



Linking tidal wetland vegetation mosaics to micro-topography and hydroperiod in a tropical estuary

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ABSTRACT

Although saltmarshes are critical coastal ecosystems they are threatened by human activities and sea-level rise (SLR). Long-term restoration and management strategies are often hampered by an insufficient understanding of the past, present, and future processes that influence tidal wetland functionality and change. As understanding vegetation distribution in relation to elevation and tidal hydroperiod is often the basis of restoration and management decisions, this study investigated the relationships between micro-topography, tidal hydroperiod, and the distribution of saltmarshes, mangroves, and unvegetated flats in a tropical estuary situated within a Great Barrier Reef Catchment in North Queensland, Australia. A combination of high-resolution unattended-aerial-vehicle (UAV)-derived digital elevation model (DEMs) and land cover coupled with 2D hydrodynamic modelling was used to investigate these aspects. Zonation was more complex than generally recognised in restoration and legislation, with overlapping distribution across elevation. Additionally, although each type of tidal wetland cover had distinct mean hydroperiods, and elevation and hydroperiods were strongly correlated, elevation explained only 15% of the variability in tidal wetland cover distribution. This suggests that other factors (e.g., groundwater dynamics) likely contribute to tidal wetland cover zonation patterns. These findings underline that simplistic rules in the causality of tidal wetlands need to be applied with caution. Their applicability in management and restoration are likely to vary depending on contexts, as observed in our study site, with varying environmental and biological factors playing important roles in the distribution patterns of tidal wetland components. We also identified strong monthly variability in tidal hydroperiods and connectivity experienced by each tidal wetland cover (e.g., 10.26% of succulent saltmarshes were inundated during lower-than-average tides compared to 66% in higher than-average tides), highlighting the importance of integrating temporal dynamics in tidal wetland research and management. Additionally, we explored the potential effects of sea-level rise (SLR) on the tidal hydroperiods and connectivity of our study site. The results show that the inundation experienced by each tidal wetland cover may increase importantly if vegetation does not keep up with SLR (e.g., under a 0.8 m sea level scenarios, mean maximum depth of succulent saltmarsh in higher-than-average tides is 184.1 mm higher than the current mean-maximum inundation depth of mangroves). This underlines the importance of acquiring detailed spatio-temporally resolved data to enable the development of robust long-term and adaptive saltmarsh management strategies. Our results are discussed from a management and restoration perspective. We highlight the uncertainties and complexities in understanding the processes influencing tidal wetland functionality, and hence, their management and restoration prospects.

1. Introduction

Tidal wetlands, including saltmarshes, are an obvious component of the coastal seascape that provide a wide range of services from supporting coastal food webs, providing habitat for fish, and increase coastal resilience through buffering stormwater surge and erosion

(Weinstein and Litvin, 2016; Gilby et al., 2021). They are also important as carbon storage sinks (“blue carbon ecosystems”) (Gonneea et al., 2019; Lovelock et al., 2022) and are a key asset in responding to climate change (Macreadie et al., 2021), while also providing multiple environmental and economical services (Lovelock and Duarte, 2019). Yet, saltmarshes are declining globally (Dixon et al., 2016; Murray et al.,

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2022), threatened by direct human activities, such as agriculture and urbanisation (Boon et al., 2011; Cherry and Battaglia, 2019), but also indirect factors such as sea level rise (SLR) and erosion (Crotty et al., 2020; Farron, 2018; Ghosh et al., 2019; Ury et al., 2021).

Concerns about the declining condition of tidal wetlands have prompted considerable investment towards restoration (Bayraktarov et al., 2016). Millions of dollars are invested annually into restoration, with mean costs to restore saltmarshes ranging from USD\$454,701/ha to USD\$1,418,770/ha (Wang et al., 2022). However, many restoration projects have poor long-term success rates (Williams and Faber, 2001; Bayraktarov et al., 2016). Failure of tidal wetland restoration projects to reach restoration objectives often result from a lack of past, current, and future contextual understanding of the “anatomy of system functioning” (Sheaves et al., 2021) that supports the ecological functions and services a system provides (Weinstein and Litvin, 2016). This “anatomy” includes complex interactions of context-specific physical (e.g., hydrology, meteorology and climate, geomorphological, and anthropogenic) and biological (e.g., physiological tolerances, competition, predation, facilitation) factors that interact at various temporal and spatial scales, which are often overlooked in restoration (Bayraktarov et al., 2016; Friess et al., 2022; Suding, 2011; Liu et al., 2021; Rogers and Krauss, 2019). For instance, the 2-year survival rate of *Suaeda australis* and *Sporobolus virginicus* in a project aiming to convert an industrial waste dump back into a tidal wetland in New South Wales, Australia, were close to 0% at elevations 10–30 cm above mean sea level (Burchett et al., 1999). This low success rate was attributed to a poor understanding of the hydrology of the site, where middle elevations had a low soil water content due to sporadic tidal inundation and freshwater input compared to lower and higher elevations, respectively (Burchett et al., 1999). Restoration and management of coastal ecosystems is also often based on an oversimplification of complex processes (Clarke, 2014; Rogers and Krauss, 2019) as well as extrapolation of paradigms and concepts elaborated in specific locations without knowing whether these apply to a similar system situated in different location (e.g., different species, landscape, human activities) (Sheaves, 2017; Sheaves et al., 2020; Sasmito et al., 2020). In addition, tidal wetland ecosystems have been commonly managed independently to each other (e.g., mangrove *versus* saltmarsh) based on arbitrary boundaries (e.g., vegetation type, intertidal zones) and on the belief that these systems are well-segregated and work in isolation (Weinstein and Litvin, 2016; Weinstein et al., 2014). These approaches ignore the complex patterns and interconnectivities characterising the coastal ecosystem mosaic (Sheaves, 2009; Beger et al., 2010; Colón-Rivera et al., 2012; Pearson et al., 2010; Rogers et al., 2014; Weeks, 2017). Concurrently, a poor understanding of the potential effects of future drivers such as sea level rise (SLR) on tidal wetland functioning and values further increases uncertainties about the long-term outcomes of current management and restoration strategies of coastal ecosystems (Sheaves et al., 2021).

Understanding the relationships between elevation, tidal hydroperiod (i.e., tidal flooding duration, depth, and frequency; tidal regime and range, Rozas, 1995; Ziegler et al., 2021) and vegetation distribution is viewed as the primary step necessary for successful restoration and management of saltmarshes (Warren et al., 2002; Waltham et al., 2021), and particularly this is the case when considering vulnerability to projected SLR and coastal change (Gesch, 2018; Colombano et al., 2021). Indeed, while studies have shown that factors such as soil water salinity, oxygen and nutrient availability, and intra- and interspecific competition play important roles in tidal vegetation patterns (Bertness and Shumway, 1993; Nunes and Camargo, 2018; Pennings et al., 2005; Ahmed et al., 2021), hydroperiod, and its relationship with microtopography, are often reported as a critical variable controlling saltmarsh distribution (Olff et al., 1988; Wang et al., 2007; Foti et al., 2012; Zhu et al., 2019b). In addition, tidal hydroperiod is an important mediator of seascape connectivity, controlling many broader values such as fish and crab habitat values and the export of trophic subsidies to coastal waters (Hollingsworth and Connolly, 2006; Davis et al., 2012;

Baker et al., 2013). Therefore, current saltmarsh and mangrove restoration and management approaches often target planting vegetation and restoring tidal connectivity, inferring that this will be sufficient to achieving the pre-defined restoration goals (Lewis III, 2005). However, variability in generally accepted relationships used to inform restoration and management strategies is described in the literature (Ziegler et al., 2021), such as distribution of species cannot only be explained by tidal hydroperiod and soil elevation alone (Silvestri et al., 2005), and that other underlying factors (e.g., groundwater dynamics) are contributing to tidal wetland distribution patterns (Moffett et al., 2012; Wilson et al., 2015).

