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Saltmarsh Connectivity in Tropical Seascapes: An Eco-hydrological Perspective

Thesis submitted by

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ABSTRACT

Saltmarsh ecosystems are some of the most productive ecosystems on earth. They are also particularly vulnerable to changes in seascape connectivity resulting from human development and sea-level rise (SLR). Although restoring and managing saltmarsh connectivity is at the centre of major conservation talks, our understanding of the drivers and values of tidal wetland connectivity is still mostly conceptual, particularly in the tropics. A quantitative understanding of the effects of tidal connectivity on ecological patterns and processes is lacking. In addition, tools that can be used by coastal managers and scientists to study tidal wetland connectivity and assess the effects of its change on tidal wetland values are limited. In this research, I questioned the extent to which tidal hydrological connectivity (expressed as tidal hydroperiod and the extent of tidal wetland inundation) mediate important ecological patterns (i.e., vegetation distribution) and processes (i.e., prey pulses) within a tropical estuarine complex composed of saltmarshes, mangroves and unvegetated flats. To investigate this research question, I developed a high-resolution digital elevation model (DEM) and land cover map using unoccupied aerial vehicle (UAV)-structure from motion photogrammetry (SfM) to parameterise a two-dimensional hydrological model used to simulate tidal wetland inundation and calculate tidal wetland hydroperiod. I then investigated (1) the variability of tidal wetland inundation across months; (2) the distribution of saltmarshes, mangroves, and unvegetated flats in relation to elevation and tidal hydroperiod; and (3) the potential effects of SLR scenarios on tidal wetland hydroperiod. I then researched to what extent the export of prey pulse under the form of crab zoea, a process symbolising the importance of seascape connectivity, was related to tidal inundation patterns and to the inundation of saltmarshes. Lastly, I used Bayesian Belief Network modelling to illustrate the trade-offs in tidal wetlands values that may result from different scenarios of changes (SLR and reduction in tidal inundation) in tidal wetland inundation patterns. Overall, this research

presents new insights into the values of tidal connectivity in tropical saltmarshes, while emphasising the importance of viewing saltmarshes as an integrated part of the tropical coastal ecosystem mosaic.

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1.1 Introduction

Tidal saltmarshes (hereafter "saltmarshes") are a coastal ecosystem initiated by halophyte vegetation and influenced by tides. While saltmarshes have often been described as being only found in temperate, subtropical and artic latitudes (Mann, 2009; D'odorico et al., 2013; Duke, 2006; Lee & Kim, 2018), they occur worldwide, with saltmarshes found in tropical latitudes, notably in the dry and arid tropics (Figure 1.1) (Mcowen et al., 2017; Murray et al., 2022). Saltmarshes are generally found within the intertidal zone from the mean sea level, but they also colonise the supratidal zone or splash zone (Wu et al., 2020). In lower latitudes, saltmarsh ecosystems usually occur as pioneers high in the intertidal zone and in the supratidal zone (Reis et al., 2019; Chapter 3) in areas where conditions for mangrove establishment are not suitable such as where tidal flooding is too infrequent or where evapotranspiration is too high (Pennings & Bertness, 1999; Pennings et al., 2005).

Saltmarshes are highly valuable ecosystems, providing multiple ecosystem services (Friess et al., 2020; Adams et al., 2021), including buffering against coastal erosion and storm surges (Leonardi et al., 2018; Temmerman et al., 2023), improve water quality (Abbott et al., 2020; Iram et al., 2022) mitigate climate change by storing and sequestering carbon (Macreadie et al., 2021), support biodiversity by providing feeding, breeding, and refuge grounds to birds (Shriver et al., 2004), fish (Rozas & Minello, 1997; Craig & Crowder, 2002; Halpin, 2000), invertebrates (Vince et al., 1981; Mazumder, 2009; Saintilan & Mazumder, 2010; Reis & Barros, 2020; Wu et al., 2019), and mammals (Spencer et al., 2009) and harbouring diverse microbial communities (Machado et al., 2012). Saltmarshes also support habitat for fishery productivity (Baker et al., 2013; Abrantes et al., 2015a; Taylor et al., 2018a; Taylor et al., 2018b). Yet, saltmarshes have suffered centuries of land reclamation/clearing and degradation (Weinstein, 1996; Kennish, 2001; Adam, 2002). Nowadays, saltmarshes are considerably threatened by anthropogenic activities and climate change (Thomsen et al., 2009; Giuliani & Bellucci, 2019; Patro et al., 2017; Gu et al., 2018; Gilby et al., 2021). Agriculture, urbanisation, invasive species and pollution are also key threats to saltmarsh functioning, integrity, and connectivity, which continue to result in saltmarsh loss and fragmentation (Thomsen et al., 2009; Gu et al., 2018; Giuliani & Bellucci, 2019). In addition, the effects of climate change, such as Sea Level Rise (SLR) and increasing global temperatures threaten current saltmarsh distribution patterns (Kelleway et al., 2017; Payne et al., 2019; Schuerch et al., 2018), with this indirect loss exacerbated by direct human activities (Silvestri et al., 2018; Gilby et al., 2021). Increasing coastal erosion due to the SLR and the increasing frequency of storm surges due to climate change also directly impact saltmarshes (Schuerch et al., 2013). Therefore, efficient management and restoration of saltmarshes is primordial for enhancing their resilience and adaptation to future changes (Gonneea et al., 2019; Nguyen et al., 2022; Waltham et al., 2021). Nevertheless, an important lack of quantitative understanding on saltmarsh functioning, their value, and contextual variability in their functioning and functions (Pétillon et al., 2023) often preclude effective management and restoration (Sheaves et al., 2021).

Although the literature on saltmarshes is substantial, most studies have been conducted in a few highly studied locations, notably in the Gulf of Mexico and along the Atlantic Coast of the United States (Minello et al., 2012; Harrison-Day et al., 2020). These studies have demonstrated that saltmarshes have many values, such as supporting habitat and nursery grounds to fish, shellfish and crustaceans (Minello et al., 2003), and trophic support of coastal fisheries (Weinstein et al., 2000). However, what is missing from our knowledge is to what extent the models developed in well-studied locations apply to saltmarshes in tropical seascapes (Connolly et al., 2009; Banerjee et al., 2017; Reis et al., 2019; Chapter 2). This represents a key knowledge gap in our understanding of coastal seascapes, notably as tropical coastlines are increasingly jeopardised by expansion and poor management of human activities (Waltham & Sheaves, 2015), climate change (Baettig et al., 2007; Corlett, 2012), and extreme weather events (Duke et al., 2017). Saltmarshes in tropical and subtropical latitudes are also threatened by "coastal squeeze" effects resulting from direct effect of landward migration of mangroves due to sea level rise (seaward) and indirect human activities (landward) (Creighton et al., 2019; Lovelock & Reef, 2020). Concurrently, the interconnectivity of coastal habitats, or seascape connectivity, entails that the degradation or alteration of one component of the coastal seascape can compromise the values and functions of others (Olds et al., 2018; Gilby et al., 2020; Henderson et al., 2020). Therefore, understanding the values and functions of saltmarshes in the tropics and their synergies with the remaining seascape is necessary so that tropical seascapes are managed and restored effectivity (Waltham et al., 2021).

Management decisions have been established on extrapolation of knowledge from data-rich locations without considering contextual variability (Bradley et al., 2020; Ziegler et al., 2021). For instance, it is common to read governmental and non-governmental publications that are not founded on scientific paradigms (Sheaves, 2017; Sheaves et al., 2020). For example "s*altmarshes* [in Queensland, tropical and subtropical Australia] *play a significant role as a feeding and/nursery area for fish*" (Jaensch, 2005, p.6). The consequence of those poorly validated paradigms is the tendency to generalise the values of saltmarshes, as if all saltmarshes have, by definition, all high and similar ecological values (Sheaves et al., 2020). This motivates management and restoration infinitives to focus on "simple structural criteria" (*sensu* Weinstein et al., 2014), often targeting specific "habitat types" defined by broad vegetation categories ("vegetation-based approach") (e.g., saltmarshes) without considering the spatial and temporal context (Sheaves, 2017). In addition, legislation, restoration, and management strategies have long targeted on only one type of habitat or ecosystem in isolation from the remaining coastal ecosystem mosaic (Liu et al., 2016; Waltham et al., 2019). This overlooks the complex synergies interconnecting saltmarshes have within other components (Sheaves, 2009; Waltham et al., 2019; Weinstein & Litvin, 2016). Concurrently, management and restoration strategies often fall short in considering the complexity of tidal wetlands, where many contextual variables may influence their values and functionality, and this at even small temporal and spatial scales (Sheaves et al., 2021).

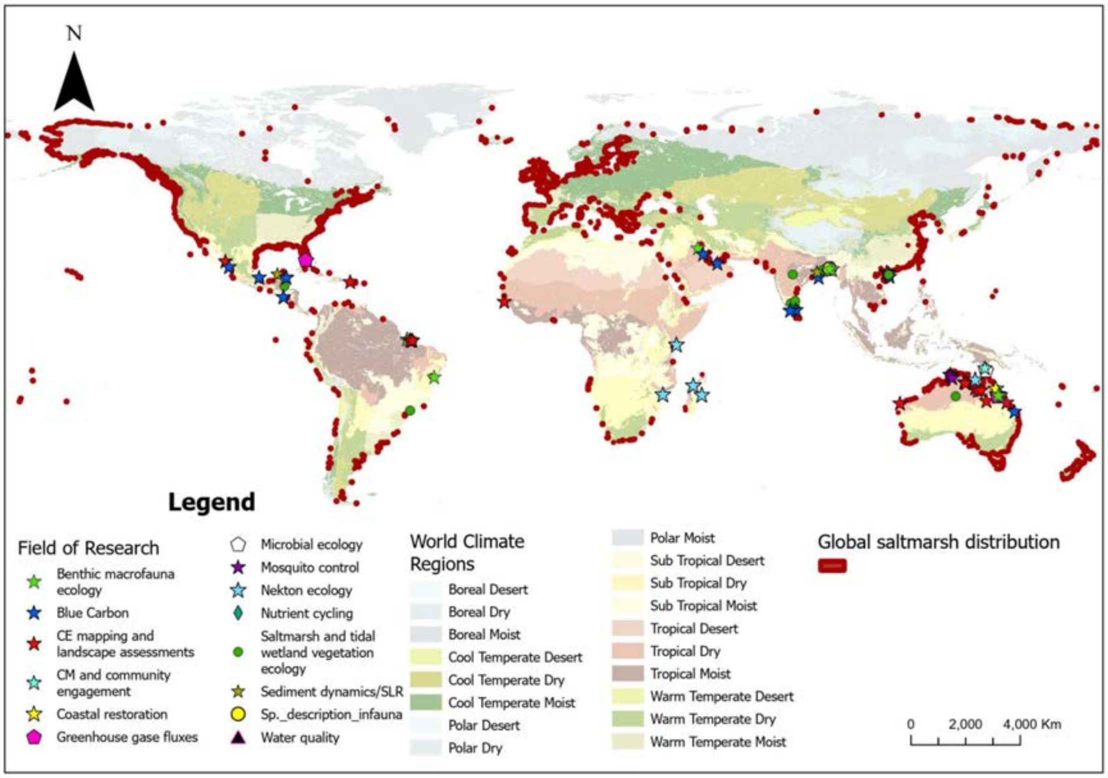


Figure 1.1 Distribution of the studies on saltmarshes occurring in the tropics by field of research. The global distribution of saltmarshes (Mcowen et al. 2017) are shown in red. World climate regions (Sayre et al. 2020) are also shown.

Defining the environmental and ecological contexts in which tidal wetland components occur should be central to modern coastal ecosystem sciences (Bradley et al., 2020; Ziegler et al., 2021). Ziegler et al. (2021) reviewed the key contextual variables that influence saltmarsh-nekton habitat relationships and concluded that the following were critical components and processes for saltmarsh function: 1) hydroperiod (flooding duration, frequency, depth, tidal regime, and average tidal range); 2) seascape configuration (e.g., distance to the nearest structural habitat); 3) geomorphology (e.g., local positioning and elevation); 4) climatic region; 5) sediment supply and riverine input; 6) salinity; 7) vegetation (e.g., plant diversity); and 8) human activities. While a holistic understanding of every contextual variable influencing saltmarsh values is likely to be problematic (Sheaves et al., 2021), it is particularly important that researchers attempt to quantitatively, or at least qualitatively, define as many of the potentially important contextual variables that may influence the patterns and processes observed at given study sites (Bradley et al., 2020; Sheaves et al., 2021).

Here, I present the first systematic review of saltmarsh knowledge in tropical latitudes. Specifically, I synthesise our understanding of saltmarshes in the tropics and whether our conceptions of the values, functions and processes of “tropical saltmarshes” are fundamentally different from temperate and subtropical saltmarshes. I also investigate whether saltmarsh studies-in the tropics report some of the key conceptual drivers of variability in saltmarshes addressed by Ziegler et al. (2021) (specifically, hydroperiod, seascape configuration metrics, geomorphology, vegetation, salinity, rivers inputs, sediment supply, and human activities).

A systematic review of the peer-reviewed literature on tropical saltmarshes was conducted using the electronic literature databases Scopus and Web of Sciences (in January 2021 and in December 2023) (Figure 1.2). The keywords used in the search were "saltmarsh OR salt marsh AND tropics OR tropical OR tropic". The term saltmarsh OR salt marsh was used following Connolly (1999) and Harrison-Day et al. (2020). Publications that did not refer to the tropics and saltmarshes were removed. Biogeographic studies not specifically on tropical saltmarshes but including methods (e.g. mapping plant distribution from herbarium data) and references to saltmarsh distribution in the tropics were retained. Book chapters and literature reviews were not included in the analyses.

Overall, this review aims to provide a summary of knowledge for scientists and practitioners, inviting them to extend studies in the tropics so that key knowledge gaps are addressed and that tropical saltmarshes become more highly valued as part of the coastal habitat mosaic.

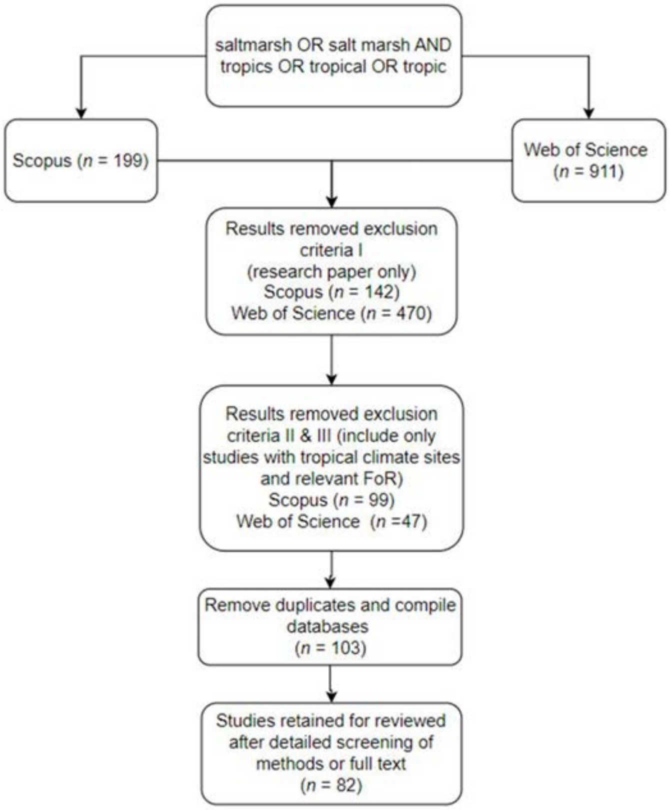


Figure 1.2 Selection process applied on the results of the online database searches related to saltmarshes in the tropics.

1.2 Geographic bias in our understanding of saltmarsh ecological values and functions across the tropics

A total of 82 studies were included in this review (Table 1.1). Studies were conducted mostly in Australia, Brazil, India, and USA reflecting a geographic bias in our understanding of saltmarsh in the tropics (Figure 1.3). Several socio-geographical, socio-economical, logistic, and biogeographic factors may contribute to this bias. Specifically, this bias may relate to the position of main universities and research centres (Stocks et al., 2008), and country economic and societal status (Skopec et al., 2020). This may explain the high number of studies from Australia here, a high-income country with high publication outputs, as well as research centres and university campuses in the dry and wet tropics (Abbott & Doucouliagos, 2004; Williams, 2010). In addition, geographic bias between the tropics and the rest of the world in environmental research remains considerable (Clark, 1985; Karlsson et al., 2007; Stocks et al., 2008; Wilson et al., 2016). For instance, Di Marco et al. (2017) estimated that 40% of conservation science studies were conducted in the UK, Australia, and the USA, compared to 10% and 6% in Africa and Southeast Asia, respectively. Another factor that may influence the low quantities of quantitative studies on saltmarshes in the tropics includes the difficulty in surveying those ecosystems (Connolly, 2009). Saltmarsh in the tropics co-occurs with mangroves, and in the arid tropics, vast areas of saltpans, often occurring in zones difficult to access by road or boat. In addition, inundated saltmarsh and creeks may be inhabited by estuarine crocodiles (in Australia) and alligators (in central and south America) or both crocodiles and hippopotamuses (in Africa), which might hinder sampling or the use of traditional sampling gear (see Chapter 4). Lastly, biogeographic factors may explain the higher publications from Australia. Australian tropical estuaries are mostly dry, except in the wet tropic bioregion, resulting in a coastal landscape mostly composed of saltmarshes, saltpans and sclerophyll forest (Sheaves & Johnston, 2009), with 76% of Australia saltmarsh flats and saltpans found in the tropics (Bucher & Saenger, 1994). Saltmarsh is therefore a conspicuous component of the Australian dry tropical coastal ecosystem mosaic, which may have contributed to the higher number of studies focusing on the functions of tropical saltmarshes, such as their role to nekton and commercially important species (see section 1.2.1 below) in this country. In addition, mangroves occupy lower elevations than saltmarshes in the tropics and are therefore more frequently inundated, contributing to higher diversity of aquatic fauna in mangroves compared to saltmarshes (Connolly, 2009; Whitfield, 2017). This has likely influenced a research bias towards mangrove ecosystems by opposition to saltmarshes in the tropics.

Table 1.1 Classification criteria for each field of research and studies classified in each field of research.

