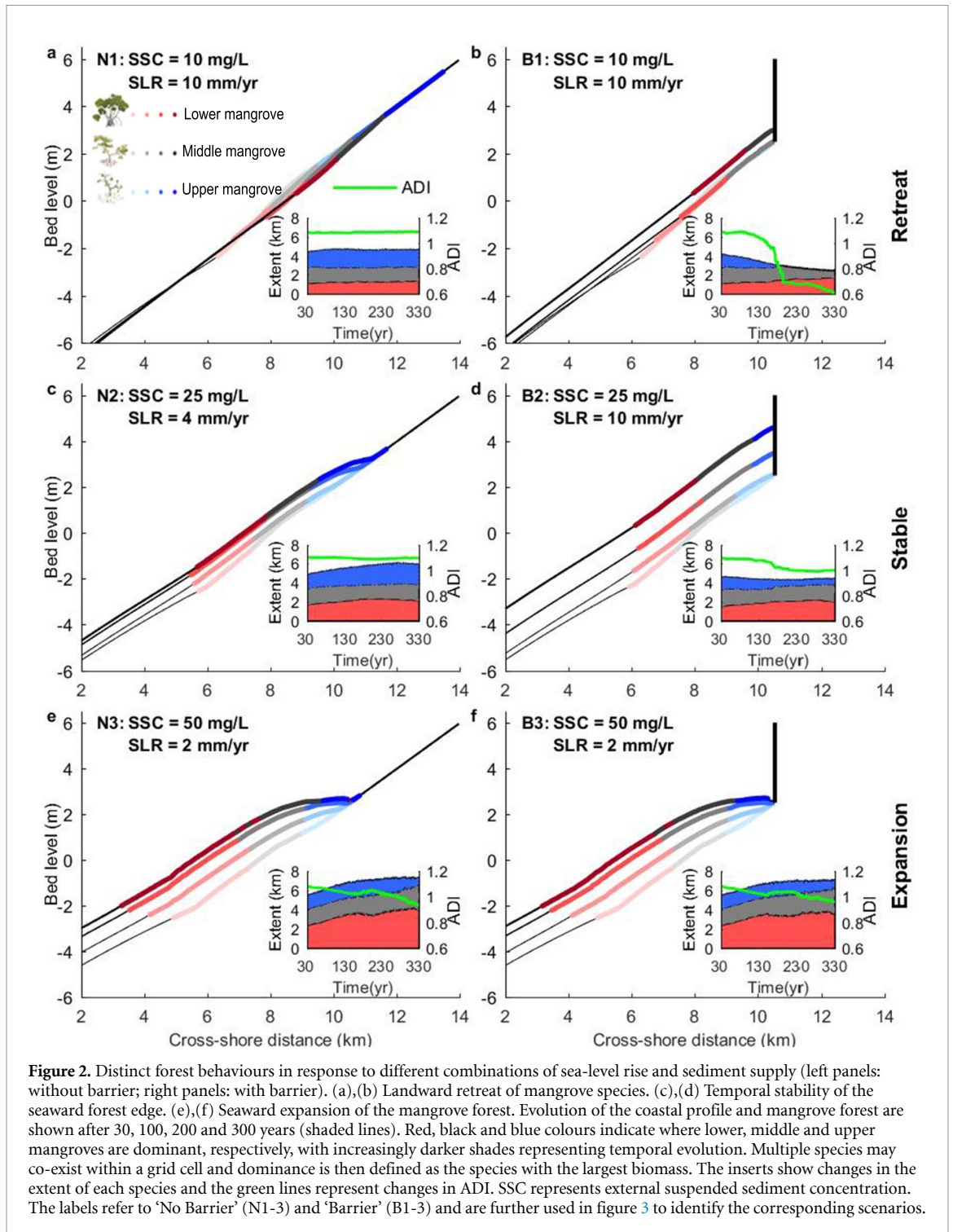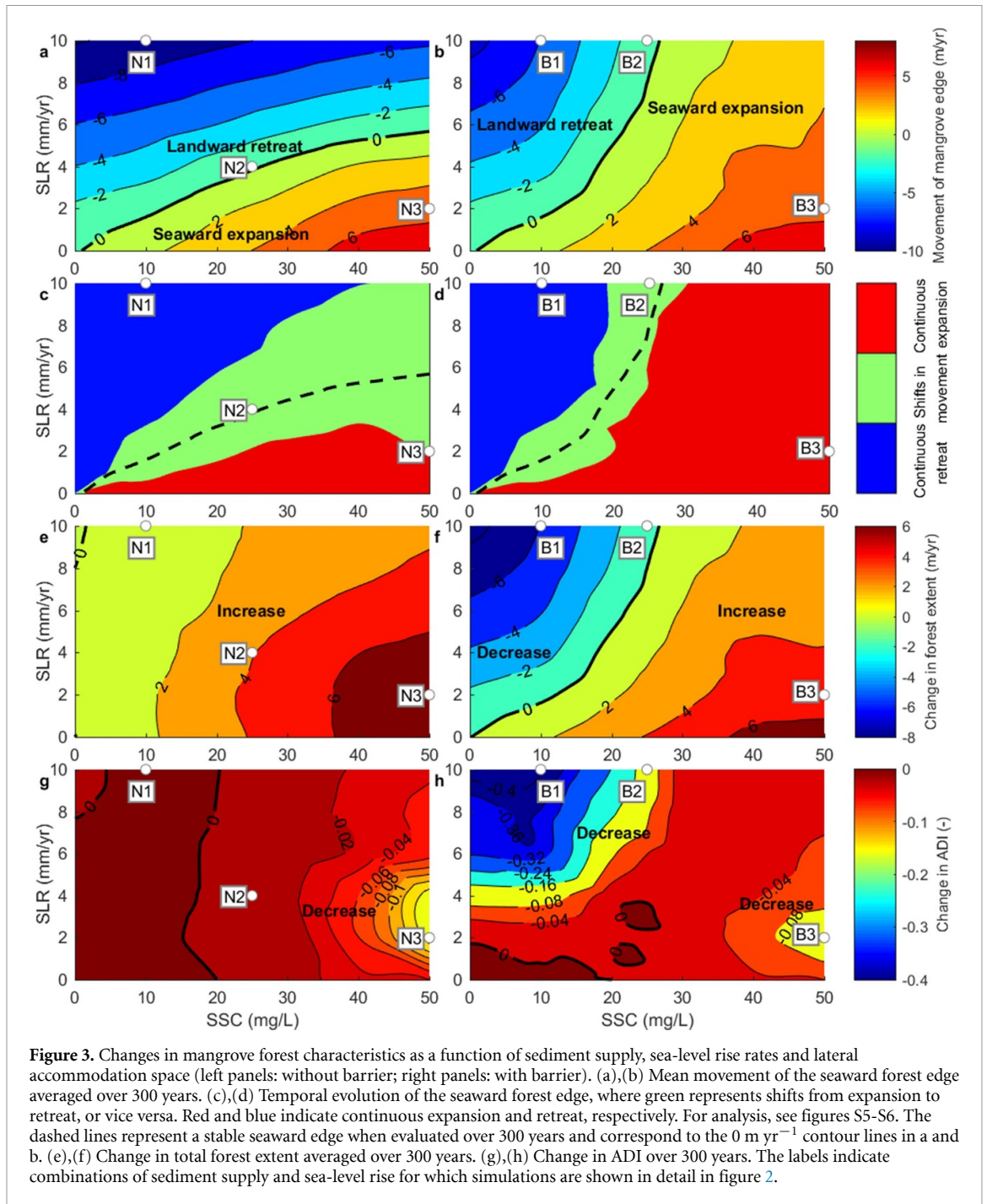
**Figure 2.** Distinct forest behaviours in response to different combinations of sea-level rise and sediment supply (left panels: without barrier; right panels: with barrier). (a),(b) Landward retreat of mangrove species. (c),(d) Temporal stability of the seaward forest edge. (e),(f) Seaward expansion of the mangrove forest. Evolution of the coastal profile and mangrove forest are shown after 30, 100, 200 and 300 years (shaded lines). Red, black and blue colours indicate where lower, middle and upper mangroves are dominant, respectively, with increasingly darker shades representing temporal evolution. Multiple species may co-exist within a grid cell and dominance is then defined as the species with the largest biomass. The inserts show changes in the extent of each species and the green lines represent changes in ADI. SSC represents external suspended sediment concentration. The labels refer to 'No Barrier' (N1-3) and 'Barrier' (B1-3) and are further used in figure 3 to identify the corresponding scenarios.