Saltmarshes in tropical seascapes have received particularly little research attention (Saintilan and Adams, 2009; Reis et al., 2019). Yet, the causality and functionality of tropical saltmarshes might be different to other regions of the world because of nuanced features that influence vegetation distribution and connectivity in complex ways (Deegan et al., 2002; Reis et al., 2019). Examples include the seasonal and yearly variability in rainfall patterns and climatic events (e.g. El Niño Southern Oscillation (ENSO) and cyclones) characterising tropical climates and the presence of hypersaline flats (“saltpans”) and mangroves in dry-tropical coastal landscapes. In addition, increasing SLR and human urbanisation makes tropical saltmarshes particularly vulnerable to the “coastal squeeze” effect – where saltmarsh areas become squeezed between migrating mangroves up elevation due to SLR and coastal development sprawl on the landward edge (Saintilan et al., 2014; Armitage et al., 2015; Raw et al., 2021). Lower latitudes will also be particularly affected by changes in coastal flooding from SLR exacerbated by increasing cyclone frequency and intensity (Woodruff et al., 2013). For these reasons, understanding the current distribution patterns of tropical saltmarshes in the context of tidal hydrology and topography remains an area of coastal ecosystem mosaic needing more research attention.

This study investigated the patterns in tidal wetland cover distributions and their relationships to soil elevation and tidal hydroperiod in a tropical estuarine complex composed of saltmarshes, mangroves, and unvegetated flats, using a two-dimensional modelling and high-resolution topographic and land cover data described fully in Vulliet et al. (2023). The key goals of this research were to: (1) explore whether saltmarsh, mangroves and unvegetated flats responded to strict zonation patterns across soil elevation; (2) test whether there was variability in the generally accepted understanding that tidal hydroperiod and elevation are strong predictors of tidal wetland zonation in the context of our study site; (3) investigate the monthly variability in tidal hydroperiod and connectivity of tidal wetland cover across lunar months characterised by average and non-average tides; and (4) investigate the potential effects and implications of future SLR scenarios on the tidal wetland hydroperiods. The implications of our findings are discussed from a management and restoration perspective, highlighting the challenges facing long-term restoration and management successes, and indicating future directions to study and manage saltmarshes in tropical estuaries more effectively.

2. Methods

2.1. Study sites

This study is located in Blacksoil Creek (19.297867,147.021333; 82.54 ha), northern Australia (Fig. 1). The site is within the Ramsar internationally important Bowling Green Bay National Park, and adjacent to the Great Barrier Reef World Heritage Area and National Marine Park (Pearson et al., 2010). The study area (82.5 ha) represents the upper tidal to supratidal area of Blacksoil Creek (>300 ha), which is a bar-built estuary (Mattone and Sheaves, 2017). It is a short estuary (<5 km saltwater intrusion) with large sandy lower reaches and tidal creeks draining coastal lowlands (Sheaves, 2006). Although similar estuaries are found in the study area (Sheaves, 2006), the creek networks of

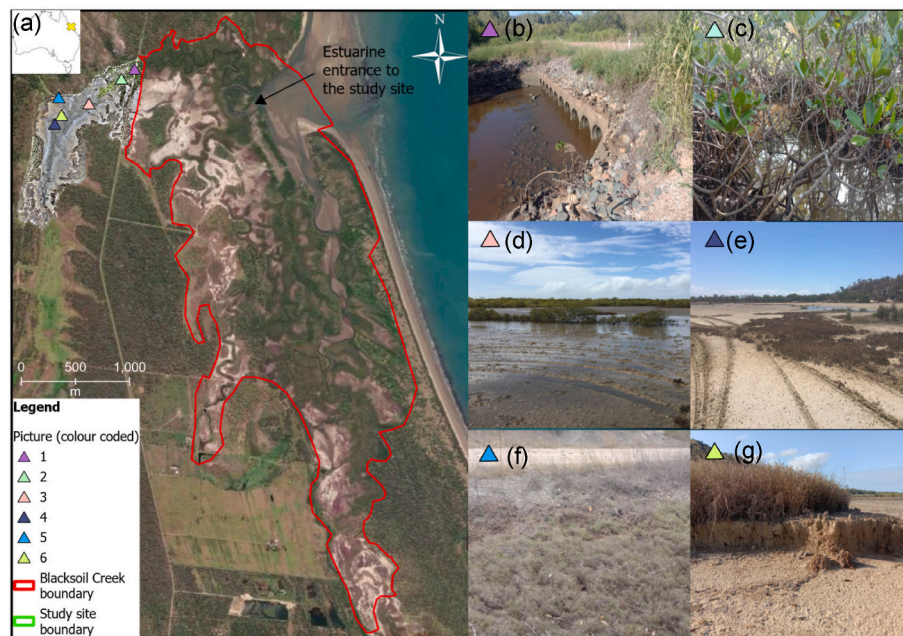


Fig. 1. (A) Study area map showing the location of the study site (in green) within the larger Blacksoil Creek estuarine complex (in red) and an indication of the estuarine entrance of the tidal creek (the “main channel”) leading to the study site. Ground pictures associated to the study site (from left to right) show (B) the main culvert at the entrance of the study site; (C) the main channel surrounded by *Rhizophora stylosa*; (D) inundated salt pans with patches of *Sarcocornia quinqueflora*; (E) drained salt pans with vehicles tracks and patches of *Sarcocornia quinqueflora*; (F) herbaceous saltmarsh dominated by *Sporobolus virginicus* with terrestrial vegetation along a dirt road; (G) salt pans and eroded banks of terrestrial grass and shrubs. Closer view and additional pictures of the study site are found in Vulliet et al., (2023). 2-Column fitting image.

Blacksoil Creek are shorter to that of other estuaries with long saltwater intrusions (>15 km) and complex creek networks draining substantial upstream areas (>1000 ha) of salt pans such as in the adjacent Cape Cleveland Bay (e.g., Crocodile Creek). Blacksoil creek has one main tidal creek (and its network of smaller tidal creeks) going to the south of the sand bar, and one, smaller, tidal creek going to the west. This creek (thereafter “main channel”) drains the study site and is interfered by a concrete road and its culverts (see below) (Fig. 1). This main channel becomes increasing narrower with higher elevation at the study site.

The extent of urban development and agricultural land within its catchment is relatively minimal (Mattone and Sheaves, 2017), which differs from others in the region (Sheaves et al., 2014), which have been largely fragmented by urban infrastructure along their shorelines (Sheaves et al., 2014). Nevertheless, cattle grazing, pastures, and sparse residential areas occur within the vicinity of the study site – a common feature of estuaries in the region (Sheaves and Johnston, 2009). The topography (Vulliet et al., 2023) and saltmarsh vegetation within the study area have been impacted by 4-wheel vehicles that use the area for recreational purposes (Fig. 1), which is a common problem in the study region (Trave and Sheaves, 2014). An important characteristic of the study site is that a concrete road, which was likely constructed in the late 1960s, restricts hydraulically tidal and rainfall runoff through a multi-pipe culvert structure (10 pipes of 1 m diameter) in addition to four small (~40 cm of diameter) single-pipe culverts along the eastern boundary (Fig. 1). The study area has an additional dirt road with a single-pipe culvert along its northern to western margin. Road crossings over tidal wetlands are a common attribute of North Queensland intertidal wetlands (Kroon and Phillips, 2015), which have created barriers to fish, invertebrates, and propagules movement (Sheaves et al., 2014).

The study area experiences a tropical-dry climate with strong seasonal rainfall, most occurring between November and April each year (900–1800 mm/yr) (Bruinsma, 2001). The tidal regime is semi-diurnal and mesotidal, with Highest Astronomical Tide (HAT) at 3.84 m above the Lowest Astronomical Tide (LAT) datum (2.15 m above the Australian

Height Datum (AHD) (Queensland, 2022). Bowling Green Bay is characterised by unidirectional coastal currents (Sheaves, 2006). Most of the main channel (>80%) at the study site remain inundated during neap tides cycle. Tides near 2.95 m (1.36 m elevation AHD) are required to start inundating the mangrove-saltmarsh ecotone in the study area (Vulliet et al., 2023), while tides greater than 2.6 m (1.01 m elevation AHD) trigger the inundation of mangroves adjacent to the main channel (Vulliet et al., 2023). The main channel is the principal source of surface tidal water exchange with the study site (Vulliet et al., 2023). The site does not receive surface freshwater upstream flow except during rainfall events.