Field of research	Topics	Studies classified
Benthic macrofauna ecology	Diversity and distribution (including environmental drivers) of benthic infauna and macrofauna in saltmarshes.	Al-Zaidan et al. (2003); Braga et al., 2009; Braga et al. (2011); Reis and Barros (2020); Reis et al. (2019); Trave and Sheaves (2014); Braga et al. (2013); Ullah et al. (2020); Santos et al. (2020); Islam et al. (2022)
	Habitat values and contribution to invertebrate diets (dietary studies, including multiple biomarkers studies)	Gorman et al. (2023)
Blue Carbon	Carbon dynamics (e.g., carbon storage, sequestration, flux)	Adame et al. (2020); Kauffman et al. (2018); Kaviarasan et al. (2019); Saha et al. (2022); Perera et al. (2022); Xia et al. (2022); Xia et al. (2021) ; Sangma et al. (2022); Radabaugh et al. (2023); Waltham et al. (2023)
	Carbon burial and storage – blue carbon, including sea-level rise (SLR)	Ruiz-Fernández et al. (2018); Saderne et al. (2018); Schile et al. (2017); Carnero-Bravo et al. (2018)
Sediment dynamics/SLR	Sea level rise records from sedimentary studies, sediment accretion	Carnero-Bravo et al. (2016); Parkinson and Wdowinski (2022)
Coastal ecosystems (CE) mapping and landscape assessments (LA)	Coastal ecosystem classification and vegetation mapping	Bucher and Saenger (1994); Rodrigues and Souza-Filho (2011); Souza-Filho and Paradella (2003); Souza Filho and Paradella (2002)
	Mapping changes in vegetation cover and coastal ecosystems distribution due to anthropogenic and/or climatic change effects (other than SLR)	Chamberlain et al. (2020); Duke et al. (2017); Berlanga-Robles et al. (2011); Paling et al. (2008); Duke et al. (2019); Lopes et al. (2022); Wang et al. (2021)
	Mapping and simulating changes in vegetation cover and coastal ecosystems distribution due sea-level rise.	Yu et al. (2019); Lopes et al. (2023)
Coastal management (CM) and community engagement	Community engagement, ecosystem ecology, biological assessments. Coastal management	Waltham et al. (2018)
Coastal restoration	Restoration of coastal ecosystems after re-establishment of natural tidal inundation	Johnston et al. (2009); Abbott et al. (2020)
	Effects of saltmarsh restoration and eco-engineering activities on climate change mitigation potential	Islam et al. (2021)
Greenhouse gas fluxes	Soil greenhouse gas fluxes from tidal wetlands, alternative agricultural land uses or freshwater impoundments	Iram et al. (2021); Cadier et al. (2022); Li and Mitsch (2016)
Mosquito control	Effects of saltmarsh hydrology and others environmental parameters (e.g. rainfall) on the abundance and population structure of saltmarsh mosquito populations	Yang et al. (2008); Jacups et al. (2011); Jacups et al. (2015)
Microbial ecology	Microbial diversity and distribution in coastal ecosystems including saltmarshes and mangroves	Shah et al. (2022)
Nekton ecology	Habitat values including contribution to nekton diets (dietary studies including isotope analyses and multiple biomarkers studies)	Sheaves et al. (2007); Abrantes and Sheaves (2010);Abrantes and Sheaves (2009); Abrantes and Sheaves (2010); Abrantes et al. (2014);Abrantes et al. (2015); Abrantes et al. (2019);
	Nekton distribution dynamics and habitat uses	Davis (1988); Davis et al. (2012); Sheaves et al. (2010); Oliveira et al. (2016); Gorman et al. (2023)
	Habitat values, seascape configuration, hydroperiod	Sheaves et al. (2012); Davis et al. (2014)
Saltmarsh and coastal vegetation ecology	Experimental studies on saltmarsh competition and facilitation (including mangrove-saltmarsh studies)	McKee et al. (2007); Nunes and Camargo (2018); Nunes and Camargo (2020)
	Distribution and diversity of saltmarsh plants	Bridgewater and Cresswell (2003); Saintilan (2009); Gopi et al. (2019); Ahalya and Suresh (2020); Viswanathan et al. (2020)
	Saltmarsh plant physiology	Ghosh and Mitra (2015)
	Drivers of saltmarsh plant zonation and distribution	Pemadasa et al. (1979); Zhang et al. (2021)
	Coastal vegetation (including mangroves and saltmarshes) distribution and relationships with environmental parameters (e.g., elevation, salinity), may include accretion rates and SLR data	Cohen et al. (2004); Lara and Cohen (2006); Krauss et al. (2011); Howard et al. (2020)
Species description (infauna)	Organismal diversity - Morphological description of species found in saltmarshes	Hossain and Hutchings (2020)
Water quality	Dynamics of water quality variables (dissolved oxygen and temperature)	Dubuc et al. (2017)

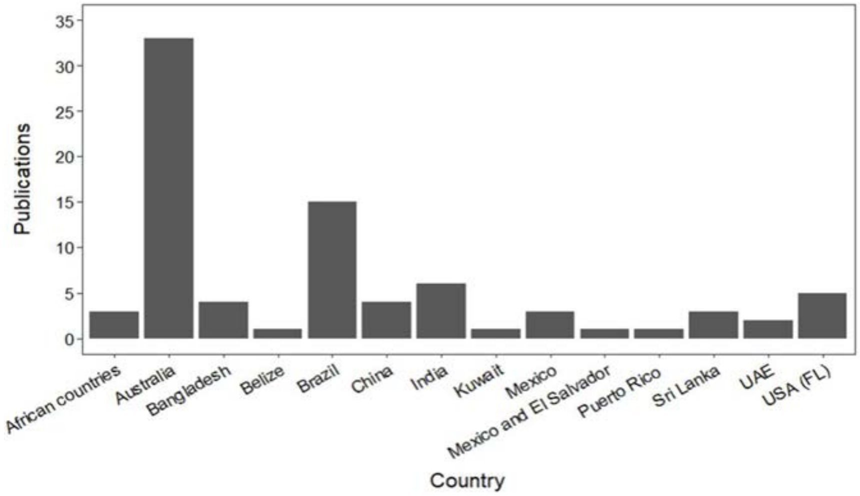


Figure 1.3 Publications on saltmarshes in the tropics per country or group of countries.

The low quantities of studies in each field of research suggest that little is known about the functioning and values of saltmarshes in the tropics (Figure 1.4). There has, however, been an increase in publications since 2017 (Figure 1.5) This is likely attributed to the increase in blue carbon publications (see section "1.2.4 Blue Carbon" below) resulting from growing interests in finding climate change mitigation strategies that offer multiple ecological and economic benefits ("blue carbon ecosystems") (Serrano et al., 2019; Alongi, 2020c; Macreadie et al., 2021). In addition, improvement in the economical and societal status of tropical countries (Harding et al., 2017) may also explain an upward trend in tropical saltmarsh publications, where research and development expenditure has increased between 2006 and 2017 in most of the tropics (Harding et al., 2017). However, highly underfunded countries for biodiversity conservation remain principally in the tropics, notably South-East Asia and West Africa, the Middle East, Northern Africa and even Australia (Waldron et al., 2013). This suggests that tropical saltmarsh ecosystems remain greatly at risk of human degradation and poor management without appropriate management attention, collaboration and funding for research.

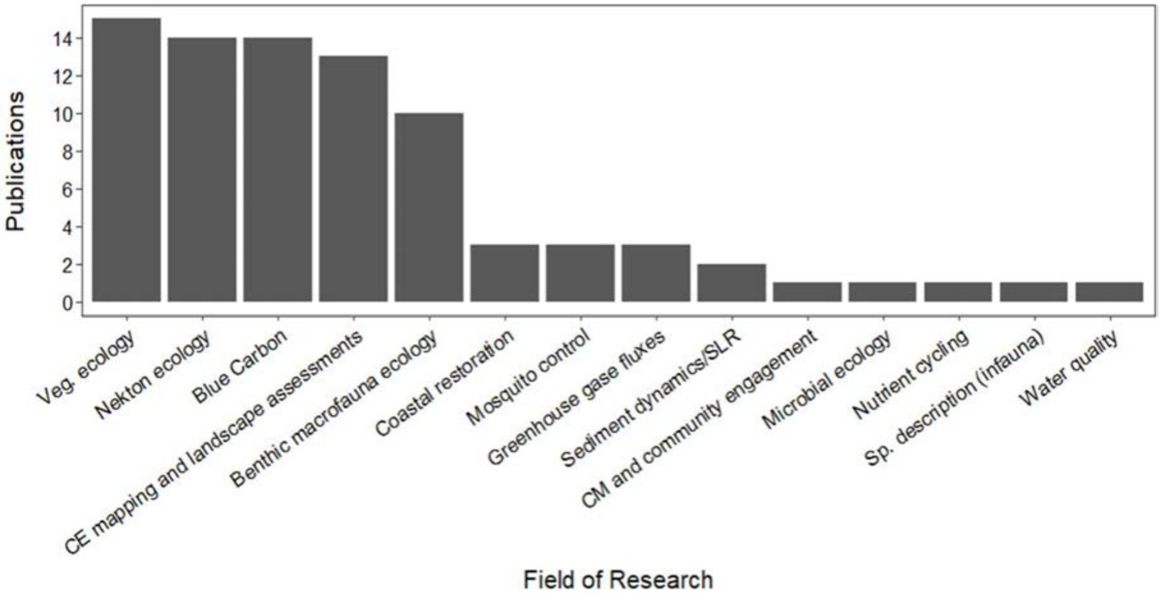


Figure 1.4 Publications on saltmarshes in the tropics per field of research “Veg. ecology” refers to the field of research “saltmarsh and tidal wetland vegetation ecology”.

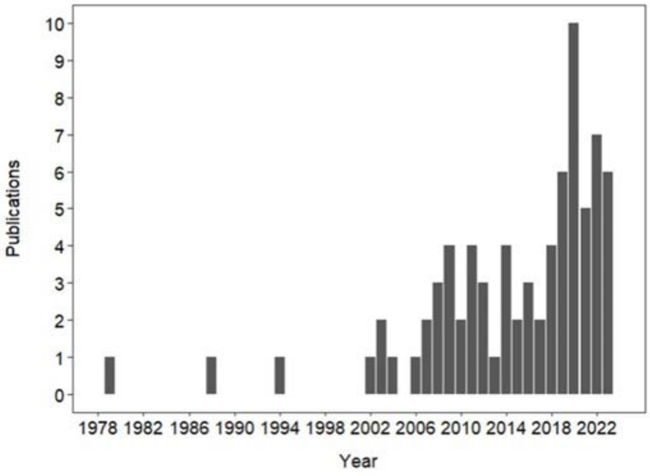


Figure 1.5 Number of publications on saltmarshes in the tropics per year (1978 - December 2023).

1.2.1 Nekton visiting saltmarshes or using saltmarsh production

Nekton ecology was the second most common field of study among the papers included in this review (Figure 1.4), however, there was a geographic bias in this research area (Figure 1.1). Out of the fourteen studies on nekton ecology, twelve were conducted in Australia, one in Brazil, and one in three African countries. There were no studies on nekton ecology in India, Sri-Lanka, Mexico, or any of the remaining countries reviewed here where studies on other field of research were conducted. This bias is likely attributed to the socio-geographical, socio-economical and perhaps logistic factors raised in section 1.2 rather than biogeographical factors (e.g., absence of saltmarsh due to wet tropical conditions). Indeed, each of these countries contain publications on tropical saltmarsh in other field of research (see sections below). In addition, these publications usually highlighted the lack of data on tropical saltmarsh functions in the country where the study was conducted (e.g., Brazil: Braga et al., 2013; India: Banerjee et al., 2017).

The contribution of saltmarsh vegetation to nekton diet was most commonly investigated, with most of the nekton ecology studies (n=8) being food web studies using stable isotopes analyses. Information on the value of saltmarsh as a habitat directly used by nekton (e.g., ontogenetic and feeding migrations), a key value of saltmarshes along the USA coasts (Minello, 2017), was limited to a small number of studies here. Specifically, only four studies focused on patterns in nekton use (other than trophic relationships) of saltmarshes. In addition, a bias in terms of study location and type of saltmarsh components (e.g., saltmarsh creek, saltmarsh flats) was observed in the present study. Six of the nekton ecology studies in Australia were conducted in the same urbanised saltmarsh location (see Sheaves et al., 2007; Abrantes & Sheaves, 2008; Davis et al., 2012; Davis et al., 2014a; Davis et al., 2014b; Dubuc et al., 2017). Furthermore, no studies investigated nekton uses (e.g., feeding migration) of other types of saltmarsh components beyond saltmarsh pools and creeks, such as saltmarsh flats and saltmarsh fringe. The lack of studies on the use of saltmarsh flats by nekton has been highlighted previously (Connolly et al., 1997; Thomas & Connolly, 2001). This represents a notable knowledge gap because saltmarsh flats (as opposed to creeks and pools) are the most ubiquitous saltmarsh habitat component in dry tropical areas such as Australia (Connolly et al., 1997). In addition, while the importance of tropical Floridan saltmarshes to wildlife has been addressed by Wingard and Lorenz (2014), their uses by nekton also appear not to have been extensively investigated. These findings underline that we still do not have a deep understanding of nekton uses of tropical saltmarshes, compared to temperate and subtropical USA marshes (e.g., Rozas, 1995; Minello et al., 2012).

The nekton studies reviewed here indicate that the values of tropical saltmarshes are controlled by physical (e.g., hydrological), ecological and landscape contexts, aligning this with what has been observed in temperate and subtropical saltmarshes (Ziegler et al., 2021). For instance, saltmarsh plants were found to be an important contributor to nekton diets supporting commercially important species such as the banana prawn, *Penaeus merguiensis* in northern Queensland (Abrantes & Sheaves, 2009b). However, their contribution was related to contextual factors such as hydrological connectivity (Abrantes & Sheaves, 2010) and the abundance of vegetation in the estuary (Gorman et al., 2023). Similarly, the contribution of saltmarsh primary and secondary production to nekton diets is viewed as one of the key values of saltmarshes to estuarine fauna in temperate and subtropical latitudes (Baker et al., 2013; Rozas & LaSalle, 1990; Baker et al., 2013; Connolly & Waltham, 2015), but is strongly controlled by saltmarsh hydrological characteristics (Baker et al., 2013) and the extent of vegetation cover (James et al., 2020). The limited number of studies that focused on direct habitat use of saltmarshes by nekton (e.g., feeding and ontogenetic migrations) also found that nekton migrations to saltmarshes were influenced by contextual variables, notably hydrological connectivity (derived from hydroperiod variables) (Davis et al., 2012), prey availabilities (Davis et al., 2014b), and nekton life histories (Oliveira et al., 2016). These are observations similar to those of temperate and subtropical saltmarshes in the USA (Rozas, 1995; Minello et al., 2012), and highlight the need to consider biological and physical processes to understand the values of saltmarsh habitats to nekton organisms (Weinstein and Litvin, 2016; Weinstein et al., 2014).

1.2.2 Benthic fauna visiting or on saltmarshes

One of the ecological functions of temperate and subtropical saltmarshes is providing refuge, breeding, and feeding grounds for benthic fauna. Temperate and subtropical saltmarshes host high benthic faunal diversity. For instance, Richardson et al. (1997) found that the crustacean and mollusc fauna sampled in Tasmanian (Australia) saltmarsh vegetation had similar diversity to South Africa and New Zealand saltmarshes. The authors found 50 species of molluscs and crustaceans, eight of which were specific to saltmarshes. Pennings and Bertness (2001) highlighted that North American saltmarshes provide refuge from predation and nursery grounds to crabs, other small crustaceans, and molluscs, outlining that, in turn, crabs stimulate plant growth by increasing soil aeration and sediment supply. Saltmarsh plants have also been described as contributing to benthic macrofauna diets. For instance, Guest and Connolly (2005) found that the carbon isotopic value ($\delta^{13}C$) of saltmarsh crabs in a subtropical Australia saltmarsh was similar to that of the saltcouch, *Sporobolus virginicus.* However, saltmarsh plants contributed little to saltmarsh crab diets in a temperate Australian saltmarsh, where fine benthic material was the dominant contributor (Mazumder 2009). Another important function of saltmarsh crabs in temperate and subtropical saltmarshes is the mass release of their zoeae following tidal connection (Mazumder et al., 2009; Qin et al., 2015; Saintilan & Mazumder, 2017), which act as an important prey pulse that can be incorporated in estuarine food webs (Hollingsworth & Connolly, 2006; McPhee et al., 2015a; McPhee et al., 2015b).

While there is a consensus relating to the important roles of saltmarsh and their benthic fauna in supporting key ecological values in temperate and sub-tropical locations, this applicability to tropical saltmarshes is not possible because of limited data available. I identified ten studies focusing on benthic fauna ecology (Figure 1.5), with six conducted in Brazil (Braga et al., 2009; Braga et al., 2011; Braga et al., 2013; Reis et al., 2019; Reis & Barros, 2020; Santos et al., 2020), two in Bangladesh (Ullah et al., 2020; Islam et al., 2022a), one in Kuwait (Al-Zaidan et al., 2003), and one in Australia (Trave & Sheaves, 2014). However, the studies reviewed here suggest that tropical saltmarsh may also have high values for benthic fauna. For instance, Islam et al. (2022a) found 118 species of benthic fauna, including 78 species of bivalve and 33 species of gastropods, on saltmarshes in their research area (dominated by the grass *Porteresia coarctata* and unvegetated flats) in Bangladesh. The value of vegetated saltmarsh areas in providing habitat for benthic fauna compared to unvegetated areas also seems similar to that described in temperate and subtropical saltmarshes (Li et al., 2018; Chen et al., 2022), where higher crab diversity occurs in vegetated patches compared to unvegetated patches (Trave & Sheaves, 2014; Reis & Barros, 2020; Reis et al., 2019). However, Reis and Barros (2020) found that juvenile fiddler crabs did not receive higher protection from temperature protection of large predators (fish and birds) in Brazilian tropical saltmarshes (dominated by *Spartina* spp.). Their findings do not align with previous temperate studies on the refuge value of saltmarshes for fiddler crabs (Powers & Cole, 1976; Nomann & Pennings, 1998). The authors warranted additional studies on the role of tropical saltmarshes to fiddler crabs, such as providing refuge from small predators and hydrodynamic forces as well as food availability.