and (h) B3) and was caused by the aforementioned coastal progradation with lower mangroves rapidly expanding while upper mangroves were overtaken by middle mangroves (figures 2(e)–(f)).

Our simulations further showed that with comparable sediment supply, the presence of a barrier enabled mean seaward expansion under higher rates of sea-level rise in comparison to the scenarios without a barrier (figures 3(a)–(b)). Investigation of temporal changes in the lateral movement

of the forests over the 300-year simulation period revealed that the forest sea edge could shift from seaward expansion to landward retreat, or vice versa (green area in figures 3(c)–(d)). The presence of a barrier in this context reduced the parameter space that led to directional shifts and, as a consequence, the likelihood for continuous seaward expansion increased (red area in figures 3(c)–(d)). Nevertheless, loss in mangrove diversity and forest extent was more pronounced in the scenarios with a barrier.

**Figure 3.** Changes in mangrove forest characteristics as a function of sediment supply, sea-level rise rates and lateral accommodation space (left panels: without barrier; right panels: with barrier). (a),(b) Mean movement of the seaward forest edge averaged over 300 years. (c),(d) Temporal evolution of the seaward forest edge, where green represents shifts from expansion to retreat, or vice versa. Red and blue indicate continuous expansion and retreat, respectively. For analysis, see figures S5–S6. The dashed lines represent a stable seaward edge when evaluated over 300 years and correspond to the 0 m yr$^{-1}$ contour lines in a and b. (e),(f) Change in total forest extent averaged over 300 years. (g),(h) Change in ADI over 300 years. The labels indicate combinations of sediment supply and sea-level rise for which simulations are shown in detail in figure 2.

### 3.2. Mangrove dynamics driven by bio-morphodynamic feedbacks

To unravel the bio-morphodynamic feedbacks that govern species-specific responses, we also assessed how key physical variables changed in the scenario with low sea-level rise (2 mm yr$^{-1}$) and high sediment supply (50 mg L$^{-1}$) as this resulted in diversity loss while overall mangrove extent was increasing (figure 4). First, we focused on mangrove behaviours and related bio-morphodynamic processes in the simulation with original root settings (first column of figure 4; figure S3). In all regions of the mangrove forest, sediment accretion was initially well above the sea-level rise rate (around 10–15 mm yr$^{-1}$)