Vegetation at the study site is dominated by the red mangrove, *Rhizophora stylosa*, along the main channel, which transitions to grey mangrove, *Avicennia marina*, and then yellow mangroves, *Ceriops tagal* and *Ceriops australis*, further perpendicular from the tidal channel (Fig. 1). The saltmarsh vegetation community is dominated by succulent marsh, notably the bead weed, *Sarcocornia quinqueflora*, with isolated patches of the glasswort, *Tecticornia* spp.; the grey samphire, *Tecticornia australasica*; pigweed, *Portulaca* spp.; pigface, *Carpobrotus glaucescens*; prickly saltwort, *Salsola australis*; and seablite, *Suaeda australis*. The herbaceous saltmarsh community is principally composed of the salt couch, *Sporobolus virginicus* with some greencouch, *Cynodon dactylon*, and jointed rush, *Juncus kraussii*.

2.2. UAV surveys and imagery processing

Details on field and UAV-SfM imagery processing methods are found in Vulliet et al. (2023). Briefly, a Phantom 4 RTK (Real Time Kinematic) connected to a DJI RTK Base Station was flown at 60 m to collect nadir images using 85% sides and forward images at both sites. Thirty-three ground control points (GCPs) were surveyed using a Real-Time Kinematic-Global Positioning System (RTK-GPS) (CHC i80) (Shanghai HuaCe Navigation Technology Ltd.) to geo-rectify the UAV imagery using Agisoft Metashape (Agisoft LLC).

The same Agisoft Metashape and ArcGIS Pro (ESRI) workflows

detailed in Vulliet et al. (2023) were used here to create orthomosaic and Digital Elevation Models (DEMs). Briefly, Digital Terrain Models were created using the in-built ground point filtering algorithms in Agisoft. The DTMs were then cleaned further from above-ground points using pixel editing tools in ArcGIS Pro and hydrologically corrected (Jarihani et al., 2015) using the “Fill” tool. Elevation accuracy of the DEM was assessed by evaluating the root mean square elevation error (RMSE), mean, standard error (SE), and standard deviation (SD) of 562 independent RTK-GPS validation points. Overall, the accuracy of the DEMs after modification in ArcGIS Pro was 0.08 m. Root mean square elevation error was 0.04 m in mangroves, 0.08 m in succulent saltmarsh and 0.12 m in herbaceous saltmarsh. Further details on the accuracy of the DEM are found in Vulliet et al. (2023).

2.3. Land cover attributes

The orthomosaic maps generated from the dense point clouds were used to classify key land cover attributes. Land cover attributes were divided into *R. stylosa/A. marina* (abbreviated as “M” for mangroves others than *Ceriops* spp.); *Ceriops* spp. (C); succulent saltmarsh (SS); herbaceous saltmarsh (HS); mudflats/salt pans (MS); main channel; human/manmade; and woodland/grass/terrestrial. Manual classification was performed in ArcGIS Pro as unsupervised and supervised object-based image classification algorithms were found to be unreliable (Vulliet et al., 2023). The manual classification process is fully described in Vulliet et al., 2023. Briefly, the orthomosaic was zoomed in so that each land cover feature could be identified and circled around to create polygons. A confusion matrix could not be used to provide an accuracy assessment. However, the high-resolution of the imagery together with expert knowledge and on-ground imagery enabled confident reliability of the classification of the land cover (Vulliet et al., 2023).

2.4. Data analyses

2.4.1. Distribution of tidal wetland cover

To relate the wetland cover to the elevation raster, wetland cover shapefiles were first converted to 0.1 m rasters and then to points, resulting in 1 point per 0.1 m. Elevation at point was extracted to obtain summary statistics to generate mean and standard elevation graphs (following Silvestri et al., 2005) as well as elevation frequency graphs for each tidal wetland cover (i.e., *R. stylosa/A. marina*, *Ceriops* spp., succulent saltmarsh, herbaceous saltmarsh and mudflats/salt pans). Note that each land cover had outliers (i.e. data points representing extreme values) due to high number of data points, DEM inaccuracies, and potential centimetre-scale errors in manual land cover classification. The data are presented without the outliers, as removing the outliers reduced kurtosis and skewness, but did not change the summary statistic results (mean, median, and mode) (more than at the 0.001–0.01 cm scale) of wetland cover elevation values. Detailed summary statistics with and without outliers are provided in Supplementary Materials (Supplementary Table 1) with a boxplot showing the distribution of the outliers (Supplementary Fig. 1).

2.4.2. Tidal wetland inundation characteristics across lunar month and wetland cover

The 2D hydrodynamic model developed by Vulliet et al. (2023) was used here to measure spatial and temporal variability in tidal inundation and to calculate the mean hydroperiod of each wetland cover class. The model was developed with the free software HEC-RAS 6.1 (Windows) using the 2D Unsteady Diffusion Wave equations. The software used a sub-grid bathymetry approach that is strongly dependent on the terrain resolution (Brunner, 2016). The data inputs were: 1) UAV-derived DEM; 2) the Land Cover dataset with associated Manning’s roughness coefficient values; and 3) tidal data corresponding to periods at which pressure loggers were deployed (Vulliet et al., 2023). To capture the variability in tidal inundation that wetlands experience across lunar

months, we decided to compute inundation simulations for three lunar months of 751.2 h (31.3 days) characterised by lower (low), average (average), and higher (high) than average spring tides using the same hydrodynamic model settings used in Vulliet et al. (2023). As in Vulliet et al. (2023), inundation patterns were well presented by the model with RMSE between observed and simulated inundation of 0–0.055 m (Supplementary Figs. 2–4). Some inundation duration and maximum depth inaccuracies were noted (Supplementary Figs. 2–4), notably at five loggers near the main mangrove channel and a small drain were inundation and maximum depth were under or overestimated (loggers 1, 6, 7, 15, 19) (Supplementary Figs. 2–4). These five loggers influenced RMSE in elevation duration (calculated as the root mean square error between the number of observed and simulated 10-min intervals above 0 m) to 35.67 h compared to 9.53 h over the entire simulation periods without these loggers. Spatial and temporal variability in model performance was likely influenced by several factors. These include model configuration and uncertainty in data inputs (e.g., DEM and spatial variability in roughness), and the use of the Unsteady Flow Equation (UFE) instead of the Shallow Water Equation (SWE). In addition, the absence of data inputs on potentially important processes influencing tidal surface flow propagation (e.g., wind, atmospheric pressure, soil morphology, eco-hydrogeomorphological feedbacks) may have influenced the accuracy of the model. The model performance is discussed in depth in Vulliet et al. (2023).

Maps showing maximum inundation area and hydroperiod characteristics (maximum depth (m), duration of inundation (hrs), and percent time inundated (%)) were generated from HEC-RAS for each simulation. The hydrodynamic outputs were then used to extract the hydroperiod characteristics of each tidal wetland class using the same method as elevation.

Relationships between maximum inundation depth, duration of inundation, elevation and tidal wetland type distribution were investigated by extracting raster values from 10,000 points randomly generated in ArcGIS Pro for each simulation and converted to a presence-absence dataset of tidal wetland cover. The BIO-ENV routine in PRIMER (Clarke and Ainsworth, 1993) was used on the presence-absence of tidal wetland land cover to investigate the extent to which elevation, duration of inundation, and maximum depth (environmental dataset) accounted for the observed distribution in tidal wetland land cover (community dataset). To address the potential effects of collinearity in the analyses, only the normalised elevation and lower-than-average duration variables were retained as the potential explanatory environmental variables pooled across simulations. Elevation showed strong relationships with higher-than-average tides (Spearman correlation test: Elevation ~ Maximum depth: $r^2 = -0.96$, $p < 0.001$; Elevation ~ Duration of inundation: $r^2 = -0.93$, $p < 0.001$) and average tides ($r^2 = -0.93$, $p < 0.001$; Elevation ~ Duration of inundation: $r^2 = -0.92$, $p < 0.001$). The relationship between elevation and lower-than-average tide hydroperiod was weaker (Elevation ~ Maximum depth: $r^2 = -0.79$, $p < 0.001$; Elevation ~ Duration of inundation: $r^2 = -0.79$, $p < 0.001$). In addition, maximum depth was strongly positively related to duration of inundation ($r^2 = 0.95$, $p < 0.001$ for higher-than-average tides; $r^2 = 0.99$, $p < 0.001$ for average tides; $r^2 = 0.98$, $p < 0.001$ for lower-than average tides).