The importance of environmental contexts on the values of saltmarsh habitats to benthic fauna was highlighted (Braga et al., 2009; Braga et al., 2011; Braga et al., 2013). For instance, Braga et al. (2011) found that the abundance of macrofauna in northern Brazil was higher in saltmarsh areas with high organic matter and water content, with tall and dense vegetation, and silt sediments, compared to areas with sandy sediments and limited vegetation. In addition, Ullah et al. (2020) found that benthic infauna diversity is less in the lower and higher marsh zone compared to the middle marsh zone. Anthropogenic activities, such as vehicle use on saltmarshes, can decrease the habitability of tropical saltmarsh for crabs (Trave & Sheaves, 2014) – a pattern also found in temperate and subtropical saltmarshes (Blakely et al., 2022; Kelleway, 2006). Pollution from sewage has been shown to reduce macrofaunal diversity in an area of a Kuwait saltmarsh compared to a more pristine area at the same location (Al-Zaidan et al., 2003). Overall, while tropical saltmarshes likely hold high values to benthic fauna, these values appear to be context-dependent. This underlines the importance of conducting additional studies on the ecological values of saltmarshes to benthic fauna. Future studies should investigate tropical saltmarsh benthic distribution in relation to potentially important contextual variables such as elevation (Dunn et al., 2023) and tidal inundation. In addition, the role of benthic macrofauna as producers of trophic subsidies via the export of crab zoeae should be an area of future investigation in tropical seascapes (see Chapter 4) because this process is considered a key value of subtropical and temperate saltmarshes (Qin et al., 2015; Saintilan & Mazumder, 2017).

1.2.3 Saltmarsh distribution in high intertidal areas

The success of long-term saltmarsh management and restoration rests in understanding the factors leading to saltmarsh vegetation establishment and survival, the variability in their distribution patterns, and their dynamics with other vegetation types such as mangroves

(Rogers & Krauss, 2019). However, this review found that a limited number of studies classified in the field of research “Saltmarsh and tidal wetland vegetation ecology” recognise the patterns and processes explaining saltmarsh distribution in tropical seascapes (Cohen et al., 2004; Lara & Cohen, 2006; Nunes & Camargo, 2018, 2020), while two studies investigated saltmarsh interactions with mangrove vegetation (McKee et al., 2007; Zhang et al., 2021). Specifically, Lara and Cohen (2006) explored the relationships between sediment porewater, salinity, inundation frequency and mangrove vegetation distribution in Brazil. These authors mentioned that saltmarsh occurred at higher elevations than mangroves, but no specific details on those relationships were provided. It was nevertheless highlighted that low-height *Avicennia* spp. occurred at the boundary of *Sesuvium* saltmarsh in an area of short inundation frequency and high-salinity, suggesting the important role of tidal inundation and salinity patterns in tropical saltmarsh zonation. Similarly, a previous study at the same location described that *Sporobolus virginicus* and *Sesuvium portulacastrum* were found with short *Avicennia* in areas of high elevation that were inundated only during the highest spring tides (Cohen et al., 2004). In India, Viswanathan et al. (2020) described tropical saltmarsh zonation patterns within three main zones delimited within broad tidal boundaries (i.e., normal high tide, neap high tide, and spring high tide). Overall, these studies highlight the important role of tidal inundation and topography in explaining tropical saltmarsh zonation, which aligns with studies conducted at higher latitudes (Kumbier et al., 2021). However, Nunes and Camargo (2018) revealed that the effects of abiotic stress and competition in a tropical Brazilian saltmarsh differ from that of temperate and subtropical studies. Specifically, the authors learned that *S. alterniflora* was absent at higher elevations due to low nutrient availability and that intra-specific competition led to the exclusion of *Crinum americanum* at lower elevations. This finding contrasts earlier studies in temperate saltmarshes describing that abiotic stress lead to species exclusion at low elevations, while competition acts at higher elevations (Crain et al., 2004; Engels & Jensen, 2010). Nunes and Camargo (2018) stressed that the processes explaining plant zonation in the tropics may be like that of higher latitude saltmarshes but that their relative importance along the intertidal gradient may be different.

Management and restoration of tidal wetlands in the tropics must include, and overcome, uncertainties and acknowledge complexity in the responses of tidal wetlands to climatic events caused by climate change (Sheaves et al., 2021). This was highlighted by three studies classified in the field of research “Coastal Ecological (CE) Mapping and Landscape (LA) Assessment” that linked patterns in vegetation distribution to climatic events in Australia (Paling et al., 2008; Duke et al., 2019; Duke et al., 2017). Important shifts in distribution patterns and cover extents between mangrove and saltmarsh were observed following tropical cyclones (Paling et al., 2008) and climatic events related to El-Nino Oscillation, such as heatwaves (Duke et al., 2017) and abnormally high rainfall (Duke et al., 2019). In addition, Duke et al. (2017) highlighted the need for a more comprehensive understanding of tidal wetlands response to severe weather events to develop long-term and adaptive management strategies. These authors underlined that management strategies should incorporate measures enhancing tidal wetland resilience to climate change-related events (Duke et al., 2017).

Understanding the factors leading to saltmarsh vegetation distribution patterns is challenging because many biological, physical, and anthropogenic factors, such as biological interactions (Costa et al., 2003), hydroperiod (Kumbier et al., 2021), groundwater dynamics (Moffett et al., 2012), wind-waves (Bendoni et al., 2014) and cattle grazing (Davidson et al., 2017) among many others (Rogers & Krauss, 2019) have the potential to influence saltmarsh dynamics and distribution patterns. Variability in saltmarsh distribution is therefore complex and context-dependent, and its understanding necessitates a multi-disciplinary approach, but is important for effective and long-term management and restoration of saltmarsh ecosystems.

1.2.4 Blue carbon value

The ability of tidal wetlands, such as saltmarshes, to sequester carbon, and thus play a role in mitigating climate change, is viewed as a key asset of coastal ecosystems ("blue carbon value") (Macreadie et al., 2019; Rogers et al., 2023). Consequently, the restoration of blue carbon ecosystems has taken an important place in the agenda of major conservation agencies (e.g., the UN Decade on Ecosystem Restoration) (Waltham et al., 2020). This is reflected here by the increase in blue carbon studies in tropical saltmarshes, where the first blue carbon study recorded here dates from 2017. In opposition to the other field of research, where Australia was often the dominant country, only two studies on blue carbon were recorded in Australia. The other countries were India (*n*=3), China (*n*=2), United Arab Emirates (UAE) (*n*=2), Mexico (*n*=1), Mexico and El Salvador (*n*=1), Sri-Lanka (*n*=1), Brazil (*n*=1), and USA (Florida) (*n*=1).

Among the studies that compared the differences between the blue carbon value of mangroves and tropical saltmarshes (Kauffman et al., 2018; Kaviarasan et al., 2019; Sangma et al., 2022; Xia et al., 2022; Radabaugh et al., 2023), four concluded that mangroves had a higher carbon sequestration and storage potential compared to saltmarshes. The higher blue carbon value of mangroves compared to saltmarshes has also been underlined in subtropical and temperate estuaries where mangroves and saltmarsh co-occur and where mangroves encroach into saltmarshes (Duarte et al., 2013; Kelleway et al., 2016). Mangrove encroachment into saltmarshes may indeed increase the blue carbon value of coastal zones (Kelleway et al., 2016). However, the dynamics of carbon in areas where mangroves encroach into saltmarshes have been shown to display spatial variability with regards to nutrients, plant composition, salinity and rainfall patterns (Yando et al., 2016; Kelleway et al., 2017), suggesting that the extent to which mangrove encroachment increase below ground carbon storage is context dependent (Yando et al., 2016).

Overall, the blue carbon studies reviewed highlight that tropical saltmarshes hold a high blue carbon value. However, several studies underlined the effects of environmental contexts on this value (Xia et al., 2022; Xia et al., 2021; Radabaugh et al., 2023; Waltham et al., 2023), aligning with observations from temperate and subtropical studies (Sasmito et al., 2020). For instance, Xia et al. (2022) found important variability in soil organic carbon (SOC) depending on edaphic variables, plant species mix, and latitudes. The authors found that SOC of saltmarshes was higher at mid-latitude (25–30° N) compared to low (20°N) and high latitude (38–40°N) in China. Furthermore, that study found that SOC density was higher in a specific saltmarsh mix (*P. australis* and *S. alterniflora*) compared to mangroves or another saltmarsh mix (*P. australis and Suaeda*). By opposition, Radabaugh et al. (2023) found that total carbon stocks in both mangrove and saltmarshes were higher in the tropical region of Florida (Ten Thousand Island and the Everglades) compared to the subtropical regions around Tampa Bay. The authors attributed this largely to the younger age of mangrove forests in subtropical regions due to recent mangrove encroachment into saltmarshes as well as difference in soil composition among other explanations (see Radabaugh et al., 2023). In addition, carbon stocks were more important in saltmarsh areas with greater tidal inundation in a tropical Australian saltmarsh, where cattle grazing was also found to negatively affect saltmarsh soil carbon stock (Waltham et al., 2023). Therefore, a nuanced understanding of the blue carbon values of tropical tidal wetlands should take a central position in blue carbon ecosystem management and restoration, particularly considering the growing interest of carbon offsetting and blue carbon ecosystem restoration to compensate CO_2 emissions (Williamson & Gattuso, 2022).

1.3 Poor reporting of contextual variables

While several studies reviewed in the present study have indirectly or directly underlined the importance of environmental and ecological contexts in determining the values of tropical saltmarshes, few studies have quantitatively measured the key contextual variables influencing saltmarsh values underlined by Ziegler et al. (2021) (Figure 1.6).

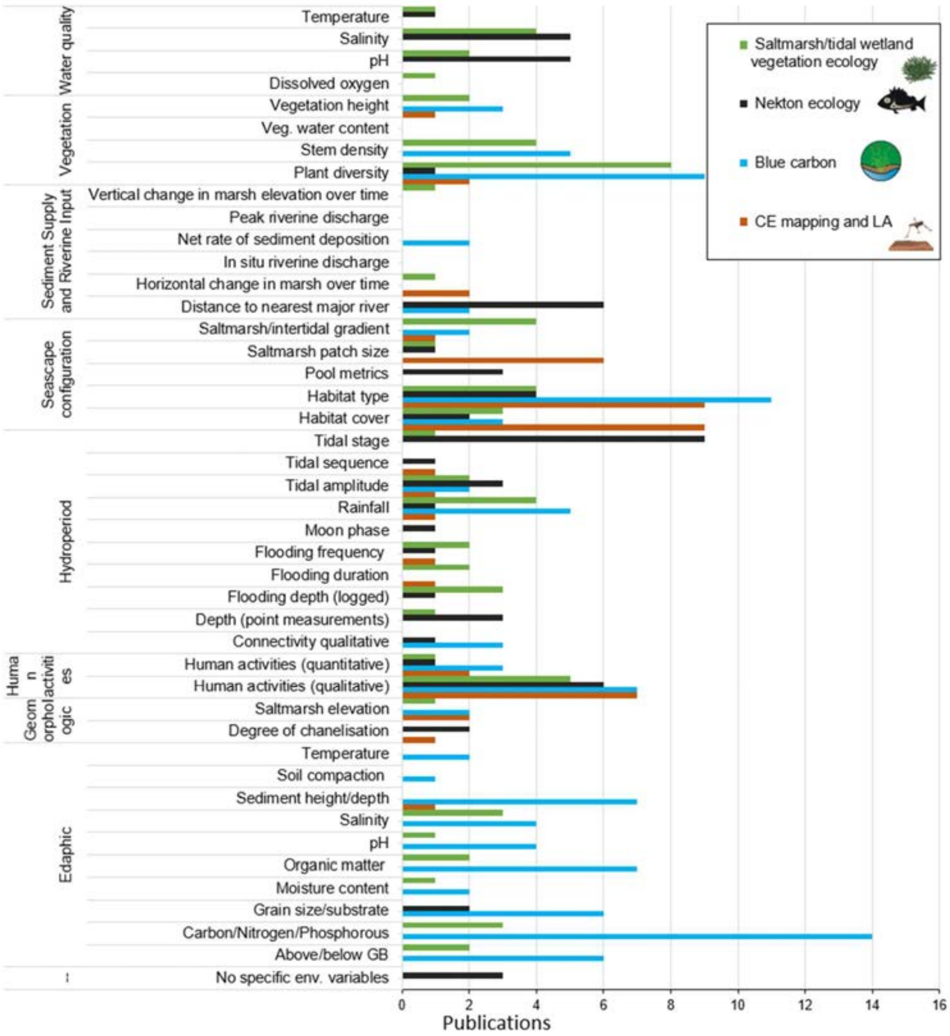


Figure 1.6 Contextual variables reported in studies classified within the four main fields of research.

The limited number of studies quantifying hydroperiod is often attributed to the challenges associated with monitoring these variables (Ziegler et al. 2021). Here, only Cohen et al.

(2004) and Lara and Cohen (2006) quantified simultaneously saltmarsh flooding depth, duration and frequency. Yet, the methods used by Cohen et al. (2004) and Lara and Cohen (2006) have some limitations as they used a bathtub model approach to examine the tidal wetland inundation, which has been criticised for its oversimplistic modelling of inundation (Traill et al., 2011). Alternatives approaches to model saltmarsh tidal inundation dynamics at the system scale (i.e., tidal wetland platform) involve two-dimensional hydrodynamic modelling (e.g., Alizad et al., 2016b; Fleri et al., 2019) and three-dimensional modelling (Temmerman et al., 2005; Xin et al., 2022) - the latter integrating multi-dimensional variability in hydrology and sediment dynamics. However, no studies in tropical saltmarshes have attempted to use these methods (but see Chapters 2 and 3)

One of the challenges in deriving tidal wetland inundation data is due to the resolution of digital elevation models (DEMs) used to parameterise hydrodynamic models (Rogers et al., 2018; Xu et al., 2021). Coarse DEMs (> 1 m) can fail to capture micro-topographic features, such as small drains that can influence tidal inundation patterns (Chassereau et al., 2011). Therefore high-resolution topographic data (< 1 m resolution) such as derived by LASAR scanners, Light Detection and Ranging (LiDAR), and more recently, Unattended-aerial-vehicles (UAV) structure-from-motion with multi-view stereophotogrammetry are potential alternatives to derive high-resolution DEM (Rock et al., 2012; Ajayi et al., 2017 ; Koci et al., 2020). In addition, UAV-borne LiDAR (Pinton et al., 2020) are a particularly promising technique for obtaining high-resolution topographic data in complex terrains such as saltmarshes (Pinton et al., 2021). However, their high cost (>30,000 USD) might preclude their application in many situations (e.g., restoration and management). Other successful techniques to model saltmarsh inundation with high accuracy consist of resampling coarser LiDAR DEM into smaller grids (see Kumbier et al. (2022) for details on this technique).

However, each of these techniques are yet to be applied in tropical seascapes (but see Chapters 2 and 3).

The remaining four studies that quantitatively monitor saltmarsh hydrological variables reviewed here used pressure loggers (Krauss et al., 2011; Davis et al., 2012; Dubuc et al., 2017; Abbott et al., 2020). For instance, Abbott et al. (2020) used pressure loggers to continuously monitor water levels following bund removal in a coastal wetland in tropical Australia. That study used both a seascape mapping and hydrological approach to recognise the effects of hydrodynamics restoration on coastal vegetation, fish distribution and water quality. That study represents one of the most exhaustive tropical eco-hydrological studies reviewed here. Dubuc et al. (2017) also used pressure loggers to understand dissolved oxygen dynamics according to water level fluctuations in tidal pools surrounded by *S. virginicus*. These studies show that the continuous record of water depth using loggers is relatively simple, inexpensive, and provides valuable information on inundation duration, frequency and depth, and can be easily linked to ecological processes. However, hydrological data derived by pressure loggers are limited as they inform only on hydrological processes at one point in space (zero-dimensional). While loggers can be placed across transects (Kumbier et al., 2021), this technique still does not enable an understanding of tidal hydrodynamics at the system scale or tidal wetland platform (Kumbier et al., 2021). In addition, depth loggers are expensive (>400 USD per loggers), which may hinder their application to cover larger scales.

1.3.2 Seascape configuration

Saltmarshes are not isolated components of the remaining coastal ecosystem mosaic (Sheaves, 2009; Weinstein et al., 2005). Their position, configuration (e.g., shape), and the connectivity with the coastal ecosystem components around them (e.g., distance to tidal creek, presence of other tidal habitats such as seagrasses and mangroves) play a major role in their values and functions (Saintilan et al., 2007; Connolly & Hindell, 2006; Fan et al., 2022; Scapin et al., 2022). For instance, higher diversity and catches of fish and crustaceans are found when saltmarshes and seagrasses are highly connected compared to when those habitats occur alone (Baillie et al., 2015). At the patch scale, the relationships between patch size and biodiversity or ecological processes are complex. For instance, even small saltmarsh patches offer high values to organisms (Becker et al., 2010). There are also mixed effects related to the patch position in the seascape (Hovel et al., 2002; Hovel & Lipcius, 2001) and patch complexity (Hovel & Lipcius, 2001), rather than patch size only. Here, a limited number of tropical studies (Braga et al., 2009; Braga et al., 2011; Davis et al., 2014a; Abrantes et al., 2014; Abrantes et al., 2015b) have attempted to understand the effects of seascape configuration on saltmarsh ecological processes (Figure 1.6). For instance, only two studies measured saltmarsh patch size to explain benthic assemblages (Braga et al., 2009; Braga et al., 2011) (Figure 1.6). Those authors found that fauna diversity was unrelated to patch size. However, these studies did not investigate the effects of patch position and other seascape configuration metrics on benthic macrofaunal distribution. In the field of nekton ecology, Davis et al. (2014a) found that the position of saltmarsh pools in the landscape influenced the uses of pools by fish species at different life stages, highlighting the importance of landscape contexts in influencing saltmarsh values to fish. Therefore, gaining further understanding of the configuration of the seascape influence saltmarsh values and function should require additional studies. Novel technologies such as UAV-SfM may facilitate the quantification of saltmarsh configuration characteristics, such as channel geomorphology (Tamminga et al., 2015), and saltmarsh spatial patterning (Zhao et al., 2021). This may advance our understanding of the effects of seascape configuration on saltmarsh values and functioning, which remains an area that require research attention not only in tropical seascapes (but see Chapter 3), but also at higher latitudes (Ziegler et al. 2021).