(figure 4(e)). Accretion then slowed down but it continued to outpace sea-level rise in the lower forest. In the upper forest, reduced accretion caused a gradually flattening profile and a progressively increasing inundation regime (blue line in figure 4(i)). Such prolonged inundation was expected to trigger accelerated surface elevation gain through enhanced sediment deposition, thus promoting wetland stability. However, our results showed a contrasting response that emerged from temporal changes in sediment delivery towards the upper part of the mangrove forest. Over time, advection of suspended material diminished because tidal currents were being dissipated more strongly as the mangroves expanded
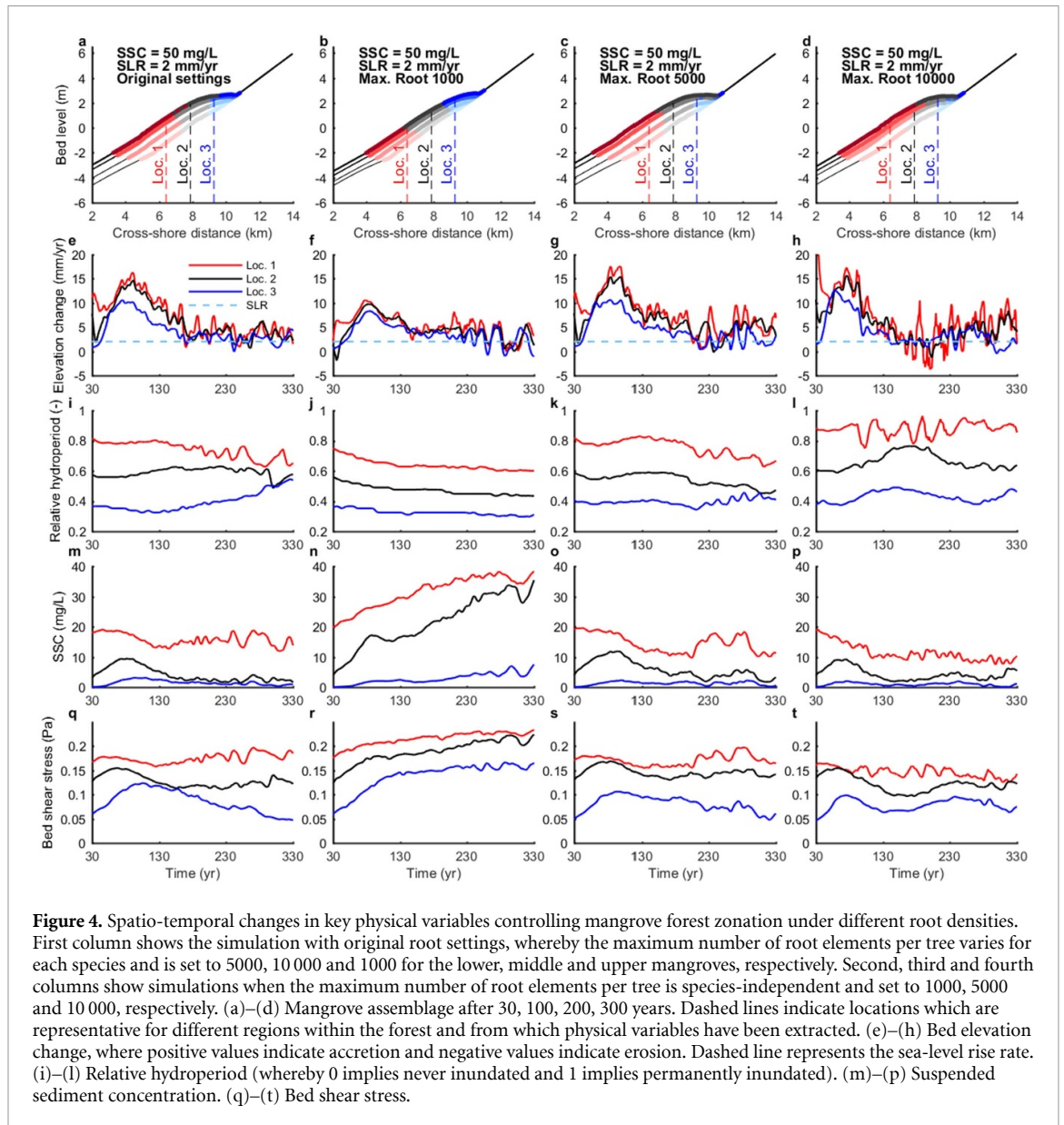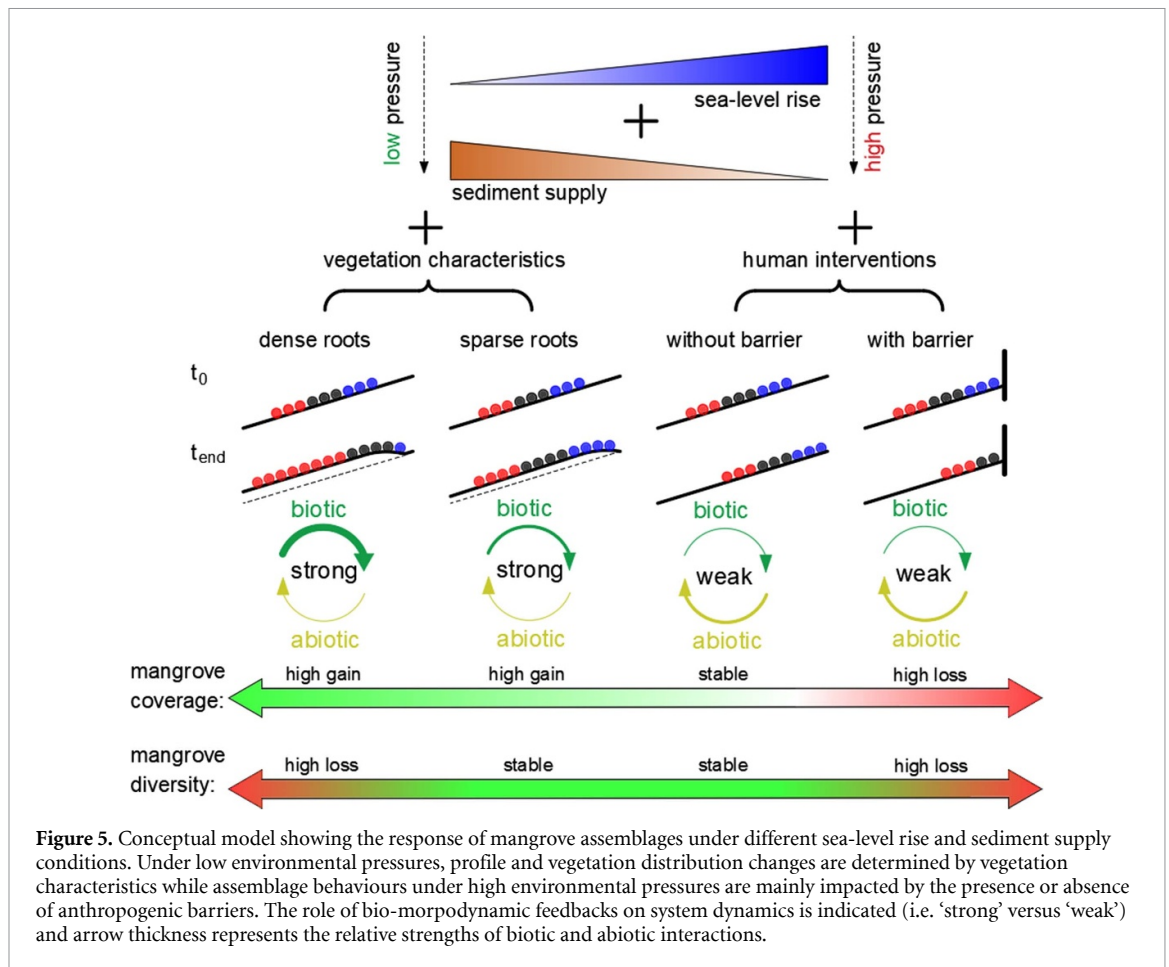
**Figure 4.** Spatio-temporal changes in key physical variables controlling mangrove forest zonation under different root densities. First column shows the simulation with original root settings, whereby the maximum number of root elements per tree varies for each species and is set to 5000, 10 000 and 1000 for the lower, middle and upper mangroves, respectively. Second, third and fourth columns show simulations when the maximum number of root elements per tree is species-independent and set to 1000, 5000 and 10 000, respectively. (a)–(d) Mangrove assemblage after 30, 100, 200, 300 years. Dashed lines indicate locations which are representative for different regions within the forest and from which physical variables have been extracted. (e)–(h) Bed elevation change, where positive values indicate accretion and negative values indicate erosion. Dashed line represents the sea-level rise rate. (i)–(l) Relative hydroperiod (whereby 0 implies never inundated and 1 implies permanently inundated). (m)–(p) Suspended sediment concentration. (q)–(t) Bed shear stress.