2.4.3. Sea level scenarios

To examine the potential effects of SLR on the hydrological connectivity and tidal inundation characteristics at the study site, sea level scenario simulations were performed by adding 0.03 m and 0.08 m (likely SLR by 2100 in the study region (Queensland, 2019)) to the tidal height data for each lunar month scenario. Tidal inundation characteristics of each tidal wetland cover were then extracted following the same method described above.

3. Results

3.1. Distribution of tidal wetland cover with soil elevation

Elevation frequency distribution graphs were computed by extracting elevation from the 0.1 m-spaced land cover point features. There was an overall pattern of changes in vegetated and unvegetated cover with elevation. Low elevations (0.15–1 m) were predominantly occupied by mangroves, followed by *Ceriops* spp., succulent saltmarshes and herbaceous saltmarshes as elevation increased. The graphs also revealed there were clear differences in elevation between some covers (e.g., *R. stylosa/A. marina* and herbaceous saltmarsh). However, there were also overlapping elevation distribution among vegetated and unvegetated covers (Fig. 2). All vegetated and unvegetated cover had non-normal elevation frequency distribution (Kolmogorov–Smirnov statistic: $D > 0.4$; $P < 0.001$ for each class). The distributions of *R. stylosa/A. marina* and *Ceriops* spp. had bimodal distributions. The distributions of herbaceous and succulent saltmarshes as well as mudflat/salt pans were quite unimodal and relatively symmetrical around the mode, most notably was the herbaceous saltmarsh. Detailed summary statistics on the elevation distribution of each wetland cover class are found in Supplementary Table 2.

3.2. Tidal wetland cover hydroperiods

Analyses of average maximum water depth, inundation duration, and percent time inundated per vegetated and unvegetated covers showed that *R. stylosa/A. marina* had the highest mean maximum depth, duration of inundation, and percentage of time inundated, followed by *Ceriops* spp., mudflats/salt pans, succulent saltmarsh, and herbaceous saltmarsh (Fig. 3). However, large standard deviations (Supplementary Table 3) suggest that there was variability in the mean tidal hydroperiod of each tidal wetland cover.

3.3. Tidal hydroperiod and elevation as drivers of tidal wetland cover zonation patterns

The BIO-ENV routine was used to determine the extent to which elevation and tidal hydroperiod variables explained the presence-absence of each tidal wetland vegetated and unvegetated cover. Higher-than-average and average hydroperiod variables were strongly correlated to elevation and were discarded from the analyses. Of the variables retained in the analyses (elevation and lower-than-average tide duration of inundation), the routine identified elevation as the factor explaining 15% of the variability of the presence-absence of tidal wetland cover pooled across the three simulations.

3.4. Variability of tidal hydroperiod and saltmarsh connectivity across lunar months

The data here revealed obvious differences in the tidal connectivity between the lunar months characterised by higher-than-average, average, and lower-than-average tides (Fig. 4) (Table 1). The model revealed that even during higher-than-average tides, which occurred 1–2 times per year in 2019–2021 (Table 2) and are shown to inundate 52.04 ha of the study site (Fig. 5), some of the saltmarsh community would have still remained disconnected from the tidal inundation. Indeed, 23% (1.37 ha) of herbaceous saltmarsh and 66% (4.24 ha) of succulent saltmarsh (Supplementary Table 3) became inundated during the higher-than-average simulation. Herbaceous saltmarsh had even more limited tidal flow connectivity in average-tide scenarios, with only 1% (0.10 h) becoming inundated and 24% (1.51 ha) for succulent saltmarsh. Considering that months with the same average-tides as simulated here are relatively frequent (6–7 times/year in 2019–2021), the model revealed that only a small proportion of the saltmarsh community is frequently connected by tides. Saltmarsh connectivity is much

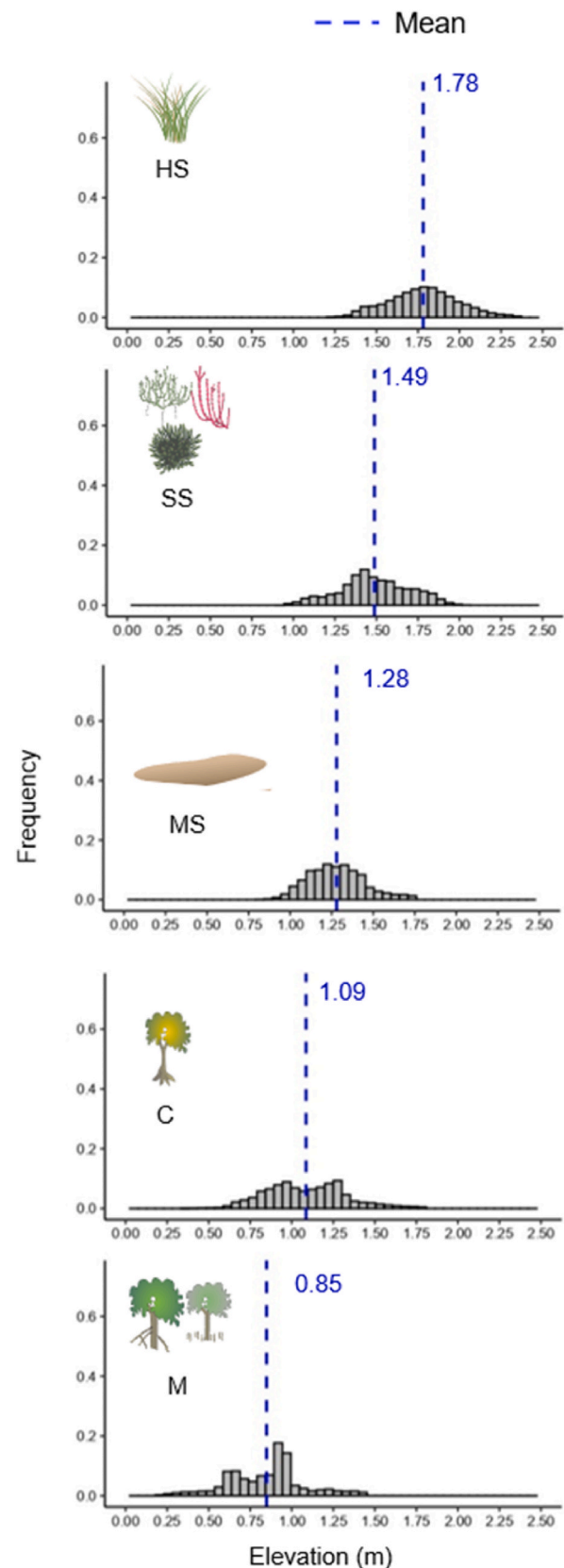


Fig. 2. Elevation frequency of tidal wetland land cover class. “HS” = Herbaceous saltmarsh; “SS” = Succulent saltmarsh; “MS” = Mudflats/Salt pans; “C” = *Ceriops* spp.; “M” = *R. stylosa/A. marina* (abbreviated as “M” for mangroves other than *Ceriops* spp.). Single-column fitting image.