1.3.3 Geomorphology

Geomorphological features such as saltmarsh elevation and degree of channelisation control saltmarsh functioning by influencing tidal flooding (Baker et al., 2013; Chirol et al., 2018), fish habitat uses (Nelson et al., 2019), saltmarsh formation (Goodwin & Mudd, 2019) and tidal wetland vegetation species zonation (Bockelmann et al., 2002; Mossman et al., 2020). Sediment supply, carbon accumulation, accretion rates and susceptibility to SLR and mangrove encroachment are also influenced by geomorphic settings (Elsey-Quirk & Unger, 2018; Fan et al., 2022). Nevertheless, the description of saltmarsh geomorphology has been the subject of virtually no attention in the tropics. For instance, none of the studies reviewed here have attempted to quantify the relationships between vegetation distribution and elevation in a degree of precision and accuracy as done in subtropical and temperate studies (Silvestri et al., 2005; Kumbier et al., 2021). For instance, while Cohen et al. (2004) and Lara and Cohen (2006) quantified the mangrove-saltmarsh elevation gradient, a specific assessment of saltmarsh-elevation relationships were not included in these studies. In addition, only two studies (Yu et al., 2019; Lopes et al., 2023) modelled the potential effects of SLR on tidal wetland vegetation patterns, both studies using the Sea Level Affecting Marshes Model (SLAMM), while in South-Florida, USA, Howard et al. (2020) determined that saltmarshes were vulnerable to SLR and mangrove encroachment by measuring relative surface elevation changes and accretion rates along a salinity gradient. The overall lack of studies that have attempted to understand the distribution of saltmarsh vegetation in relation to elevation and their vulnerability to SLR represents a significant knowledge gap in the tropics considering the obvious and continuing threat of climate change (e.g., erosion, D'Alpaos et al., 2007), mangrove encroachment (Krauss et al., 2011) and anthropogenic activities (e.g., alteration of sediment supply, Wolanski & Hopper, 2022) on the geomorphology of coastal ecosystems. This knowledge gap was underlined by Parkinson and

Wdowinski (2022) in the context of south floridan coastal wetlands and their resilience to SLR. The authors highlighted that while there are additional types of coastal wetlands than mangroves in this region, most of the sediment accretion studies (97%) conducted in South Florida were in mangroves.

1.3.4 Saltmarsh vegetation

Saltmarsh vegetation composition, density and height can influence the functioning and values of saltmarsh habitats, too (Sullivan et al., 2007). Different saltmarsh vegetation community structures may have different trophic values (Guest & Connolly, 2005) and carbon storage potential (Xia et al., 2021) and hold different benthic assemblages (Luk & Zajac, 2013). For instance, the invasion of *S. alterniflora* in tropical Chinese saltmarshes composed of *P. australis* was found to increase SOC storage but decreased SOC storage in invaded mangroves (Xia et al., 2021). Shift in plant composition due to introduced saltmarsh species (e.g., *P. australis* invasion into *S. alterniflora* in New England saltmarshes) can alter food web structure (Dibble & Meyerson, 2014). In temperate Australia, different saltmarsh vegetation was found to hold different crab assemblages (Mazumder, 2004), where *Sarcoconia quinqueflora* held higher abundances of the crab species *H. cordiformis*, while saltmarshes dominated by *S. virginicus* and *Juncus kraussii* held a greater number of *H. haswellianus*. These examples underline that differences in saltmarsh plant composition may be important in understanding variability in saltmarsh functions.

Table 1.2 Saltmarsh family and species recorded in the 82 studies analysed. The numbers represent the number of publications (out of 82) that listed the species. The total number of species at the bottom of the table refer to the count of species per each country as recorded across the studies.

Family and species	African Countries	Australia	Bangladesh	Belize	Brazil	China	El Salvador	India	Kuwait	Mexico	Puerto Rico	Sri Lanka	UAE	USA (FL)	Total
Acanthaceae															**1**
Acanthus ilicifolius	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Aizoaceae															**9**
Sesuvium portulacastrum	-	-	-	1	1	-	-	4	-	-	-	-	-	2	8
Sesuvium spp.	-	-	-	-	1	-	-		-	-	-	-	-	-	1
Bataceae															**4**
Batis agrillicola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Batis maritima	-	-	-	-	-	-	1	-	-	2	-	-	-	1	3
Boraginaceae															**1**
Heliotropium curassavicum	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Chenopodiaceae (Amaranthaceae)															**57**
Arthrocnemum indicum	-	-	-	-	-	-	-	3	-	-	-	-	-	-	3
Atriplex spp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Blutaparon vermiculare	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Halocnemum strobila	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Halopeplis perfoliate	-	-	-	-	-	-	-	-	-	-	-	-	1		1
Maireana spp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Rhagodia spp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Salicornia brachiata	-	-	-	-	-	-	-	4	-	-	-	2	-	-	6
Salicornia europaea	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Salicornia pacifica	-	-	-	-	-	-	1	-	-	2	-	-	-	-	3
Salicornia spp.	-	1	-	-	-	-	-	-	-	-	-	-	-	1	2
Sarcocornia quinqueflora	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Sarcocornia virginica	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Sclerolaena	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Suaeda arbusculoides	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Suaeda australis	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Suaeda fruticosa	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2
Suaeda maritima	-	-	-	-	-	-	-	4	-	-	-	2	-	-	6
Suaeda monoica	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2
Suaeda nudiflora	-	-	-	-	-	-	-	3	-	-	-	-	-	-	3
Suaeda salsa	-	1	-		-	-	-	-	-	-	-	-	-	-	1
Suaeda spp.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Suaeda vermiculata	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2
Tecticornia australasica	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Tecticornia pergranulata subsp. *Queenslandica*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Tecticornia indica subspp.	-	3	-	-	-	-	-	-	-	-	-	2	-	-	5
Tecticornia spp.	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Convolvulaceae															
Cressa cretica	-	-	-	-	-		-	1	-	-	-	-	-	-	1
Cyperaceae															**6**
Eleocharis spp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Fimbristylis ferruginea	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Fimbristylis polytrichoides	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Schoenoplectus spp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Schoenoplectus subulatus	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Scirpus littoralis	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Juncaceae															**4**
Juncus articulatus	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Juncus roemerianus	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Juncus usitatus	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Poaceae															**59**
Distichlis spicata	-	-	-	1		-	-	-	-	-	-	-	-	2	3
Distichlis spp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Leersia hexandra	-	-		-	1	-	-	-	-	-	-	-	-	-	1
Myriostachya wightiana	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2
Paspalum vaginatum	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Panicum spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Phramites australis	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Porterersia coarctata	-	-	2	-	-	-	-	3	-	-	-	-	-	-	5
Spartina alterniflora	-	-	2	-	10	3	-	-	-	-	-	-	-	1	16
Spartina bakeri	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
Spartina brasiliensis	-	-	-	-	3	-	-	-	-	-	-	-	-	-	3
Spartina patens	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Spartina spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Sporobolus virginicus	-	16	-	-	1	-	-	-	-	-	-	-	-	1	18
Urochondra setulose		-	-	-	-	-	-	1		-	-	-	-	-	1
Xerochloa imberbis	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Portulacaceae								-		-	-	-			**2**
Portulaca bicolor	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Portulaca oleracea	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Total number of species (incl. "spp.")	**-**	**20**	**2**	**2**	**10**	**3**	**2**	**15**	**2**	**2**	**-**	**5**	**1**	**13**	**61**
Presence of "samphire" specified	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Studies not reporting species	3	9	-	-	4	1	-	-	-	2	1	-	-	-	20

Saltmarsh flora diversity was not systematically described in the studies reviewed (Figure 1.6). For instance, here 20 studies (16.4%) did not specify the type of saltmarsh vegetation species or genus that occurred in their study locations (Table 1.2). The reasons for not specifying saltmarsh vegetation depends on the research questions being investigated and the level of specificity needed. For instance, in the food web studies reviewed here, tidal wetland vegetation was usually broadly categorised into two categories: mangrove and saltmarsh vegetation (pooling herbaceous and succulent species) (e.g., Gorman et al., 2023) or C_3 and C_4 tidal wetland vegetation (e.g., Abrantes et al., 2013). In addition, determining saltmarsh vegetation species at the system scale can be laborious, necessitating usually both ground truth and remote sensing approaches such as satellites imagery (Gopi et al., 2019), LiDAR (Pinton et al., 2020; Rogers et al., 2018; Wang et al., 2017) or UAV-SfM (Kaneko & Nohara, 2014; Li et al., 2017). Species-level mapping of saltmarshes can be challenging due to the similar colour, texture, and wavelength across saltmarsh species, but also between terrestrial vegetation (Sadro et al., 2007). Yet, gaining a better understanding of the distribution of saltmarsh vegetation species and their ecological functions is particularly important for the conservation, restoration, and management of diversity in saltmarsh ecosystems. Multispectral (Nardin et al., 202) and hyperspectral (Li et al., 2017; Cao et al., 2021) imagery acquired from remote sensing techniques such as sentinel-2 imagery (Blount et al., 2022; González et al., 2023) and UAV (Horrocks, 2018) have shown important progress in mapping saltmarsh and mangrove vegetation. Applying these novel techniques in tropical saltmarshes should be an area of future research.

1.4 Poor understanding and increasing threats

There is a paradox between the scarcity of data on saltmarsh values and the increasing threats to these ecosystems – this presents a major challenge for managers responsible for saltmarsh conservation while also approving more land use changes and disturbance that threatens saltmarsh areas. Indeed, studies classified in the field of research coastal ecosystem mapping and landscape assessment were similar in that most reported coastal vegetation changes. For instance, Chamberlain et al. (2020) detailed an overall decrease in vegetation cover (saltmarsh, mangroves, open forest) in the Great Barrier Reef Catchments in Australia, with suggested causes such as cyclones, anthropogenic changes in hydrology, extreme weather events, changes in sediment profiles, SLR variability, direct trampling, and transgression of estuarine wetlands to human land. Similar observations have been made in Brazil (Souza-filho Souza-Filho & Paradella, 2003) where coastal erosion and land mismanagement have led to mangroves and saltmarsh loss along the Bragança coast. In Mexico, Berlanga-Robles et al. (2011) found that 75% of the shrimp aquaculture was built on saltmarshes. In Puerto Rico, Yu et al. (2019) simulated SLR using land cover analyses and the SLAMM. These authors estimated that saltmarshes (defined as herbaceous saline wetlands) would be most affected by changing sea levels. The authors also estimated that saltmarsh would lose 10.3% of their extent with a 1-m SLR scenario and 66.5% with a 2-m SLR scenario will have slight possibility of migrating landward due to urban development and the island topographic features. Gopi et al. (2019) reported saltmarsh vegetation loss in the Southeast coast of India due to mangrove plantations. Thus, while these studies report changes in seascape configuration, the low number of studies on the functioning and values of saltmarshes in these same countries suggests that prompt research attention is needed.

1.5 Conclusion and directions for future studies

Peer-reviewed and grey literature on saltmarshes often introduce their studies by stating that saltmarshes have many values. For instance, Jaensch (2005) states that "s*altmarshes* [in Queensland, tropical and subtropical Australia] *play a significant role as a feeding and/nursery area for fish*" (Jaensch 2005, p.6). Despite this there are very few studies that have investigated the values of saltmarshes in the tropics and, consequently, such paradigms on the values of saltmarshes are not likely founded on quantitative information. While I did not consider technical reports where unpublished (peer-reviewed) mapping and monitoring information of tropical saltmarshes has been gathered (e.g., North-Queensland, Australia: Wegscheidl et al., 2015; South-Florida, USA: Radabaugh et al., 2017), the study advocates major knowledge gaps in the understanding of tropical saltmarshes functioning and their values to nekton, benthic macrofauna, vegetation, and susceptibility to climate change. There are also considerable knowledge gaps in the understanding of how different patterns defined by contexts influence processes, functions, and values.

The paucity of information on the role of saltmarshes should encourage scientists and practitioners to further document the functioning and values of saltmarsh ecosystems in the tropics so that these ecosystems become an integrated part of the tropical seascape. An increasing body of studies have highlighted the importance of contexts in shaping functions and values. Thus, scientists are encouraged to quantify key variables such as hydroperiod to define the context in which a function of interest (e.g. nursery) might occur. Emerging technologies will play an important role in assisting scientists in developing a contextual understanding of saltmarshes values. Understanding saltmarshes functions and values should involve cross-discipline collaboration involving hydrologists, ecologists, statisticians, geologists and managers, but also collaboration among research groups across the world so that methods and frameworks can be consistently and simultaneously applied across a variety of tropical seascape contexts.

1.6 Thesis rationale and structure

The aim of this thesis is to investigate some of the important information gaps in tropical saltmarsh ecosystems. To this end, this thesis investigates the extent to which tidal hydrological connectivity (expressed as tidal hydroperiod and the extent of tidal wetland inundation) mediate important ecological patterns (i.e., vegetation distribution) and processes (i.e., prey pulses) within a tropical estuarine complex composed of saltmarshes, mangroves and unvegetated flats. The specific objectives are:

1. Investigate the potential of UAV-SfM to obtain high-resolution DEMs and parameterise a two-dimensional hydrodynamic model of tidal wetland inundation (**Chapter 2**)
2. Analyse the relationships between tidal hydroperiod and micro-topography on tidal wetland vegetated and unvegetated cover distribution (**Chapter 3**)
3. Investigate the effects of tidal wetland connectivity patterns on the export of crab-mediated prey pulses (crab zoeae) (**Chapter 4**)
4. Apply Bayesian-Belief-Networks to illustrate the trade-offs in tidal wetland values considering different scenarios of changes (SLR and reduction in inundation) in tidal wetland inundation patterns (**Chapter 5**).

In Chapter 2, I address the methodological challenges of obtaining high-resolution topographical and hydrological connectivity data. In this chapter, I develop a high-resolution digital elevation (DEM) and land cover data derived from UAV-SfM that I used to parameterise a two-dimensional hydrodynamic model of tidal wetland inundation. This chapter provides the methodological foundation for the subsequent chapters of the present thesis and offers important preliminary insights on the tidal hydrological context of the study site.

- Vulliet, C., Koci, J., Jarihani, B., Sheaves, M. and Waltham, N., 2023. Assessing Tidal Hydrodynamics in a Tropical Seascape Using Structure-from-Motion Photogrammetry and 2D Flow Modelling. *Estuaries and Coasts*, pp.1-24.

In Chapter 3, I investigate the relationships between the distribution patterns of tidal wetland vegetation and unvegetated flats in relation to tidal wetland hydroperiod and micro-topography. This chapter highlights the importance of gaining a more holistic understanding of the factors leading to tropical saltmarsh vegetation patterns. This chapter investigates the potential effects of SLR on tidal wetland hydroperiod, illustrating the complexities and uncertainties in our understanding of tidal wetland functioning in the future.

- Vulliet, C., Koci, J., Sheaves, M. and Waltham, N., Submitted December 2023, In Review. Linking tidal wetland vegetation mosaics to micro-topography and hydroperiod in a tropical estuary.

In Chapter 4, I examine the relationships between tidal connectivity and the export of crab zoea, a process symbolising the importance of seascape connectivity in temperate and subtropical saltmarshes but that had never been investigated in tropical saltmarshes. This chapter highlights the critical importance of tidal connectivity in mediating the export of crab zoeae, but also underscores the importance of considering additional biological and physical factors that lead to meaningful ecological connectivity.

- Vulliet, C., Koci, J., Sheaves, M. and Waltham, N., Submitted January 2024, In Review. Intertidal crab prey pulse export quantifies importance of tidal wetland connectivity.

Lastly in Chapter 5, I applied a Bayesian Belief Network (BBN) approach building upon the datasets derived in the previous chapters to introduce how decision tools can be used by coastal managers to assess the potential effects and trade-offs of modifications of tidal connectivity due to SLR and reduced tidal inundation.

Overall, this thesis emphasises the importance of viewing saltmarshes from a holistic perspective and as integrated components of the wider coastal ecosystem mosaic connected at various spatial and temporal scales by both physical and ecological processes. This thesis provides important tools and scientific insights that I believe will be important in assisting coastal managers in developing more effective and long-term management and restoration strategies to manage tropical saltmarshes. In addition, this thesis will provide guidance for future scientific research in tropical saltmarshes.

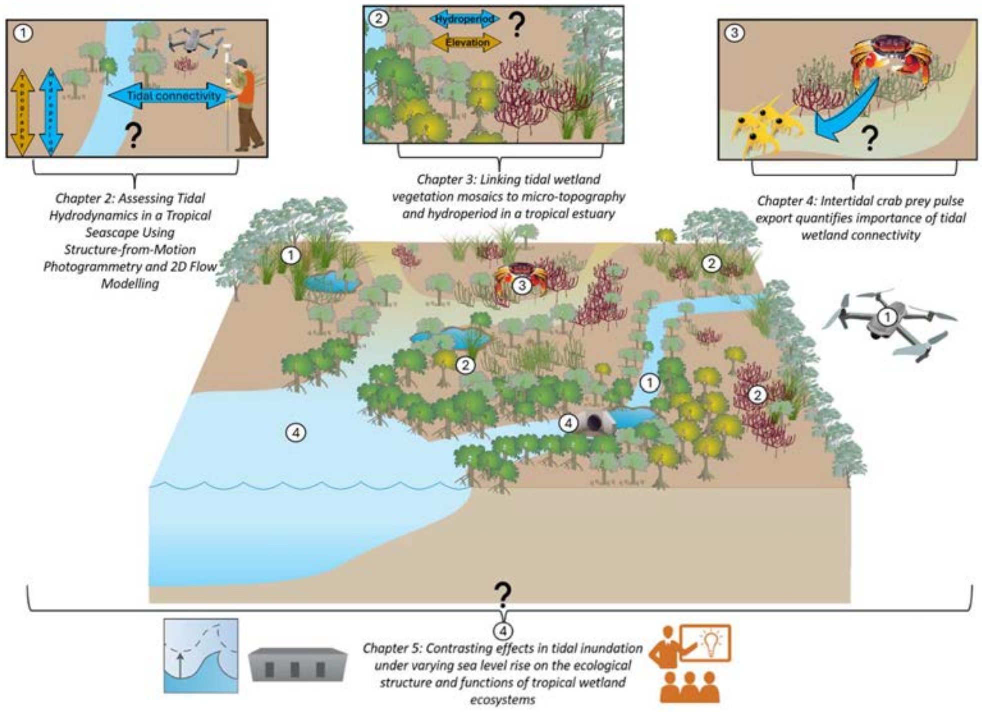


Figure 1.7 Summary of the thesis structure and rationale where (1) novel technologies will be applied to derive high-resolution digital elevation model and land cover data. These data will be used to derive a high-resolution two-dimensional hydromodel of saltmarsh tidal inundation. (2) The models developed in (1) will be used to investigate the effects of hydroperiod and elevation on the distribution tidal wetland vegetated and unvegetated cover; (3) The data developed in (1) and (2) will be used to derive an understanding of the export of prey pulses from intertidal crab to understand the extent to which this process occurs in tropical tidal wetland and to what extent it is influenced by tidal inundation patterns and the extent of tidal connectivity; and (4) A decision tool (Bayesian Belief Network) will be developed to investigate the potential effects of sea-level rise and a reduction in tidal inundation on the habitability of the site to tidal wetland vegetation and the probability of the site in holding crab zoea export and blue carbon value.