seaward (figure 4(q); figure S7). Thus, while inundation periods increased in the upper forest (from 0.3 to 0.6) (figure 4(i)), bed level accretion was hindered as sediment availability became limited (from 5 to ~0 mg L$^{-1}$) (figure 4(m)). This caused a shift in species occurrence where middle mangroves replaced upper mangroves. The transition to supply-limited conditions occurred under constant sea-level rise and external sediment supply and was thus purely controlled by internal system dynamics. Essentially, the lower mangroves expanded, and by mediating the physical processes they reduced the extent of upper mangroves, implying that indirect species interactions played a critical role in driving forest diversity changes.

Model simulations indicated that forest behaviours regarding mangrove seaward and landward movement (figure 2) remained consistent under the additional sensitivity runs with different species distribution criteria and root densities (figures

S8 and S9). However, interestingly, root density exerted a major influence on the ADI in the case of coastal progradation and seaward mangrove expansion, where higher root densities caused a greater loss of diversity (figure S9(m)–(p)). Although general accretion trends along the profile and through time were comparable among different root settings, the maximum accretion rate increased with increasing root density (figures 4(f)–(h)) and overall deposition in the lower and middle intertidal area was approximately half a meter more under higher root densities (figures 4(b)–(d) and figure S10). Increased root density accelerated mangrove seaward expansion, but it thus also reduced the extent of upper mangroves at a faster rate (figures 4(b)–(d)). Although accretion was typically slower under low root densities, it was also more uniform across the forest and profile flattening was therefore less profound (figure 4(b) and figure S10). In contrast to the scenarios with higher root densities where hydroperiods increased in the

**Figure 5.** Conceptual model showing the response of mangrove assemblages under different sea-level rise and sediment supply conditions. Under low environmental pressures, profile and vegetation distribution changes are determined by vegetation characteristics while assemblage behaviours under high environmental pressures are mainly impacted by the presence or absence of anthropogenic barriers. The role of bio-morpdynamic feedbacks on system dynamics is indicated (i.e. 'strong' versus 'weak') and arrow thickness represents the relative strengths of biotic and abiotic interactions.

upper forest causing changes in dominant species, hydroperiods decreased throughout the entire forest when root density was low (figure 4(j)) and species distributions remained relatively constant.

## 4. Discussion and conclusions

To summarize the findings of our numerical experiments, we propose a conceptual model to illustrate the response of mangrove assemblages and related bio-morphodynamic feedbacks under low and high environmental pressures, represented by different combinations of sea-level rise and sediment supply (figure 5). We demonstrate that under low sea-level rise rates and high sediment supplies, system dynamics are dominated by coastal progradation and seaward mangrove expansion, while anthropogenic barriers exert little stress. As our approach uses idealized numerical simulations to unravel the controlling processes driving changes in mangrove forests, model testing should involve an evaluation of model behaviours and trends (Murray 2013). In this context, our simulations of seaward mangrove expansion are in agreement with observations at locations that experience large sediment inputs (Anthony *et al* 2010, Lovelock *et al* 2010, Nardin *et al* 2016, Liu *et al* 2018). In such settings, mangroves are able to colonize elevated mudflats, stressing the importance

of hydro-sedimentary processes in the unvegetated intertidal area fringing the mangrove forest combined with dynamic vegetation growth. In northern Australia, mangrove coverage along particular coastal sections has recently increased not only through seaward but also landward expansion, the latter being driven by the combined effects of sea-level rise and prolonged inundation of coastal lowlands (Asbridge *et al* 2016). Our modelled scenarios qualitatively capture such behaviours and, in addition, they highlight the conditions that can lead to sea-level rise driven expansion of mangrove forests.

What is more, at low environmental pressures, the bio-morphodynamic feedback, whereby vegetation influences hydro-sedimentary processes and morphological evolution in turn affects vegetation growth, plays a key role in driving mangrove species distributions. Our model results indicate that the density of root elements, and thus the strength of biotic interactions, will influence this feedback and steer changes in diversity. For the same environmental conditions, sparse roots allow more sediment to be transported towards the upper region of the forest as tidal currents are stronger, causing a uniform accretion across the forest such that coastal profile shape and species zonation remain relatively stable. Dense root structures, as also supported by field studies (Furukawa *et al* 1997, Mazda *et al* 1997,

Kumara *et al* 2010, Swales *et al* 2019), cause dampening of tidal currents and enhance sediment trapping, and this may then lead to upper-forest sediment starvation. Here we show that such interactions can cause variations in accretion across the forest resulting in profile change and, more importantly, trigger diversity loss (figure 5). Bio-morphodynamic feedbacks thus generally promote vertical accretion and seaward expansion, which enhance overall forest resilience, but at the same time these feedbacks reduce sediment delivery to the more landward region of the forest, thus preventing upper species to capture sediment with sea-level rise and making them more vulnerable to be replaced by species adapted to higher inundation time.