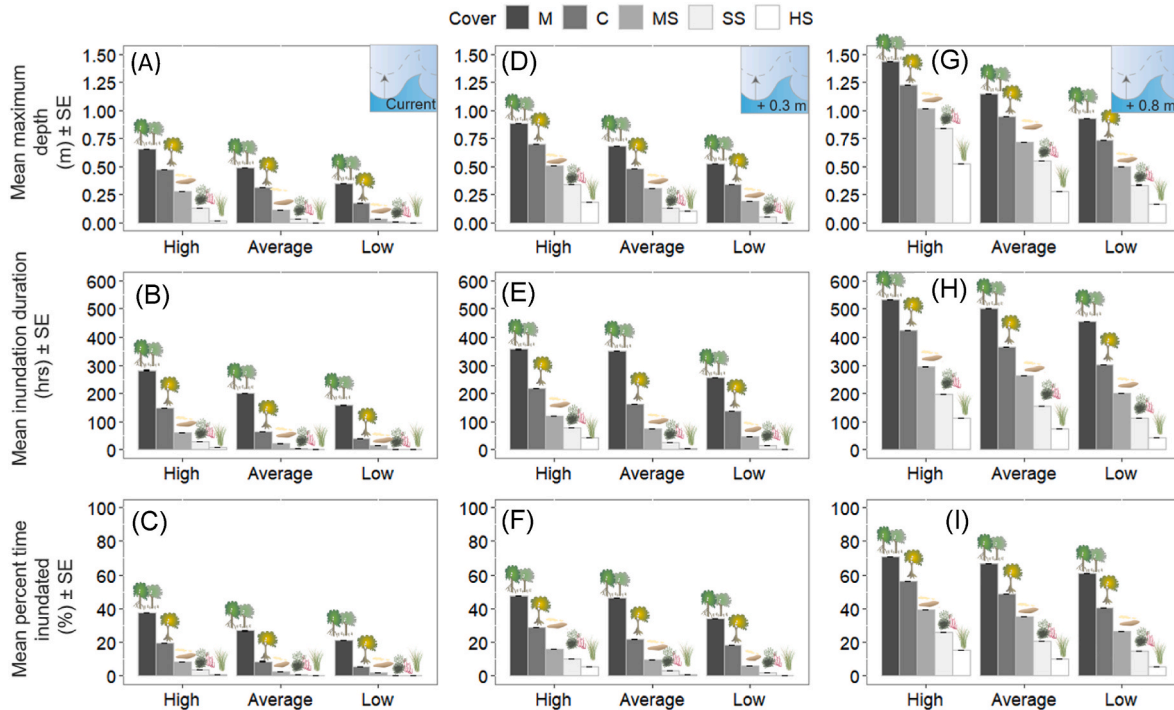


Fig. 3. Mean maximum depth, duration of inundation (hours) and percent time inundated \pm standard error (SE) per tidal wetland land cover for: (A–C) current, (D–F) +0.3 m, and (G–I) +0.8 m sea level rise scenarios for the higher-than-average tide (High), average (Average), and lower-than-average tide (Low) scenarios. “HS” = Herbaceous saltmarsh; “SS” = Succulent saltmarsh; “MS” = Mudflats/Salt pans; “C” = *Ceriops* spp.; “M” = *R. stylosa/A. marina* (abbreviated as “M” for mangroves other than *Ceriops* spp). **2-Column fitting image.**

lower in months with lower-than-average tides, which occurred 1–3 times/year in 2019–2021, with respectively 0.1% (0.01 ha) and 10.3% (0.66 ha) of herbaceous and succulent saltmarsh being inundated within this study.

3.5. Sea level rise

Projected SLRs of +0.3 m and +0.8 m were simulated here without considering processes of accretion and landward migration of tidal vegetation (Fig. 5). Overall, the inundation extent increased from 52.94 ha (current) to 62.58 ha (+0.3 m) and 72.18 ha (+0.8 m), in the higher-than-average simulation, from 37.38 ha (current) to 53.42 ha (+0.3 m) and 68.12 ha (+0.8 m) in average tide simulation, and from 19.60 ha (current) to 41.49 ha (+0.3 m), and 61.85 ha (+0.8 m) in lower-than-average tide simulation. This suggests that in a +0.8 m projected SLR scenario, lower-than-average tides would increase the inundation of the study site by 8.91 ha when compared to the current higher-than-average tides.

An increase in hydroperiod was observed for each land cover class under the sea level scenarios (Fig. 4). For instance, in higher-than-average tides +0.8 m sea level, succulent saltmarsh would have a mean-maximum inundation depth that is 184.1 mm higher than the current mean-maximum inundation depth of *R. stylosa/A. marina*. Changes in the duration of inundation would also be important. For instance, at +0.8 m, succulent saltmarsh mean inundation duration would be higher than the current *Ceriops* spp. Inundation in all tides.

4. Discussion

Tidal wetland ecosystems such as saltmarshes are threatened by ongoing degradation from human land use and climate change-driven factors such as rising sea levels. While ecosystem restoration is an increasingly appealing mitigation strategy to compensate for the losses in services that tidal wetlands provide (Waltham et al., 2020; Adams

et al., 2021), restoration success is dependent on a careful understanding of past, present, and future contexts that might influence restoration outcomes (Sheaves et al., 2021). Increasing our understanding of the distribution of tidal wetland vegetation in relation to elevation and tidal hydroperiod and the potential effects of future SLR on current hydrological patterns, such as established in this study, is particularly important to direct future research and assisting coastal managers in developing long-term strategies to manage and restore tidal wetland ecosystems.

4.1. Overlapping elevation: the need for a holistic understanding of habitat functioning

The vegetated and unvegetated zonation pattern observed in the tropical tidal wetland studied here is characteristic of eastern Australian intertidal wetland seascape configuration (Saintilan and Adams, 2009), with an overall succession pattern of mangroves at lower elevations near mean sea level (MSL) and transitioning to herbaceous saltmarsh at higher elevations around HAT. Our findings reveal that tidal wetland cover did not display well-segregated zonation patterns but displayed overlapping and mosaic patterns across micro-topographic gradients. Mosaic patterns in the distribution of saltmarshes and mangroves at similar elevations have been described in tropical northern Australia (Saintilan et al., 2009) and elsewhere (Osland et al., 2013; Saintilan et al., 2019), and advise that tidal wetland distribution does not respond to strict zonation arrangements that might be commonly applied in management and legislation (e.g., Marine Estate Management Act, 2014; Rogers et al., 2016). Understanding the biological and physical processes that facilitate co-existence compared to the conditions that result in more segregated zonation patterns between saltmarsh, mangroves, and unvegetated flats would provide valuable insights in our understanding of the zonation of those systems. In addition, the results support that research and restoration effects should prioritise a more holistic or system understanding (e.g., “whole-of-catchment strategies”,