Chapter 2:Assessing tidal hydrodynamics in a tropical seascape using structure-from-motion photogrammetry and 2D flow modelling

This chapter has been published in *Estuaries and Coasts*:

- Vulliet, C., Koci, J., Jarihani, B., Sheaves, M., & Waltham, N. (2023). Assessing Tidal Hydrodynamics in a Tropical Seascape Using Structure-from-Motion Photogrammetry and 2D Flow Modelling. *Estuaries and Coasts*, 1-24. DOI:10.1007/s12237-023-01288-6

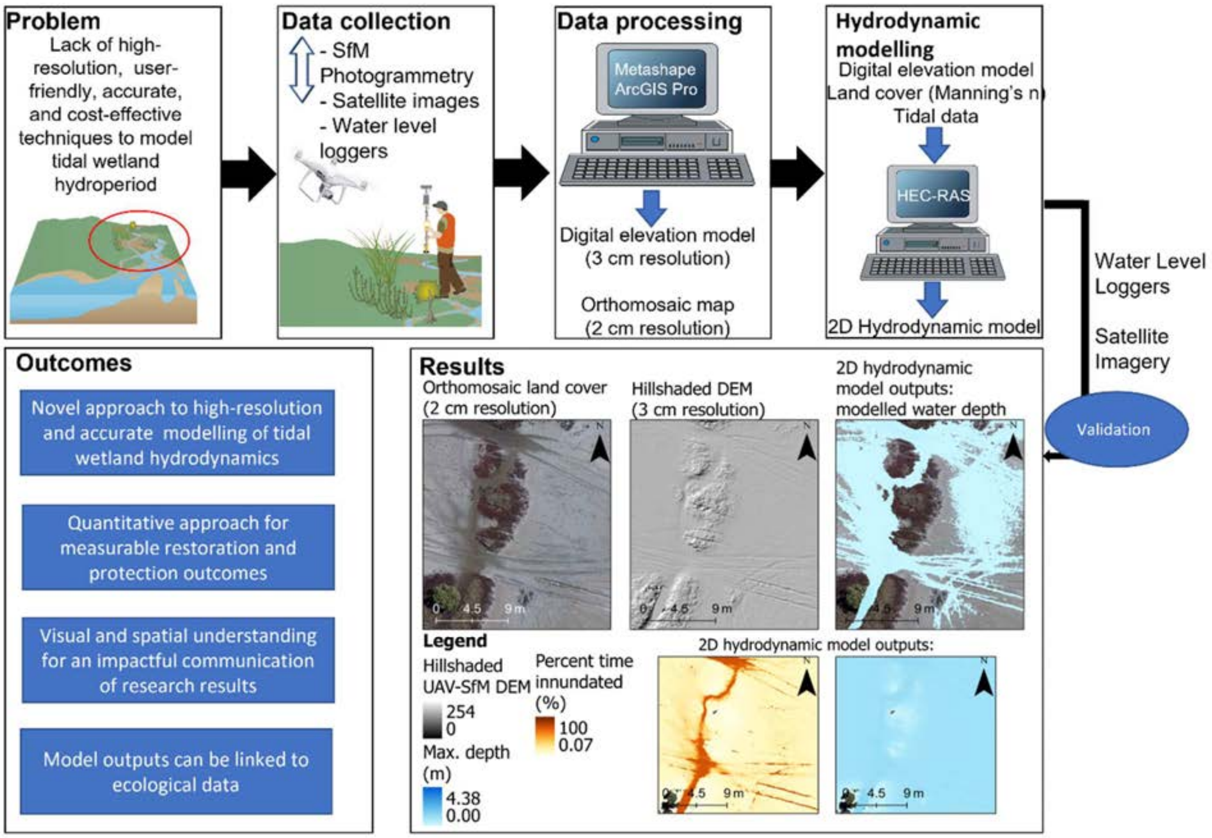
The submitted manuscript has been modified to fit with the style of the thesis.

Authors contributions: **Vulliet:** Conceptualisation, Methodology, Investigation, Data curation, Formal analyses, Writing-original draft, Visualisation, Funding acquisition, Project administration. **Koci:** Investigation, Formal analyses, Validation, Writing - Review & Editing, Supervision, Resources. **Jarihani:** Formal analyses, Validation, Writing - Review & Editing. **Sheaves:** Validation, Writing - Review & Editing. **Waltham:** Conceptualisation, Validation, Visualisation, Writing - Review & Editing, Supervision, Resources.

2.1 Abstract

Reliable and parsimonious models that can be used by managers and practitioners to simulation tidal wetland hydroperiod dynamics (duration, depth, and frequency of tidal inundation) at high-resolution are limited presumably because these ecosystems have very low elevation across their flooding plain. Here, I developed a two-dimensional hydrodynamic model parameterised using a high-resolution (3 cm) and accurate (8 cm RMSE elevation error) digital elevation model (DEM) and land cover map (2 cm resolution) derived from unoccupied aerial vehicles (UAVs) structure from motion photogrammetry (SfM) to assist in the understanding of tidal wetland hydroperiod and hydrological connectivity of an upper tidal Australian tropical seascape. Ground-based water level datasets were used to calibrate and validate the model with higher accuracy (RMSE=7 cm between maximum observed and simulated depth). The high-resolution approach demonstrates how small changes in topography such as vehicles tracks can interfere with hydrological connectivity. Centimeter-changes in tidal height resulted in important variations (10 ha) in the total area of the wetland being inundated, suggesting that small anthropogenic modifications of tidal inputs (e.g., culverts and sea-level rise) might have important implications on tidal wetland inundation patterns. Despite challenges related to reconstructing topography in densely vegetated areas and obtaining bathymetric data, the method developed here represents an accurate and cost-effective approach to quantify tidal wetland hydroperiod. This approach assists in planning, defining, and implementing effective and measurable restoration and protection projects of tidal wetland ecosystems.

2.2 Graphical Abstract



2.3 Introduction

Tidal wetlands (saltmarshes, mangroves, mudflats, and saltpans) are located at the land-sea boundary and hold significant ecological and economic value. For instance, they provide critical resources to commercially targeted species (e.g., European seabass, *Dicentrarchus labrax* and sea mullet, *Mugil cephalus*) (Deegan et al., 2002; Raoult et al., 2018; McCormick et al., 2021), assist with nutrient processing (Rivera-Monroy et al., 2011), and are basal carbon sources supporting coastal food web production (Abrantes & Sheaves, 2009a; Connolly & Waltham, 2015; Jinks et al., 2020). Tidal wetlands are also incredibly effective in absorbing greenhouse gas emissions (Wang et al., 2021a), thereby counteracting anthropogenic carbon emissions and mitigating climate change.

Despite recognition of their values, tidal wetlands continue to be jeopardised by direct ecosystem destruction and degradation (Murray et al., 2022) as a result of urbanisation and agriculture (Saintilan & Wilton, 2001), including installation of engineered barriers (e.g., roads, culverts, and tidal gates) and coastal infrastructures (e.g., seawalls and dikes), which alter inundation regimes, leading to modifications in seascape connectivity and configuration (e.g., vegetated patch distribution and structure) (Bishop et al., 2017; Rodríguez et al., 2017). Climate change (e.g., sea-level rise, changes in temperature and rainfall patterns, and extreme weather events) also modifies seascape connectivity patterns via changes in hydrological, morphological and biological processes (Gilby et al., 2021; Colombano et al., 2021; Finotello et al., 2022), which can be exacerbated by human activities (Gedan et al., 2009). An example is the coastal squeeze effect where saltmarshes become reduced between urbanisation and mangroves migrating to higher elevations due to increases in mean sea level (Torio & Chmura, 2013). Implementation of effective restoration projects and urban planning that minimise environmental loss is, therefore, urgently needed. However, this is constrained by a poor understanding of the location-specific tidal wetland hydroperiod nuisances, which can be influenced by a combination of vegetation mosaic and impediment on ingress, inundation depth and frequency of wetland inundation (Bradley et al., 2020; Karim et al., 2012; Ziegler et al., 2021; Waltham et al., 2021).

Tidal hydroperiod determines the depth, duration, and timing of flooding and, as a result, influences hydrological connectivity and, subsequently, many critical eco-hydrological and morphodynamical processes such as the movement of biota throughout seascapes (Rozas, 1995; Minello et al., 2003; Davis et al., 2014a), soil-vegetation interactions (Liu et al., 2021a), carbon sequestration (Wang et al., 2021b), and coastal erosion (Finotello et al., 2022). These processes ultimately contribute to coastal productivity and resilience (Olds et al., 2012) hence, tidal wetland restoration success can be closely linked with hydrological processes (Zhao et al., 2016).Tidal wetland hydroperiod is most strongly influenced by topography, but also by many hydrological, geomorphic, edaphic, biological, and climatic variables (Xin et al., 2022). Complex interactions among these factors means, for managers, that hydroperiod is challenging to quantify accurately (Passeri et al., 2015).

Over the past decade, advancements have occurred in the development of techniques to examine hydroperiod and connectivity of these ecosystems within nearby estuaries and coasts. Direct measurement approaches have used water level loggers (or pressure loggers) deployed at single points in space (Peterson & Turner, 1994; Davis et al., 2014a) or along transects (Kumbier et al., 2021). For instance, Minello et al. (2012) used tidal gauge data, which was checked using point elevation measurements, to more accurately investigate spatial variability in saltmarsh hydroperiod. That study enabled comparisons of hydroperiod across multiple locations, but it still required manual water level measurements, which can be prone to measurement error.

There has been growing interest in using complex empirical and physical numerical models to understand tidal wetland hydrodynamics, notably to recognise the relationships between hydrology, saltmarsh evolution and morphology (Kirwan et al., 2010; Fagherazzi et al., 2013; Xin et al., 2013b; Bouma et al., 2016; Fagherazzi et al., 2020; Xin et al., 2022). These models range from zero-dimensional (i.e., process at single points) (Allen, 1995) to one-dimensional (e.g., channel transects) (D'Alpaos et al., 2007; Karim et al., 2014), two-dimensional (2D) (e.g., tidal wetland platform) (Temmerman et al., 2007; Alizad et al., 2016b; Fleri et al., 2019; Finotello et al., 2022), and three-dimensional (3D) models that encompass multidimensional variability in hydrology and sediment transport (Kirwan & Murray, 2007; Xin et al., 2022). There have also been attempts to combine these models (Moffett et al., 2012; Kumbier et al., 2022). For instance, Alizad et al., (2016) investigated saltmarsh response to sea-level rise by combining a 2D hydrodynamic model developed by Bacopoulos et al. (2012) that uses tides, wind, pressure, and bathymetric-topographic datasets to understand saltmarsh hydroperiod, with a zero-dimensional model of saltmarsh accretion and biomass productivity derived from Morris et al. (2002). While these models represent an important advancement in our ability to understand saltmarsh functioning, the complexity and high input data requirements may preclude their broader application by environmental scientists, ecologists and practitioners, particularly in data-sparse situations.

Recent advances in remote sensing techniques, coupled with freely available modelling software with user-friendly Graphical User Interfaces (GUIs), are opening the door to readily applicable approaches to quantify tidal wetland hydroperiod dynamics and connectivity. These new approaches might be more easily communicated and integrated into tidal wetland studies (e.g., fish habitat uses) and restoration. For example, using 2D simulation software such as, but not limited to, MIKE 21 (Warren & Bach, 1992), TELEMAC-2D (Morris et al., 2013a), TUFLOW 2D (Syme, 2001), Delft3D (Temmerman et al., 2005; Horstman et al.,

2015) or HEC-RAS can offer a detailed spatial and quantitative understanding of tidal inundation with minimal data input (Symonds et al., 2016; Karim et al., 2021; Muñoz et al., 2021). The basic input for hydrodynamic models includes bathymetry or topographic datasets (Digital Elevation Models; DEMs), land cover to account for surface roughness, and water level or discharge time series. Nevertheless, the low-gradient and narrow-width (< 1 m) draining channels in coastal areas could be completely missed or mis-represented depending on DEM resolution and uncertainty level in data acquisition (Chassereau et al., 2011).

High- or Very High-resolution DEMs (< 1m) are traditionally developed using ground-based LASER scanners (Sampson et al., 2012) or LiDAR instruments (Goodwin & Mudd, 2019) and recently, by using Unoccupied Aerial Vehicles (UAV) technology (Shaad et al., 2016; Pinton et al., 2020; Zhu et al., 2019a; Li et al., 2021a; Annis et al., 2020). Structure-from-motion with multi-view stereophotogrammetry (SfM) (e.g., Koci et al., 2020) has emerged as a low-cost alternative to UAV-LiDAR (0.6-40% of LiDAR cost (e.g., Hu et al., 2021). UAV-SfM produces 3D point clouds and DEMs with comparable resolution and accuracy to that of LiDAR in most environments (Nouwakpo et al., 2016; Annis et al., 2020; McNicol et al., 2021). In addition to high-resolution topographic models, UAV-SfM generates high-resolution orthomosaic maps providing detailed information on surface features (e.g., vegetation, roads and trails). UAV-SfM can thereby fulfil two essential data requirements for 2D hydrodynamic modelling (i.e., DEM and land cover) (Annis et al., 2020). This approach might be particularly useful in tidal wetlands characterised by low-relative gradient with yet complex topographies (e.g. tidal channels), where subtle variations in topography cannot be captured with coarse DEMs (Chassereau et al., 2011).

This study aimed to test the potential of a UAV-derived DEM with a 2D flow model to simulate inundation patterns in a tidal wetland. Specifically, the main purposes of this study were (1) to attempt to parameterise a detailed hydrodynamic model of the upper region of an intertidal tropical seascape using a UAV-SfM derived DEM, a UAV-SfM derived land cover dataset, and tidal data; (2) to try to derive information on tidal wetland hydrological connectivity and quantify tidal wetland inundation extent, depth, and duration based on the hydrodynamic model outputs; (3) to investigate the importance of high-resolution DEMs in low relative relief; and (4) to assess the advantages and weaknesses of UAV-SfM to study tidal wetland hydroperiod.

2.4 Materials and methods

2.4.1 Study site

The study site is in the upper intertidal region of Blacksoil Creek in north Queensland, Australia (-19.297867, 147.021333), covering 82.54 ha (Figure 2.1). The study site represents a dry tropical estuarine complex consisting of mangrove forests dominated by the red mangrove, *Rhizophora stylosa* at the seaward and channel edges transitioning to the grey mangrove, *Avicennia marina* and the yellow mangrove, *Ceriops tagal,* in the upper intertidal area furthest from the open water channel. In the upper to supratidal zone, saltpans and saltmarshes dominate, including the bead weed *Sarcocornia quinqueflora*, and the salt couch, *Sporobolus virginicus.*

There is no freshwater stream inflow, only entering via groundwater and direct runoff during rain events. The estuary downstream of the study area is semi-diurnal mesotidal, with the highest tides occurring during the day in Austral summer and night in Austral winter. The Highest Astronomical Tide (HAT) is 3.84 m above the Lowest Astronomical Tide (LAT) datum (2.150 m above the Australian Height Datum (AHD)) (Queensland, 2022). The 1991-2021 average tidal height is 1.72 m (Queensland, 2022). The climate is dry-tropical, with most rainfall (900-1800 mm/annum) (Bruinsma, 2001) occurring during the wet season (Nov-Apr). There is a road with a multi-pipe culvert (10 pipes of 1 m diameter) downstream of the study area on the main drainage creek (Figure 2.1b). Four small (~ 40 cm of diameter) single pipe culverts are found across the road, south of the main culvert.

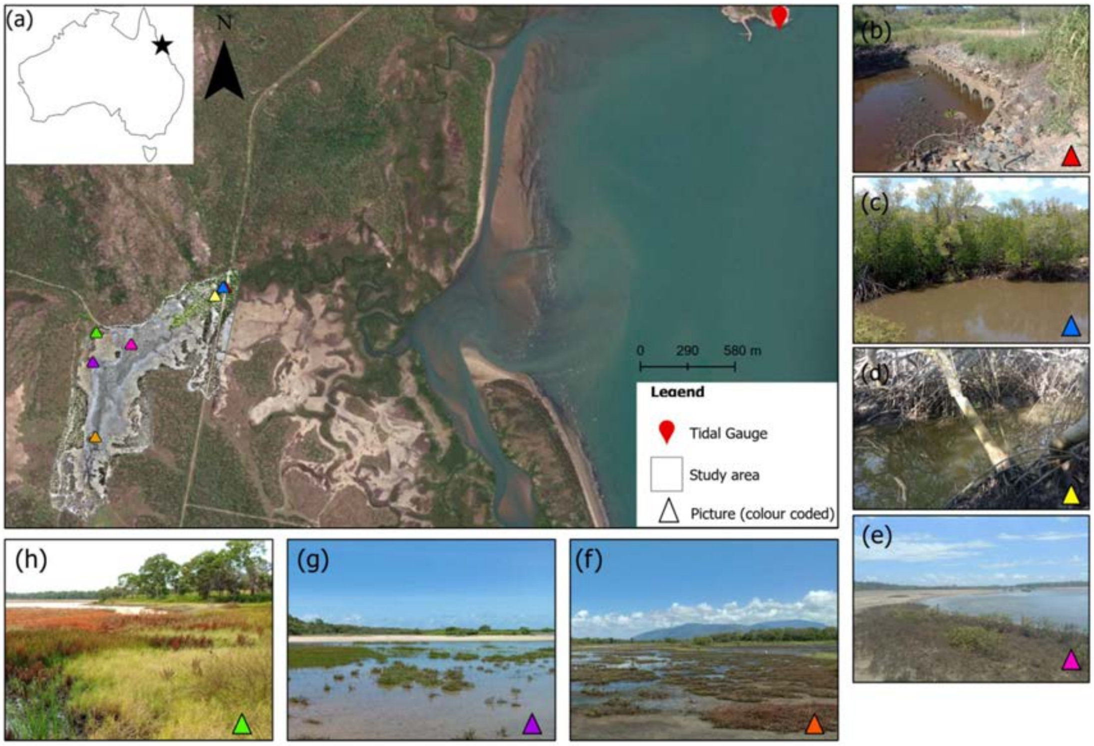


Figure 2.1 (a) Study area map showing the location of the study site on the Australian East coast and location of tidal gauge: (b) photo of the culvert at the north-eastern boundary of the study site; (c) photo of the culvert (shown in b) during low tide bordered by *Rhizophora stylosa* and *Avicennia marina*; (d) tidal channel draining the upper portion of the site surrounded by *R. stylosa*; (e) succulent saltmarsh dominated by *Sarcocornia quinqueflora* with encroaching *A. marina*.; (f) succulent saltmarsh patches dominated by *S. quinqueflora*; (g) patches of herbaceous saltmarsh dominated by *Sporobolus virginicus*; and (h) herbaceous saltmarsh community at the transition between saltpan/saltmarsh and fully terrestrial vegetation.