Under high environmental pressures, when sea-level rise is fast and sediment input is low, mangrove behaviours are mainly controlled by the abiotic drivers (i.e. enhanced inundation caused by sea-level rise) instead of bio-morphodynamic feedbacks. Hereby the presence of anthropogenic barriers exerts a major impact on the fate of mangrove assemblages. Barriers prove to be mainly detrimental for both mangrove coverage and diversity while species distributions can remain stable if landward habitat is available (figure 5). Globally, anthropogenic activities, including urbanization and the construction of flood protection works, heavily impact coastal ecosystem resilience with an estimated loss of up to 30% of wetland area within this century if no further lateral accommodation space is created (Schuerch *et al* 2018). Clearly, for coastal systems where sediment supplies are in decline and losses are irrevocable, removing barriers that obstruct inland migration is of critical importance to safeguard mangrove survival.

The degree to which such bio-morphodynamic feedbacks and anthropogenic pressures control wetland behaviour may rely on wetland characteristics (e.g. vegetation type and density, surface area and slope) and hydrodynamic forcing (e.g. tidal range, waves) and thus depends on the overall biogeomorpholocial setting (Balke and Friess 2016, Woodroffe *et al* 2016, Bryan *et al* 2017). As such, parameterizing our model for a range of real world mangrove settings to predict mangrove responses at specific field sites should be further explored in the future. In addition, sub-surface processes can play an important role in controlling substrate elevation change and wetland resilience (Krauss *et al* 2014). Mangrove root accumulation helps raising bed elevations (Mckee *et al* 2007, Mckee 2011), which is not included here. Our modelling approach may therefore underestimate the ability of mangrove forests to cope with sea-level rise. However, subsidence due to decomposition and sediment auto-compaction limits mangrove elevation gain (Rogers *et al* 2005). The mechanisms governing subsurface processes are still not fully understood and the net effect is highly dependent on site conditions (Krauss *et al* 2014, Sasmito *et al* 2016). As such, our model focusses on above-ground interactions between vegetation and hydro-sedimentary processes and provides new insights into the dynamics that govern bio-morphological response to changing environmental drivers.

Our results indicate that above-ground bio-morphodynamic feedbacks cause spatio-temporal variations in sediment accretion. As mangrove vegetation modulates tidal currents, transport of sediment inland is reduced resulting in varying accretion rates across the mangrove forest. Our simulations show this can cause counterintuitive behaviours with respect to sea-level rise as accretion rates and inundation time are being decoupled. As such, wetland accretion may fail to accelerate despite extended inundation and, in the longer term, this can cause a loss in mangrove diversity. Changes in mangrove coverage and composition are of course also affected by other major drivers, including mangrove poleward migration with the potential of mangroves encroaching into salt marsh areas (Saintilan *et al* 2014). A bio-morphodynamic modelling approach, as presented here, will be useful to study the loss or gain in coastal ecosystem diversity in the face of such global change impacts.

Overall, our study implies that projections of mangrove assemblages in the face of sea-level rise need to capture the complex interactions between multi-species mangrove dynamics and hydro-sedimentary processes across the coastal profile, as well as the impacts of surrounding anthropogenic conditions. As the loss of mangrove species will have dramatic ecological and economic implications, comprehensive evaluations of species-specific responses are crucial in order to evaluate the future extent and diversity of mangrove forests, and to develop nature-based, integrated coastal zone management approaches to protect these vulnerable ecosystems.

## Acknowledgments

## Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5281/zenodo.3749866. Data will be available from 01 January 2021.

## Supporting information

Attached file with supplementary figures, texts and tables.

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