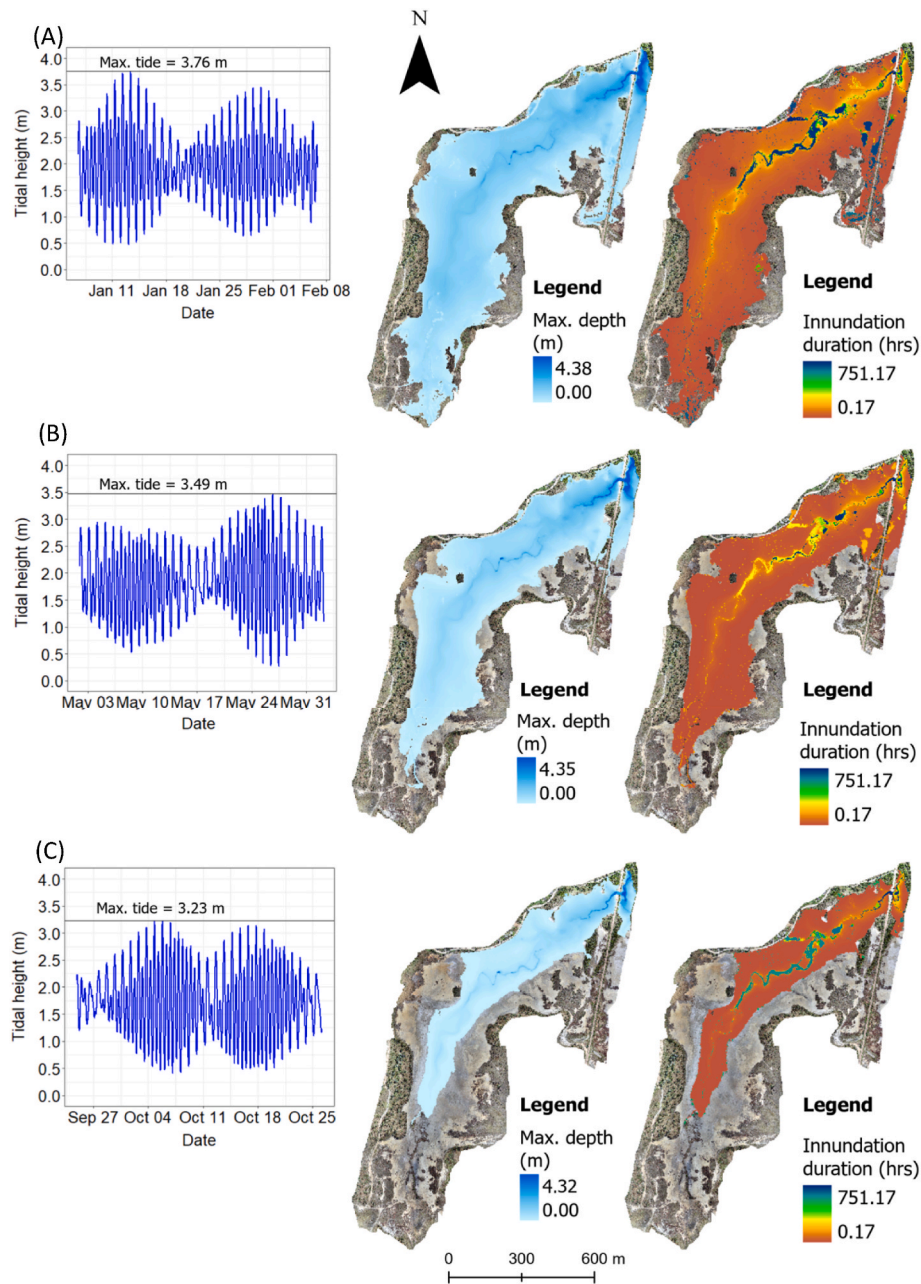


Fig. 4. Observed tidal height (m) recorded at Cape Ferguson tidal gauge (−19.277208; 147.060908), Australia with associated maps of simulated maximum depth and inundation duration (hours) for each lunar month: (A) Higher-than-average tides observed in January 2021; (B) Average tides observed in June 2022; and (C) Lower-than-average tides observed in September 2021. **2-Column fitting image.**

Table 1

Maximum tidal height (m) and inundation extent (ha) in the higher-than-average tide lunar month (January 2022, “High”), average tide lunar month (June 2022, “Average”), and lower-than-average tide lunar month (September 2022, “Low”) for the current sea level rise and +0.3 m and +0.8 m sea level rise scenarios.

	High			Average			Low		
	Current	0.3 S L	0.8 S L	Current	0.3 S L	0.8 S L	Current	0.3 S L	0.8 S L
Maximum tidal height (m)	3.76	4.06	4.56	3.49	3.79	4.29	3.23	3.53	4.33
Inundation extent (ha)	52.94	62.58	72.18	37.38	53.42	68.12	19.60	41.49	61.85

State of Queensland, 2016) of these habitats, encompassing their interconnectivities and functionality as closely adjacent and overlapping habitats and ecotones (Begam et al., 2017; Yando et al., 2018; Ghosh et al., 2022).

In the case of managing tidal wetland values to aquatic biota such as

fish and crabs, the presence of overlapping tidal wetland cover and varying tidal connectivity for similar vegetation presents a model that managers need to move beyond a “vegetation-based approach” (e.g., mangrove versus saltmarshes) to a more contextual or process-based approach (e.g., tidal connectivity) (Bradley et al., 2020). For instance,

Table 2

Number and percentage of lunar months in 2019, 2020, and 2021 with maximum tide categorised as higher-than-average (“High”), average (“Average”), and lower-than-average (“Low”).

Year	Type of tides		
	“High”: $\geq 3.76 \pm 0.1$ m	“Average”: $\geq 3.49 \pm 0.1$ m	“Low”: $\geq 3.23 \pm 0.1$ m
	Number of tides ≥ 3.86 ; ≥ 3.76 ; ≥ 3.66 (Percentage of total maximum tides)	Number of tides ≥ 3.59 ; ≥ 3.49 ; ≥ 3.39 (Percentage of total maximum tides)	Number of tides ≥ 3.33 ; ≥ 3.23 ; ≥ 3.13 (Percentage of total maximum tides)
2019	0; 2; 3 (0%; 16.7%; 25%)	4; 7; 8 (33.3%; 58.3%; 66.7%)	9; 10; 12 (75%; 100%; 100%)
2020	0; 1; 3 (0%; 8.3%; 25%)	5; 7; 10 (41.7%; 58.3%; 83.3%)	10; 12; 12 (83.3%; 100%; 100%)
2021	0; 1; 1 (0%; 8.3%; 8.3%)	4; 6; 11 (33.3%; 50.0%; 91.7%)	11; 11; 12 (91.7%; 91.7%; 100%)

the present study raises questions on the difference in the values to aquatic biota of mangrove and saltmarsh occupying similar elevations or between saltmarshes that are tidally connected compared to saltmarshes that are not connected even during higher-than-average tides. Many studies have demonstrated that similar vegetation types might have different causality and hence functions and values to aquatic biota (Bradley et al., 2019; Rozas, 1995; Minello et al., 2012; Morley et al.,

2020), which might vary at small spatial scales (e.g., saltmarsh pools within the same location) (Davis et al., 2014). This is important for management given that tidal wetlands might not necessarily require similar prioritisation or management and restoration actions depending on their contextuality (Neal et al., 2018; Rabinowitz et al., 2023), even if they contain the same species or type of vegetation (e.g., mangroves; Sheaves, 2017).

4.2. Elevation and hydroperiod as drivers of vegetation patterns

The important role of tidal inundation in influencing tidal vegetation patterns was highlighted by the distinct maximum depth, duration of inundation, and percent time inundated of each tidal wetland cover. Nevertheless, the expected linear and strong relationships between tidal vegetation distribution and elevation and tidal hydroperiod, which usually form the scientific basis of restoration decisions (Friess, 2017), lacked “appropriate evidence” (sensu Sheaves et al., 2020) in the case of our study site. This likely suggests that other factors not studied here (Table 3) more strongly contribute to the observed vegetation patterns at the study site (Fig. 6) than elevation and tidal hydroperiod. This is consistent with previous studies that did not establish strong links between saltmarsh distribution patterns and tidal hydroperiod and elevation (e.g., Eleuterius and Eleuterius, 1979; Silvestri et al., 2005; Moffett et al., 2012). These findings are particularly important because they highlight the complexities and uncertainties facing coastal managers challenged to restore and manage these inherently complex and dynamic systems (Harris and Heathwaite, 2012; Bayraktarov et al., 2016;