2.4.2 Modelling framework and set-up

The free software HEC-RAS 6.1 (Windows) was used to develop a 2D hydrodynamic model of the study site using the 2D Unsteady Diffusion Wave equations. HEC-RAS uses a high-resolution sub-grid system, allowing water movement in each cell to be strongly controlled by the terrain model (Shustikova et al., 2019). Although the Diffusion Wave equations are not recommended for tidally driven system and the Shallow Water equations should be used instead, the Shallow Water equations did no yield stable simulations. 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. The model was first built by manually delimiting the perimeters around the study site. The 2D flow areas was then generated using the “Computation Points with All Breaklines” tools with computation point spacing of 2 x 2 m, which generated an irregular mesh of 195131 cells (mostly of 4 sides and up to 8 sides along mesh boundaries). The 3 cm resolution UAV-DEM (see below) was used to extract the sub-grid level information. To reduce computational time while keeping information on the high-resolution terrain, HEC-RAS uses a sub-grid bathymetry approach that enables the use of coarser grid-size on finer terrain model (Brunner, 2016; Shustikova et al., 2019). The approach consists of a pre-processing step that calculates hydraulic radius, volume and cross-sectional from the finer topographic data for each computational grid cells (Shustikova et al., 2019). This sub-grid bathymetry approach allows the information from the fine scale terrain model to be accounted for in the coarser grid through mass conservation (Casulli, 2009; Brunner, 2016). Hence, DEM resolution influences model accuracy (Yalcin, 2018). For instance, Yalcin (2018) demonstrated that a decrease in the Digital Surface Model (DSM) resolution (0.25 m/pixel – 10 m/pixel) with the same grid size (2m x 2m) linearly increases depth and inundation area inaccuracies compared to the 2m x 2m grid size with a 0.0432 m DSM. By opposition, no notable differences in model accuracy were observed between simulations computed with the 0.0432 m DSM and grid sizes of 2m x 2m to 10m x 10m. An abrupt decrease in model performance was only observed with a grid size equal to or greater than 15m x 15m. Numerical details on the sub-grid bathymetry approach used by HEC-RAS can be found in Brunner (2016).

The boundary condition (tidal flow data) was implemented using the Stage Hydrograph with the Initial Stage used. The initial conditions were left blank. Only one boundary condition was used, which was placed manually downstream of the culvert in the main channel, outside of the 2D flow area, which is presented in Appendix A (Figure A2). Note that tides only enter to the study site via the culverts found across the road at the eastern boundary of the study site (Figure 2.1).

2.4.3 Input data

2.4.3.1 UAV-derived DEM

UAV surveys were conducted over two days in September 2021. A DJI Phantom 4 RTK (Real-Time Kinematic) (SZ DJI Technology Co., Ltd.) connected to a DJI RTK Base Station set over a known benchmark was flown at 60 m altitude (62 m ground sample distance) on a one-grid mission planned to use the DJI RTK App (SZ DJI Technology Co., Ltd.). The camera model was FC6310R with maximum image size of 5472 x 3648, focal length of 8.8 mm, and pixel size of 2.41 x 2.41 µm. Full specifications of the Phantom 4 RTK can be assessed on the official DJI website (https://ag.dji.com/fr/phantom-4-rtk/specs). Images were collected at nadir with 85% side and forward image overlap. The UAV was flown each day between 9:30 to 15:00, with short interruptions to change the battery (i.e., each flight was approximately 20-25 minutes) totaling to 6488 images. RTK-GPS measurements recorded by the UAV ended up not being used for data processing due to the difficulties and time limitations in finding a workflow leading to high accuracies. Thirty-three ground control points (GCPs) were evenly distributed in the corner, along the boundary, and across the study site to maximise DEM accuracy (Sanz-Ablanedo et al., 2018). The GCPs consisted of rectangular black and white checkerboards of 60cm x 60cm. To georeference the model with centimeter-level accuracy (Koci et al., 2017; Taddia et al., 2021), the centre of the GCPs were surveyed with Real-Time Kinematic-Global Positioning System (RTK-GPS) (CHC i80) (Shanghai HuaCe Navigation Technology Ltd.) (taking the average of 10 readings) (Figure 2.2a). The accuracy of the RTK-GPS was calculated using the GCPs (33) and validation points (562, see details below), resulting in an RTK-GPS mean horizontal error of 0.015 ± 0.000 m (standard error, SE) (standard deviation, SD of 0.005 m) and mean vertical error of 0.027 ± 0.000 m (SD of 0.009 m). The coordinates were recorded in the

GDA2020 MGA Zone 55 reference system and orthometric elevation in the Australian Height Datum (AHD). Agisoft Metashape (Agisoft LLC) was used to create dense point clouds and orthomosaics from UAV-SfM. The DEM was generated following dense point cloud classification of ground points. Point cloud density (calculated as the total of points divided by the total area surveyed) was 4.81 points per m^2. Detailed processing steps and parameters are provided in Table 2.1.

The DEM was exported towards ArcGIS Pro 2.8.6 (Esri) for further cleaning of above-ground control points and reconstruction of the main channel. Dense vegetation cover precluded accurate reconstruction of the channel bathymetry using aerial imagery in those areas where mangrove forest did not allow the survey of ground points. In addition, the RTK-GPS received no to very low signal in the mangrove forest. Hence, in these areas, on-ground GPS points (Garmin hand-held GPS) were taken along the channel banks, in addition to five cross-sectional profiles of the channel surveyed with RTK-GPS. The low RTK signal in the mangrove forest prevented additional cross-sectional profiles. It is noted that GPS accuracy is low compared to RTK-GPS (5-15 m horizontal error), which added to uncertainties in channel delimitation and reconstruction (see discussion). Channel bathymetry was reconstructed using Natural Neighbor (or Sibson) interpolation (the “Interpolate from the Edge” tool in ArcGIS Pro). This interpolation technique creates a smooth surface using a local and spatially adaptive method that retains the original values at the reference points (Etherington, 2020).

Table 2.1 Workflow and parameters used to process the Unoccupied Aerial Vehicle (UAV) imagery in Agisoft Metashape

Process	*Description*
1. Convert geographic coordinates and camera reference setting	Convert the coordinate systems and camera reference setting to the coordinate system of the GCPs surveyed with the RTK-GPS (I.e., from WGS84 to GDA2020/ MGA zone 55 and AHD) using the "Convert" tool
2. Align image, generate sparse point cloud, and detect markers	Align photos using: • "High" accuracy • Select generic preselection and reference preselection. • Set Key point limit at 40,000 and Tie point limit at 10,000 • Apply masks to None • Uncheck "Exclude stationary tie points"; Guided "Image matching": and "Adaptive camera model fitting"
3. Detect Markers	Using the "Detect Markers" tool
4. Import GCPs	Import GCPs coordinates from CSV file • Set marker accuracy at 0.002 m • Adjust markers on image when necessary
5. Uncheck cameras and check all markers	Uncheck all cameras to force to optimisation process to use the markers surveyed using the RTK-GPS
6. Spare point cloud cleaning and optimisations	Using the gradual selection tool to delete the selected points: • Reckon uncertainty (level 15) and optimise (Default parameters: f, cx, cy, k1-k3, p1, p2, no adaptative camera model fitting) • Reprojection error (level 0.4) and optimise • Reprojection error (level 0.3) and optimise • Projection accuracy (Level 30) and optimise
7. Build Dense Cloud	Build dense point cloud using "High" accuracy and "Mild" depth filtering. Density of Dense Cloud = 4.81 points/m2.
8. Build Orthomosaic	
9. Build DSM	
10. Build DEM	Use “Classify Ground Control Point” with parameters set at default

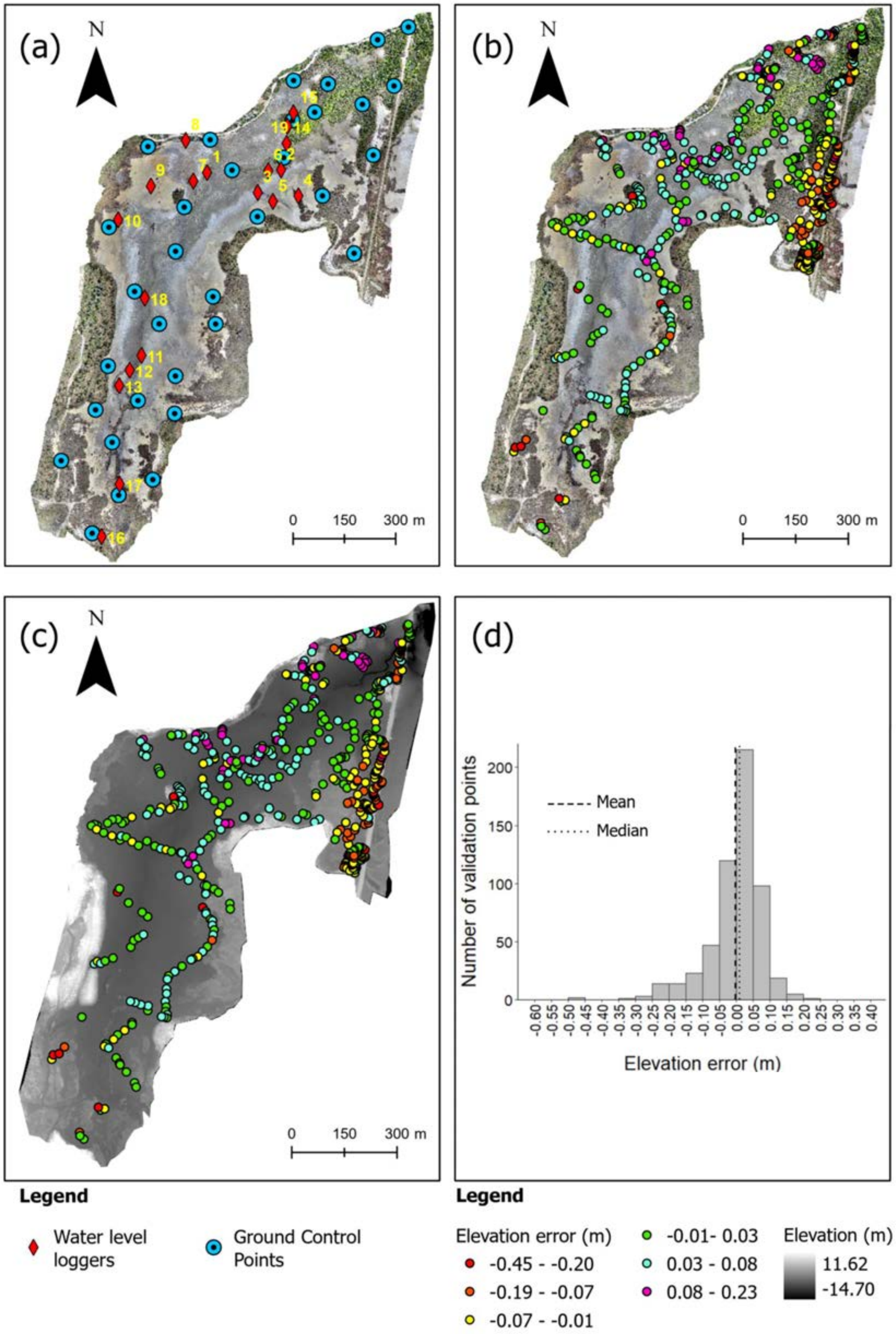


Figure 2.2 (a) UAV-derived topographic map and DEM showing loggers and ground control points position: (b) validation points colour coded according to elevation error on the topographic map; (c) and on the DEM; and (d) and graph of the distribution of elevation error of validation points.

This tool was also used to remove mangrove trees. A conservative terrain filter tool (available in the Pixel Editor tools) that detects and removes above ground points while conserving natural slopes was used to remove remaining vegetation from the DEM surface. The DEM was hydrologically corrected (Jarihani et al., 2015) using the “Fill" tool. Elevation accuracy was assessed by comparing extracted values from the elevation raster to the elevation of 562 RTK-GPS random validation points (the number was not initially set but the aim was to collect the maximum number of RTK-GPS validation points across the study site during the allocated time). DEM error is expressed as the root mean square error (RMSE).

2.4.3.2 Land cover

Key land cover attributes, totaling to eight main cover classes were identified. These cover classes included vegetation (i.e., Herbaceous Saltmarsh, Succulent Saltmarsh, *Ceriops* spp., Other Mangroves (“Mangroves”), and Woodland/Grass Terrestrial), main channel, artificial structures, and unvegetated flats (mudflat/saltpan). Land cover classes were identified with the orthomosaic generated from UAV-SfM to specify Manning’s roughness coefficient. Multiple attempts were made to classify the orthomosaic using unsupervised and supervised object-based image classification algorithms in ArcGIS Pro, but the results were deemed unreliable. A manual classification was performed using the drawing tools in ArcPro and assisted with field data (GPS points and photography). To achieve this, the entire orthomosaic was zoomed in so that each land cover feature could be circled around to create polygons of each land cover categories. The polygons were then merged into individual land cover categories. The final land cover shapefile was made by assigning the entire study site as a mudflat/saltpan polygon (the dominant land cover). Each land cover shapefile was then erased to the mudflat/saltpan polygon in their order of overlapping in the field and then merged to create the final land cover map (Figure A1). The manual classification did not allow the uses of a confusion matrix to provide an accuracy assessment. Nevertheless, the very high-resolution of the UAV-SfM imagery together with expert knowledge of the site coupled and on-ground imagery allowed confident reliability of the classification of land cover (Figure 2.3).

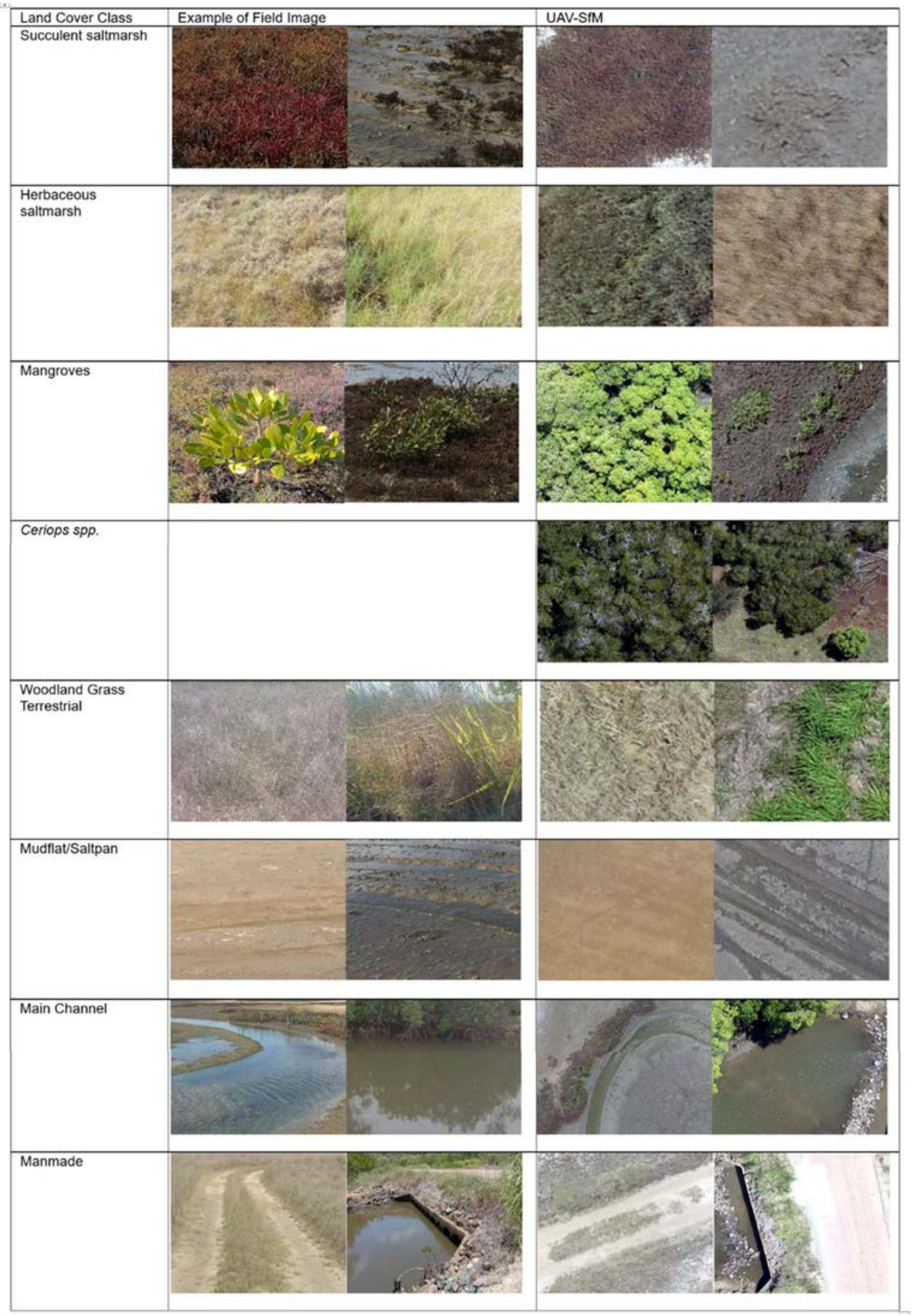


Figure 2.3 Land cover class identified in the field for classification and corresponding examples viewed from the orthomosaic map derived from UAV-SfM.

Table 2.2 Information on the three simulations computed to calibrate and validate the hydrodynamic model. Simulation starting elevation refers to the elevation at which the tidal level was at the beginning of the simulation. Associated loggers used for calibration and validation are also shown (their position can be cross-checked with Figure 2.2.1b).

Simulation	Start time	End time	Maximum tide elevation (m, AHD)	Simulation starting elevation	Loggers
January	07/01/2021 14:00	17/01/2021 07:10	2.07	0.54	1; 2; 3; 4; 5; 6; 7
June	18/06/2021 01:20	30/06/2021 07:30	1.96	0.55	8; 9; 10; 11; 12; 13; 14; 15
August	17/08/2021 15:00	28/08/2021 14:50	1.96	0.57	16; 17; 18; 19

2.4.4 Validation data

2.4.4.1 Water level by loggers

Water levels were monitored from November 2020 to March 2022 using pressure loggers (HOBO Water Level Data Logger (30 Meter U20L Series)) (Onset Compute Corp.) deployed over the study site (Figure 2.2a). The loggers were rotated to new locations based on wetland terrain characteristics every 3 to 4 months due to a low number of loggers available at any time (4-8 loggers). This practice evaluated model performance across the entire study site to maximise spatial and temporal representation of water levels (Johnson & Pattiaratchi, 2004). A logger was placed in a tree in the study area, approximately 1.5 m above ground, to log barometric pressure to compensate recorded pressure by the loggers (the logger remained in the same location for the entire study). The software onset HOBOware Pro was used to convert pressure to water depth, which is calculated using fluid density (saltwater), reference water level (measured at the time of the logger deployment) and barometric pressure data.

2.4.4.2 Inundation by Sentinel-2

The second validation method consisted of comparing satellite imagery to compare observed and simulated inundation extent (Reid et al., 2014; González et al., 2023). Sentinel-2 imagery was downloaded from Planet Labs PBC 2022. As it was not possible to determine whether the inundated area occurred by a preceding tide or was inundated on the satellite imagery, we opted to compare the maximum inundation extent for each simulation period to the first satellite imagery available following the highest tide of the simulation. In January, satellite imagery was taken four days after the highest tide (1/13/2021 at 09:20), with corresponding imagery taken the 21/01/2021 at 09:54. In June and August, the highest tide occurred at night (25/06/2021 at 0120 and 21/08/2021 at 20:10, respectively). Imagery was only available two days after the highest tide in June (27/06/2021 at 10:00) and three days after the highest tide in August (23/08/2021 at 09:44).

2.4.5 Model calibration and validation

The hydrodynamic model was built and calibrated by simulating tidal dynamics over the ~10 days period in January, June and August (Table 2.2), representing different logger positions. A central focus of the analysis was to simulate days representing a neap to spring tidal cycle (Table 2.2), with similar starting and ending tidal elevation across the simulations. Although temporal variations in saltmarsh morphodynamics have been described elsewhere (Sun et al., 2018; Jin et al., 2022) (e.g., 0-10 cm increase in soil elevation within six months following months with higher inundation frequencies in *Spartina alterniflora* saltmarshes, Jin et al., 2022), it was assumed here that the site seasonal variability in morphodynamics was negligible across the simulation period, and the same DEM was used for all simulations.

The Manning's roughness coefficient is the principal calibration target in 2D HEC-RAS (Muñoz et al., 2021). Modelling performance was first assessed with an overall Manning’s roughness coefficient of 0.025-0.035, which are the values recommended in the 2D HEC-RAS manual for bare land with minimal impediment on flow. At that stage, model parameters, including the Theta Implicit Weighting Factor were adjusted (Table 2.3). The Theta value is a weighting factor involved in the solving of the shallow water equations and is responsible for increasing model stability and output accuracy (Hicks & Peacock, 2005). The Theta value was reduced from 1 to 0.6 to improve model stability and better represent tidal wave propagation (Pasquier et al., 2019). The model was then manually calibrated by adjusting the Manning's roughness coefficient of each land cover class (Table 2.4) starting with initial values suggested in the 2D HEC-RAS manual for similar cover classes and rising and adjusting the values until the simulated water level visually best matched the observed water levels. For instance, the 2D HEC-RAS manual recommends range values of 0.023-0.03 for barren land; 0.03 was used here for the mudflat/saltpan category. Similarly, the range of values suggested for emergent herbaceous wetland (0.05-0.085) were used as a basis to calibrate the values of herbaceous (*S. virginicus*) and succulent saltmarsh (*S. quinqueflora*). The friction values are considered in the middle to upper range of the suggested values from 2D HEC-RAS manual to compensate DEM and bathymetric errors (Mardani et al., 2020). Examples of model performance with constant Manning’s and with the manual adjustments can be found in Appendix A (Figure A3)

After trial simulations to calibrate the model by modifying Manning's roughness coefficient and model parameters, we observed a consistent offset of 0.3-0.4 m between observed and simulated water levels. We attributed that to a site-specific offset in datums (likely due the distance to tidal gauge used to parameterise the model) and uncertainties in the DEM (including bathymetry, notably in the area where the mangrove forest was removed, and the channel was reconstructed) (see discussion for details on DEM sources of inaccuracies) and subtracted 0.35 m to observed tidal data. Note, the above description of the calibration of the

Manning coefficients to obtain the final Manning values was carried out after correction for the offset.

Table 2.3 Parameters used for the final calibrated 2D hydrodynamic model in HEC-RAS 6.1.

Computation settings (2D Flow)	*Value*
Theta	0.6
Theta Warm-up	0.6
Water Surface Tolerance	0.003 (default)
Volume tolerance	0.003 (default)
Maximum iterations	20 (default)
Equation set	Diffusion Wave
Initial Conditions Ramp Up Fraction	(default)
Number of Time Slices	1 (default)
Computation Time Step Base	1 min
Base Output Interval	10 min
Hydrograph Output Interval	10 min
Mapping Output Interval	10 min
2D Flow Area	
Points Spacing (m)	2 x 2 m (smaller cell size did not improved the model but significantly increased processing times)
Default Manning's Value	0.035

Table 2.4 Manning's n roughness coefficient used in the validated model based on the range of the recommended values by the HEC-RAS manual.

Land Cover	Manning's n
Mudflat/Saltpan	0.03
Woodland Grass Terrestrial	0.04
Herbaceous saltmarsh	0.06
Succulent Saltmarsh	0.05
Ceriops spp.	0.08
Other mangroves (*Avicennia* spp. and *Rhizophora* spp.)	0.08
Manmade (gravel and concrete roads)	0.1
Main Channel	0.035

The model was validated by comparing the depth recorded by the loggers and the depth simulated by the model. Differences between the maximum observed and predicted depth are *presented* for each logger, together with RMSE of maximum depth error and R^2. RMSE and R^2 between observed and simulated water depths are also presented. RMSE and R^2 of inundation duration were computed by calculating the number of 10-minutes time step being greater than 0 m for both the depth recorded by the loggers and the depth simulated by the model. The number was then multiplied by 10 and converted to hours. The extent of inundation was further validated by comparing the inundation boundary from satellite imagery (Sentinel-2 at 3-m resolution) to the simulated boundary.

2.5 Results

2.5.1 DEM generation and accuracy assessment

The UAV-SfM generated a 3 cm resolution DEM (Figure 2.2), with a RMSE in elevation of 8 cm (Table 2.5). The distribution of elevation error is leptokurtic, with some outliers in vegetated areas (Figure 2.2d). Elevation tended to be overestimated in vegetated areas (Table 2.5). RMSE in elevation was higher in vegetated wetlands (4 cm in mangroves to 12 cm in herbaceous saltmarsh) compared to unvegetated areas (mudflat/saltpans RMSE = 5 cm)

(Table 2.5). The lower elevation error in the mangroves compared to herbaceous saltmarsh is likely because only two successful validation points were surveyed with the RTK-GPS in the mangrove forests (Table 2.5). This made it difficult to assess DEM errors for the mangrove land cover.

Table 2.5 Assessment of elevation error between RTK-GPS validation points and UAV-DEM elevation. Positive mean values indicate elevation underestimation, while negative mean values indicate elevation overestimation.

	Land cover	**n**	**RMSE (m)**	**Mean (m)**	**SD (m)**	**SE (m)**
	Whole DEM	562	0.081	-0.002	0.081	0.003
Unvegetated	Mudflat/Saltpan	357	0.054	0.022	0.050	0.003
Vegetated	Succulent s.	76	0.078	-0.008	0.078	0.009
Vegetated	Herbaceous s.	59	0.123	-0.081	0.096	0.011
Vegetated	*Ceriops* spp.	4	0.080	0.059	0.060	0.031
Vegetated	Mangroves	2	0.041	-0.013	0.055	0.039
Vegetated	Grass/wood.	46	0.155	-0.088	0.128	0.019
Water	Main channel	5	0.107	-0.058	0.101	0.045
Manmade	Manmade	13	0.064	-0.011	0.058	0.016

2.5.3 The hydrodynamic model

Overall, simulated water levels and timing fitted the observed water levels (R^2=0.51 to 0.71 and RMSE = 0 to 0.05 m) (Figure 2.4a). This gives confidence that the model performed well in predicting water level and inundation across the study site. Simulated maximum depth at each logger point was close to that observed, with an RMSE of maximum depth of 0.07 m and a correlation coefficient R^2= 0.93 (Figure 2.4b). RMSE between observed and simulated depth ranged from 0 m (loggers 9, 10, 16, 4 – in areas that remained dry during the study period) to 0.053 m. Correlation coefficients indicate moderate to strong correlation (0.506-

0.712) between simulated depth and observed depth, with the exception at logger 17 where R^2 was 0.24 (Figure 2.4a). Some specific exceptions in model performance in simulating depth are noticeable, notably at logger 2, 3, and 14 where simulated maximum depth were greater than 9 cm of the observed depth. At logger 2, which was positioned adjacent to the mangrove channel, the difference between maximum simulated and observed depth was 0.19 m - the highest recorded. Without this outlier, the RMSE was 0.05 m and the correlation coefficient R^2= 0.98. In addition, the model simulates a constant water level following inundation at logger 17, a logger placed in the isolated channel at the southern part of the study site. When pooling all loggers, simulated inundation durations were lower than observed inundation durations with a R^2 of 0.79 and a RMSE of 24.55 hours (Figure 2.4c). The large RMSE in inundation duration was largely driven by the underestimation of inundation duration in the main channel at loggers 1, 6, 15, 18, 19 and a small drain at logger 7. Without these six loggers, the RMSE dropped considerably, reaching 5.09 hours and a R^2 of 0.99. Model performance was also notably reduced as simulated arrival time and maximum water level tended to be 10-60 minutes earlier than observed. When adjusting for this delay, overall model performance improved in most logger emplacements ($R^2 > 0.789$) (Table A1). For instance, if simulated inundation had arrived 60 minutes later at logger 2, the R^2 would have increased from 0.672 to 0.946 (Table A1).

Comparisons between satellite imagery and simulated inundation extent for each of the three simulation periods (Figure 2.5) support that the model accurately modelled tidal inundation. In January, observed inundation extent was 49.82 ha compared to the simulated extent of 53.02 ha. In June, observed and simulated inundation extents were respectively 41.13 ha and 43.07 ha, while in August, it was 43.20 ha (observed) and 42.89 ha (simulated).

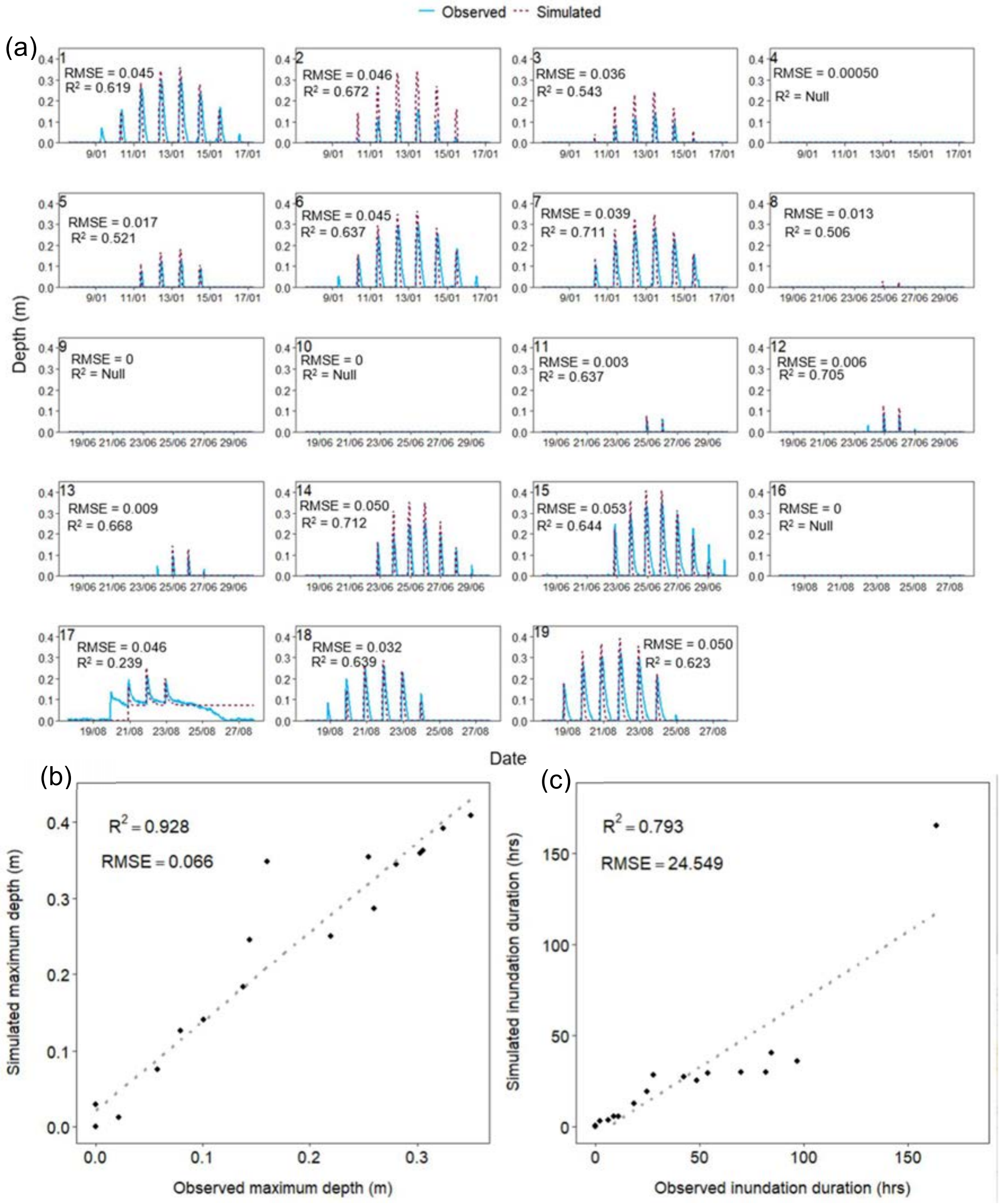


Figure 2.4 (a) Simulated depth over recorded depth (HOBO water level logger) at each logger position with root-mean-square error (RMSE) and correlation coefficient (R2); (b) Distribution of maximum observed and simulated depth (for all simulations) with R2 and RMSE; (c) Distribution of observed and simulated inundation duration in hours with R2 and RMSE.

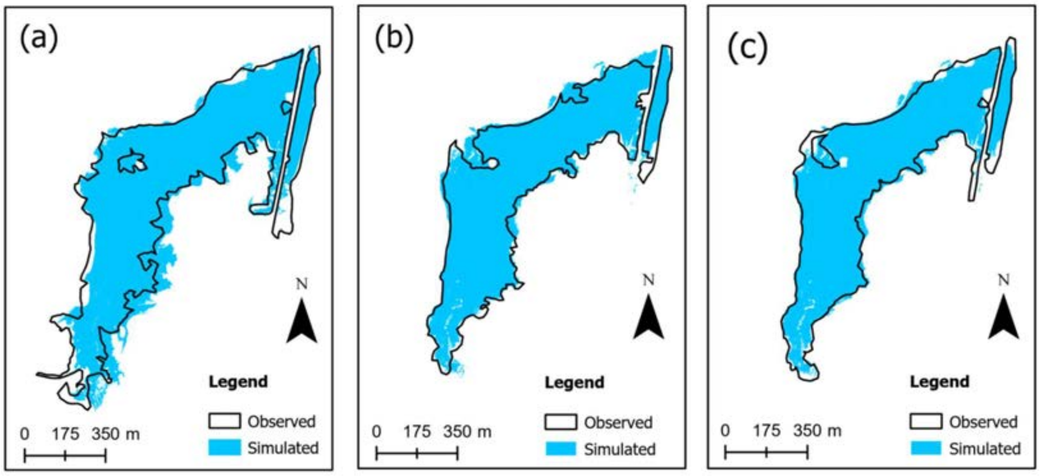


Figure 2.5 (a) Comparison of simulated and observed (Sentinel-2 imagery) inundation boundaries for January; (b); June; and (c) August simulations.

2.5.4 Hydroperiod

The model developed here indicated that a tidal height of near 2.95 m (1.36 m elevation AHD) is required to start inundating the wetland above the mangrove-marsh ecotone (i.e., saltmarshes and saltpan) in the study area upstream of the culvert. In addition, the higher tides observed in January (0.2 m higher compared to June and August) resulted in an increased inundation extent of 10 ha of tidal wetland (Figure 2.6).

Maximum inundation depth across most of the study site and simulation periods remained shallow at <0.4 m (Figure 2.6). Specifically, 68.2%, 82.5%, and 83.5% of the total inundation extent for the January, June and August, respectively, simulations had a maximum depth of less than 0.4 m. Inundation frequency is low across most of the tidal wetland (Figure 2.6). More specifically, in all simulations (January, June and August), more than 50% of the maximum tidal boundary was inundated less than 23.3, 29.4 and 26.4 hours respectively (Table 2.6). Only the defined mangrove channel areas remain inundated 80-100% of the simulation period (Figure 2.6).