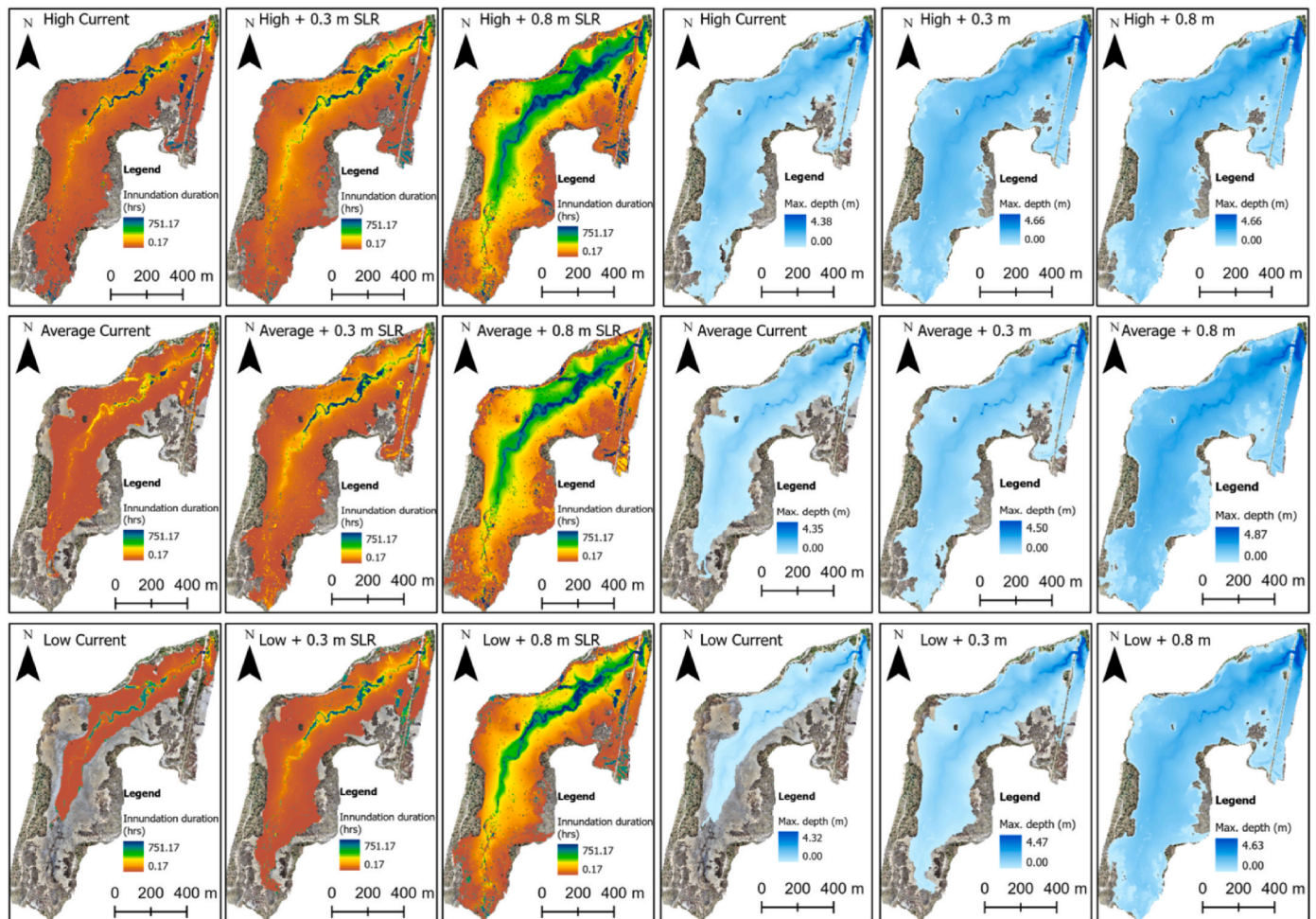


Fig. 5. Simulations of inundation duration (hrs) and maximum depth (m) under current, +0.3 m and +0.8 m sea level rise for the higher-than-average tide (High), average (Average), and lower-than-average tide (Low) scenarios. 2-Column fitting image.

Table 3

Additional potential abiotic, anthropogenic, and biotic factors beyond soil elevation and tidal surface hydrology that might interact with each other and influence wetland vegetation and unvegetated flats distribution patterns at the study site.

Factors	Examples of abiotic and biotic factors that might influence tidal wetland vegetation patterns	Abiotic and biotic effects	Examples of studies
Abiotic	Subsurface flow and groundwater dynamics	Soil properties (e. g., soil type, conductivity, redox potential) Soil aeration Root respiration Germination and seedling growth	Moffett et al., 2012; Wilson et al., 2015; Wilson and Morris, 2012; Xiao et al., 2017; Xin et al., 2013; Xin et al., 2022
	Past rainfall and climatic events	Periods of droughts and rainfall influence stress gradients, which may favour the establishment of some species over others.	Duke et al., 2019; Duke et al., 2017
	Wind-induced waves	Increase/decrease tidal inundation extent	Bendoni et al. (2014)
	Atmospheric pressure	Increase/decrease tidal inundation extent	Goodman et al. (2018)
	Creek densities and morphologies	Influence surface and subsurface water exchange, sediment dynamics, propagule dispersal	Fleri et al., 2019; Whitt et al., 2020
	Soil type and properties (including salinity) Soil moisture Nutrient availability	Oxygen availability Root respiration Germination and seedling growth Growth limitation (specific responses)	González-Alcaraz et al., 2014; Xin et al., 2017 Rogel et al., 2000 Morris et al., 2013; Redelstein et al., 2018; Simpson et al., 2013 Rodríguez et al., 2017; Xin et al., 2022
Anthropogenic	Culverts and roads	Influence surface, subsurface and groundwater dynamics. Influence flow attenuation with consequences on water retention time, inundation depth, and periods of wetting and drying.	
	4WD vehicle uses	Affect cover distribution and composition; influence soil compactness and local hydroperiod;	Kelleway, 2006; Trave and Sheaves, 2014; Vulliet et al., 2023
Biotic	Competition	Competition of one species over the other	Nunes and Camargo, 2018, 2020; Pennings et al., 2005; Bertness and Shumway, 199
	Facilitation	Facilitate intra and inter-specific establishment (e.	Bertness and Shumway, 1993; Ghosh et al., 2022

Table 3 (continued)

Factors	Examples of abiotic and biotic factors that might influence tidal wetland vegetation patterns	Abiotic and biotic effects	Examples of studies
	Propagule dispersal and establishment	g., soil accretion, salt removal) Propagule establishment depends on the abiotic and biotic conditions at the time of establishment (highlighting that past conditions are important in explaining current patterns).	Robert et al., 2015; Van der Stocken et al., 2015; NOE and Zedler, 2001
	Crab burrowing activity	Influence porewater and subsurface water exchange	Xin et al. (2009)

Sullivan et al., 2018; Williamson and Gattuso, 2022). The processes determining the successful establishment and development of tidal wetland vegetation at a given location may be more complex (Fig. 6) than “oversimplistic rules” based on tidal hydroperiod and elevation alone (Bertness and Pennings, 2002; Silvestri et al., 2005; Clarke, 2014; Friess, 2017; Lee and Kim, 2018; Rogers and Krauss, 2019; Xin et al., 2022), or attempts to replicate the environmental conditions of a reference state (Sullivan et al., 2018). This suggests that a comprehensive understanding of the contextual factors likely to influence a successful ecological outcome in a given context (e.g., Table 3) might be more necessary than generally thought for management and restoration plans (Friess, 2017; Sheaves et al., 2021). This is notable in the context of our study site which represents high intertidal to subtidal areas punctuated by roads where factors other than surface tidal inundation, notably groundwater dynamics (Moffett et al., 2012) and past climatic events (Duke et al., 2017, 2019), among additional factors (Table 3), might exert a high control on vegetation patterns (Huckle et al., 2000; Rodríguez et al., 2017; Goodwin and Mudd, 2019).

The approach taken here to investigate monthly variability in tidal hydroperiod was important in profiling the substantial variability in tidal conditions and hydrological connectivity experienced by each type of intertidal wetlands across lunar months. Monthly variability in tidal inundation, including non-average tides are rarely integrated in restoration studies (Van Loon et al., 2016), but as demonstrated here, requires careful consideration in order to understand how non-average tides might influence tidal wetland communities and their connectivity.

4.3. Sea level rise: an additional driver of uncertainty

An important aspect of this study was the demonstration of the complexities facing managers and long-term restoration success when considering SLR. Our results show significant changes in tidal wetland inundation characteristics in response to future sea levels projected in the study region. This supports the requirement of coastal managers to acknowledge that current patterns in the hydroperiod of sites might not be the same in the future (Sheaves et al., 2021). For instance, while tidal hydroperiod was not found to be the most predominant factor of zonation here, it might become more of a contributing attribute describing vegetation patterns in the future with rising sea levels. Because the factors contributing to tidal vegetation distribution patterns are spatially and temporally variable (Rogers and Krauss, 2019), effective management requires strategies that can adapt to new knowledge and changes

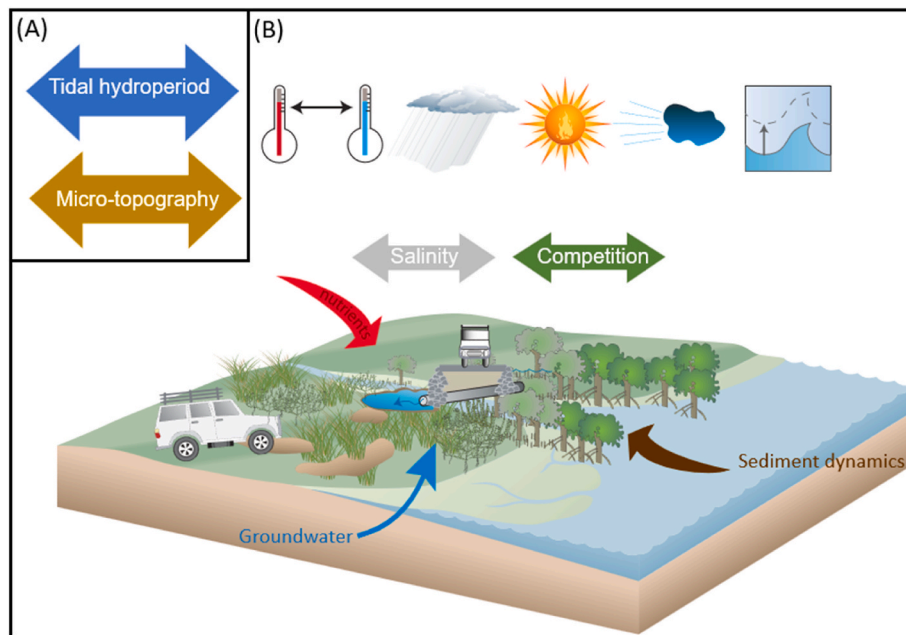


Fig. 6. Conceptual diagram of (A) the processes studied in the present study by opposition to (B) the likely interacting processes, together with tidal hydroperiod and microtopography, (B) that shape saltmarsh and mangrove zonation patterns in tropical seascapes. **2-Column fitting image.**

in contextual factors (“adaptive management”) (Waltham et al., 2021). In addition, it supports the need for additional research on how, and how fast, tropical tidal wetlands such as saltmarshes and mangroves will adapt to future SLR projections. Our ability to predict their adaptation to SLR largely depends on our current understanding of the many interacting climatic, hydrological, geomorphological, ecophysiological, and anthropogenic processes and factors (and their feedbacks) influencing wetland distribution (Rogers and Krauss, 2019). For instance, higher SLR may favour more sediments supply, which may contribute to higher accretion rates, and thus the ability for saltmarsh and mangroves to keep up with SLR (Kirwan and Megonigal, 2013). Therefore, the present tidal hydroperiod results here under SLR likely represent an overestimation of the effect of SLR (Kirwan et al., 2016). In the case of the study site and the study region in general, there is an urgent need to start acquiring current information on context-specific and species-specific saltmarsh and mangrove accretion rates and feedback with hydrological and sediment dynamics (Krauss et al., 2014; Fagherazzi et al., 2020) as well as the availability of space for landward migration (Schuerch et al., 2018). This data will be necessary to start developing more accurate models of their potential responses to SLR (e.g., Kumbier et al., 2022) and plan their management and accommodation under SLRs with greater certainties (Roman, 2017; Schuerch et al., 2018; Kumbier et al., 2022).

4.4. Limitations of the approach

The present study experienced uncertainties in obtaining information on tidal wetland hydroperiod and elevation that have been discussed in Vulliet et al., 2023. Similar to Sadro et al. (2007), the lack of normality in the elevation frequency distribution of each vegetated and unvegetated cover might result from the misclassification of land cover features. Notably, the misclassification of herbaceous saltmarsh with terrestrial vegetation might have inaccurately represented this category with higher elevation, contributing to the low inundation duration within this category. Additionally, tidal inundation might have been underestimated in the areas further away from the main tidal creek, where densely vegetated areas such as herbaceous saltmarsh increased DEM inaccuracies (RMSE = 0.12 m in herbaceous saltmarsh). Additional pressure loggers placed below the ground (e.g., Kumbier et al., 2021)

rather than at the surface might have provided additional insights into the hydrological dynamics of these distant saltmarshes. Also, the pooling of similar species for classification purposes might have affected the accuracy of the results. For instance, the bimodal distributions for *Cerriops* spp. and *R. stylosa/A. marina* may be due to the species mix in addition to the other factors explained above. Using a multi-spectral camera and UAV-Lidar (Pinton et al., 2020; Zhu et al., 2019a) may improve vegetation classification, DEM accuracies, and, subsequently, the relationships between vegetation distribution, topography, and inundation characteristics. In addition, the fact that only one UAV survey was conducted and used as the basis for each hydrodynamic modelling simulations assume that vegetation distribution and soil elevation are temporally static. This is a limitation of the modelling approach discussed in Vulliet et al. (2023) as tidal wetland vegetation cover and soil elevation in saltmarshes can vary seasonally such as in response to tidal dynamics (Oloff et al., 1988; Jin et al., 2022) and rainfall (Duke et al., 2019) – although no interannual variability in saltmarsh vegetation cover has also been described (Teal and Howes, 1996). Despite these limitations, it is worth noting that high-resolution spatial investigations of wetland vegetation distribution to tidal inundation, as developed here using UAV technology, are relatively new and might reveal more variability in intertidal wetland zonation than currently understood using transect studies (which has been highlighted by Zhu et al., 2019a).

5. Conclusions

Given the accelerating degradation of coastal wetland ecosystems and increasing interest in restoration of coastal ecosystems, understanding how coastal ecosystems are likely to deal with future projected climate change is becoming more necessary for long-term conservation and management positive outcomes. Restoration and management practices are often based on generalised understandings of mangroves and saltmarshes causality (Rogers and Krauss, 2019), such as that zonation patterns are strongly linked to tidal hydroperiod and soil elevation. However, the present study has established that, in the context of our study site, patterns in tidal wetland zonation could well respond to micro-topographic changes in soil elevation and tidal inundation, but could not be explained solely by those variables. For

example, groundwater dynamics may be important at explaining some of the patterns at the study site. These complex patterns in the distribution and tidal connectivity of tidal wetlands observed here, together with the uncertainties in explaining zonation patterns, support the need to approach coastal ecosystems from a holistic, multidisciplinary approach. This approach should consider interactions and uncertainties associated with the many processes that shape the functions and values of intertidal wetlands (Sheaves et al., 2021). In addition, this study raises many questions that warrant future research, such as: a) the variability of the present findings in varying spatial and temporal contexts; b) the effects of factors not studied here (Table 3) on explaining zonation patterns; c) the values and functions of different vegetation types occupying similar elevations or similar vegetation types with different tidal connectivity; and d) the adaptive and contextual response of tidal wetlands to SLR.

The workflow presented here, combining a high-resolution DEM from a UAV and a 2D hydro-model derived from UAV data, presents a novel approach that can be used by managers and practitioners to obtain a preliminary understanding of tidal wetland zonation patterns, and their causality and tidal hydrological connectivity. Replicating similar spatial works in additional sites will enable to establish in which contexts generally accepted relationships may be more confidently applied in decision-making or restoration plans or, conversely, when they require further scrutiny and additional data collection before being used as a basis for management and restoration strategies (Bradley et al., 2020; Sheaves et al., 2020, 2021). However, modelling approaches that consider multiple contextual factors in the distribution of tidal wetland vegetation, including their temporal and spatial variability (Rogers and Krauss, 2019), will ultimately be necessary to develop robust understanding and management of these important but intrinsically complex ecosystems.

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CRediT authorship contribution statement

Cécile Vulliet: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jack Koci:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Formal analysis. **Marcus Sheaves:** Writing – review & editing, Supervision, Resources. **Nathan Waltham:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106485>.

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