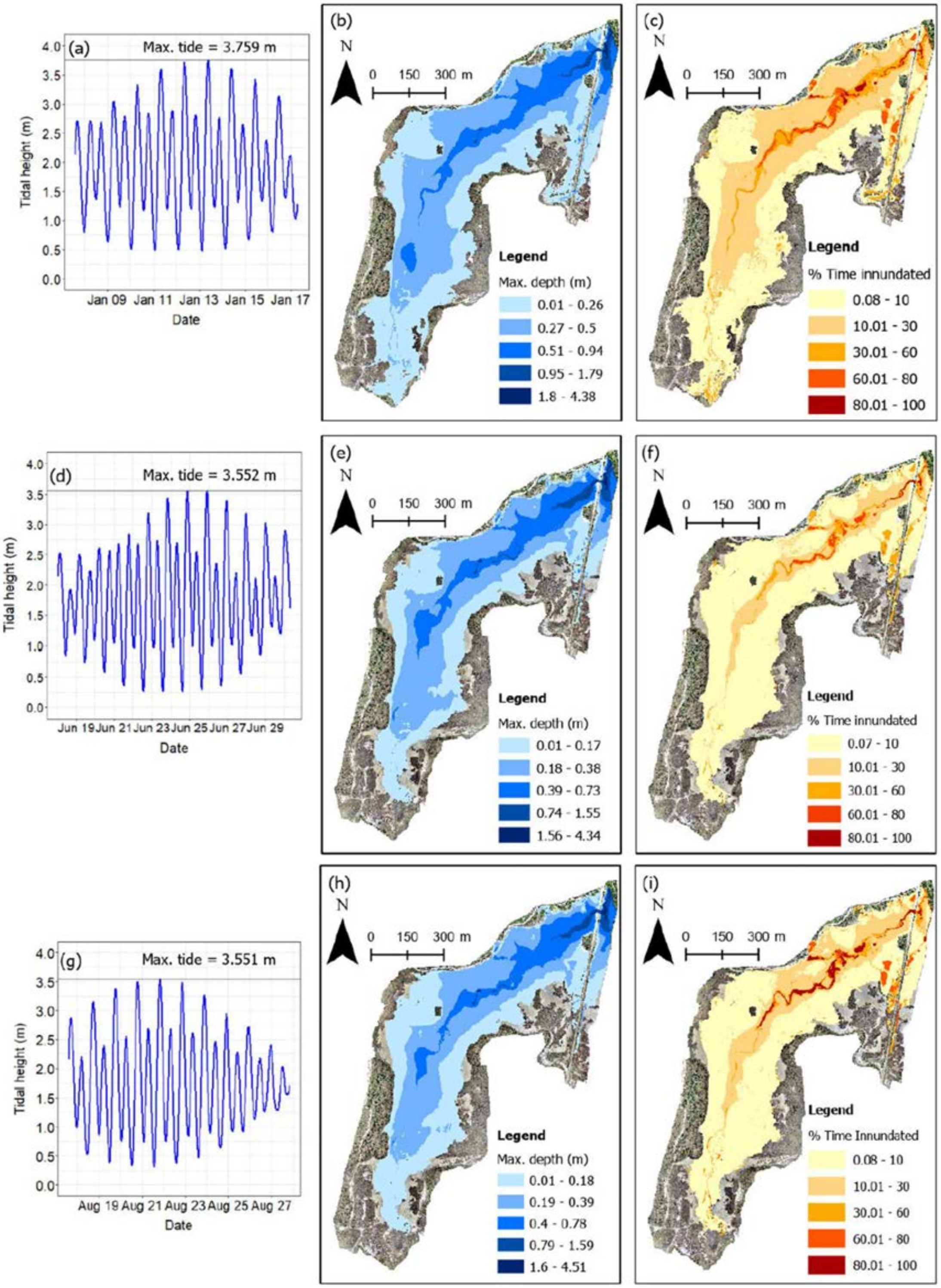


Figure 2.6 Examples outputs for each simulation. Observed tidal height (a, d, g) for January, June and August respectively) recorded at Cape Ferguson tidal gauge (-19.277208; 147.060908), Australia and corresponding spatial distribution of maximum depth (b, e, f) and percentage of time of inundation (c, f, i).

Table 2.6 Maximum (max.) observed tidal height for each simulation and associated maximum simulated tidal extent area (ha). The percentage of the area inundated for a given number of hours (expressed in brackets) is also shown. The number of hours represents <10%, 10-30%, 30-60%, 60-80%, and 80-100% of time of each simulation.

	January 2021	June 2021	August 2021
Max. tidal height (m)	3.76	3.55	3.55
Max. inundation extent (ha)	52.95	43.01	42.84
Simulation time (hours)	233.17	294.17	264.00
Percentage of area inundated less than 10 percent of simulation time (hrs)	50.98% (< 23.32 hrs)	76.15% (< 29.42 hrs)	68.47% (< 26.40 hrs)
Percentage of area inundated between 10-30 percent of simulation time (hrs)	36.40% (23.32- 46.63 hrs)	15.29% (29.42 – 88.25 hrs)	22.34% (26.40 -79.20 hrs)
Percentage of area inundated between 30-60 percent of simulation time (hrs)	6.47% (69.95-139.90 hrs)	5.07% (88.25-176.50 hrs)	2.78% (79.20-158.40 hrs)
Percentage of area inundated between 60-80 percent of simulation time (hrs)	4.54% (139.90-186.53 hrs)	2.59% (176.50 -235.33 hrs)	2.45% (158.40-211.20 hrs)
Percentage of area inundated between 80-100 percent of simulation time (hrs)	1.29% (186.53-233.17 hrs)	0.38% (235.33 – 294.17 hrs)	3.50% (211.20-264.00 hrs)

2.6 Discussion

Low-lying tidal wetlands are at threat owing to changes in tidal inundation due to sea-level rise and anthropogenic disturbances giving rise to the urgent need to develop modelling tools for managers to better implement coastal management and restoration planning decisions. This study presents a workflow that can be used by managers to develop a relatively simple 2D hydrodynamic model, computed using freely available software (HEC-RAS) that requires minimal data inputs (UAV-SfM derived DEM and land cover, and water level data). The resolution and accuracy presented here makes this approach particularly useful for managers challenged with working in low relief coastal wetlands where centimeter scale changes in topography is the difference between water connection or not.

2.6.1 The importance of high-resolution topographic data in coastal studies

The model presented here illustrates how small changes in topography (e.g., vehicle tracks) can interfere with surface hydrology in shallow water environments (Figure 2.7). For instance, a 20 cm increase in tidal height was related to a 10-ha increase in upper tidal areas being inundated. This suggests that even minor alterations in tidal inundation due to anthropogenic activities (e.g., culverts and tidal gates; Kroon & Phillips, 2015) or sea-level rise might affect the extent of intertidal wetland (e.g., saltmarshes) inundation. Vehicle uses on saltmarshes has been shown to cause direct saltmarsh degradation and disappearance (Trave & Sheaves, 2014; Blakely et al., 2022). In this study, vehicle tracks through the wetlands were found to influence tidal inundation pathways and create unnatural flow paths that remain wet. The present observations support the model that vehicle uses on saltmarshes might affect tidal wetland hydrological connectivity and potentially interfere with eco-hydrological processes at the local scale. For instance, constant inundation might affect soil properties (e.g., water content, salinity, compactness) and in turn vegetation distribution and soil suitability to burrowing organisms (Trave & Sheaves, 2014). In light of these findings, and in line with several other studies (Hannaford & Resh, 1999; Kelleway, 2006), coastal management authorities must carefully consider whether these activities should occur in such sensitive ecosystems. These observations also support the importance of utilising fine resolution DEMs (Annis et al., 2020), where employing a coarser DEM resolution (e.g., 1 m) would not have detected road tracks and small channels that would seemingly influence inundation (Figure 2.8).

2.6.2 Key considerations for hydrodynamic modelling of tidal wetlands

2.6.2.1 Choice of model

With an RMSE error between maximum observed and simulated depth of 7 cm, and similar trends between simulated and observed depth, the present model was considered a reliable tool to understand tidal wetland hydroperiod. The largest difference between maximum observed and simulated depth (19 cm) also is lower than reported in other coastal flooding studies (e.g., 33 cm in Kumbier et al., 2022). Correlation coefficients between observed and simulated depths were nevertheless lower than reported in another hydrodynamic study of a tidal wetland complex composed of similar saltmarshes and mangroves species (r^2=0.98-0.99, Kumbier et al., 2022).

Spatial variability in model performance was observed, notably near the mangrove channel, where simulated depths were higher than recorded depth (notably at loggers 2, 3, and 14). Previous studies have attributed spatial variability in hydrodynamic model performance to model configuration and uncertainty in inputs data (e.g., DEM, mesh structure, grid size, spatial variability in roughness, boundary condition, and processing parameters) (Ganju et al., 2016; Anees et al., 2017). For instance, it is possible that a combination of DEM inaccuracies and the fact that the tidal gauge was placed outside of the study area could have resulted in the observed difference of 0.3-0.4 m in water depth during calibrations, and resulted in the need to subtract 0.35 m to the tidal data. The use of the Unsteady Flow Equation (UFE) instead of the Shallow Water Equation (SWE) that considers local and advection acceleration might also have decreased water depth accuracy (Yilmaz et al., 2023) and led to the need to correct the 0.3-0.4 m offset. Solving the UFE instead of the SWE might also have led to the shortened arrival time as the UFE tends to simulate higher flow velocities (Marangoz & Anilan, 2022), although slower propagation has also been described with UFE (Martins et al., 2017). DEM

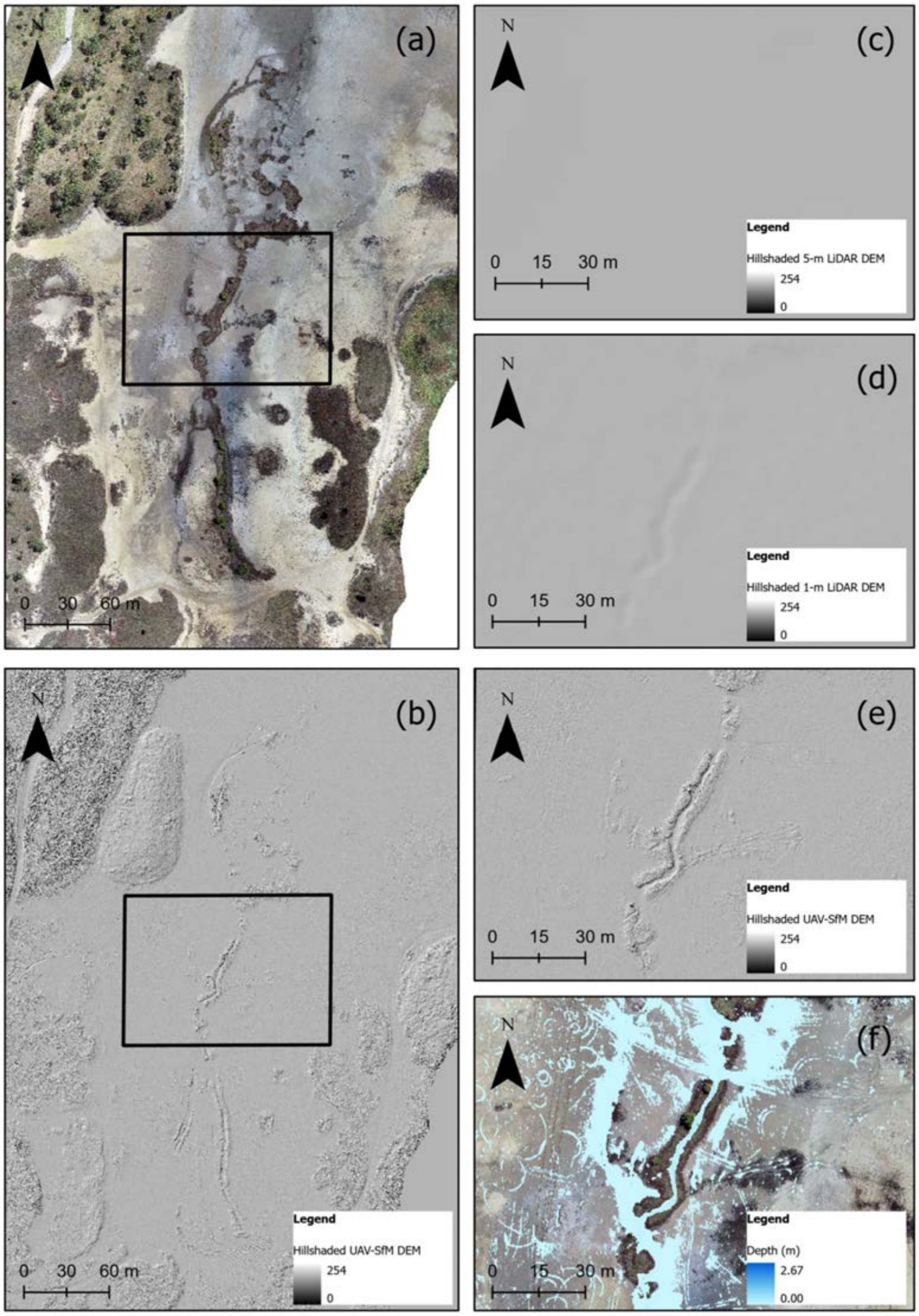


Figure 2.7 (a) Orthomosaic map of 0.02 m resolution and (b) associated 0.03 m digital elevation model (DEM) (this study) generated from UAV-SfM. (c-f) Examples of the effects of DEM resolution on the representation of topographic features are shown. (c) The same area (black rectangle in a and b) is represented by a 5-m DEM derived from LiDAR (Geoscience Australia); (d) 1-m DEM derived from LiDAR (QLD Government; and (e) 0.03 m DEM derived from UAV-SfM (this study). (f) The effects of microtopographic features represented by the 0.03-m UAV SfM on tidal flow trajectory and depth are shown, where tidal inundation simulated by the 2D hydrodynamic model developed in this study is overlaid on the orthomosaic map.

(including bathymetry) inaccuracies could also have led to the higher simulated depths and shorter simulated inundation compared to the loggers placed in the mangrove channel as well as the overall earlier simulated arrival times. Manning's n values are the only parameter that needs to be adjusted in HEC-RAS and seemed not to importantly influence arrival time in the present study (Figure A3). Hence, it is more likely that other choices (DEM and boundary condition) leaded to the lower performance in the model near the mangrove channel and in arrival times. A detailed sensitivity analysis and calibrations of the model are essential to understand the effects of model configuration and/or uncertainty in input data on model performance (Hall et al., 2009). Detailed sensitivity analyses were not conducted in the present study, but might have improved the assessment and calibration of the model (Pan et al., 2011).

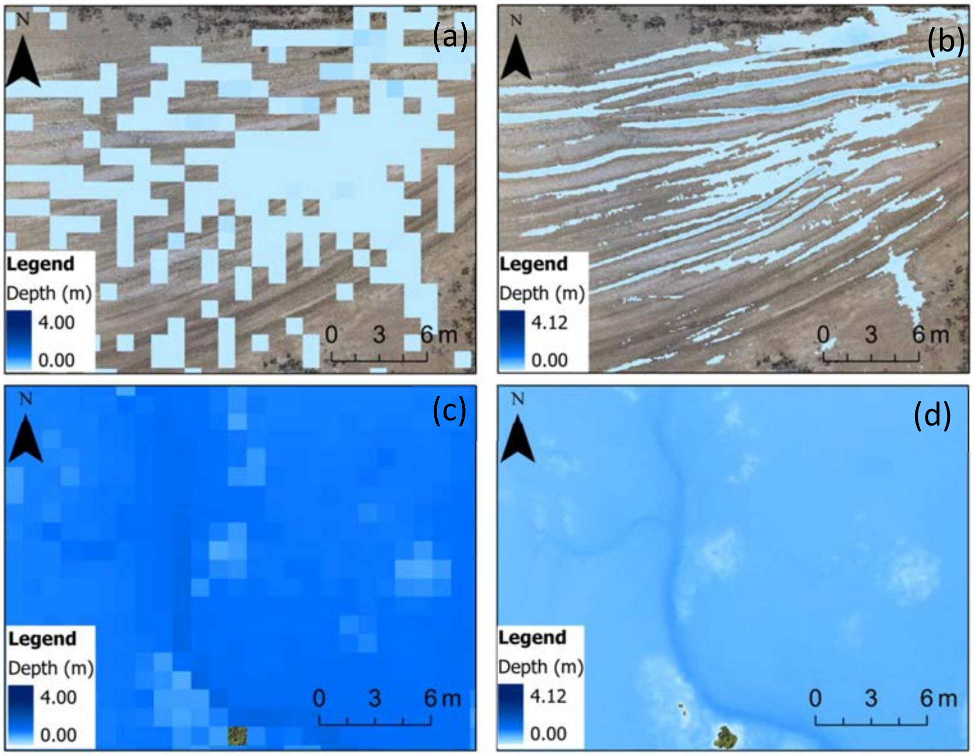


Figure 2.8 Comparisons between the hydrodynamic modelling outputs based on the DEM derived from UAV-SfM resampled at 1-m resolution (a, c) and the 0.03 m- UAV-SfM (b, d) showing depth overlaid on the orthomosaic map.

Eco-hydrological processes such as variability in soil characteristics (e.g. stratigraphy and chemistry), groundwater dynamics (e.g., Willson and Morris 2012), or macropores (Xin et al., 2009) can also influence surface and sub-water flow interactions, and thereby spatio-temporal variability of tidal wetland inundation. Monthly variability in tidal inundation frequency and sediment availability can also lead to seasonal changes in soil elevation (Jin et al., 2022). For instance, a 0-10 cm increase in soil elevation was reported in *S. alterinflora* saltmarshes (Jin et al., 2022). The increase occurred over a six-month period following months with higher inundation frequencies. These processes might have caused some of the differences between observed and simulated water depth, notably near draining channels and vegetated areas as bare flats are less prone to seasonal changes in soil elevation (Jin et al., 2022).

Dynamic mechanistic numerical models (e.g., ecogeomorphic models), that take into account hydrology and soil morphology (e.g., Marois & Stecher, 2020) and feedback processes between ecology and hydrogeomorphology (e.g., Alizad et al. 2016), may better represent small-scale processes that influence tidal wetland hydrology.

Similarly, adding rainfall, barometric, evapotranspiration, and wind data to the present 2D hydrodynamic model could enhance model applicability in wider meteorological contexts (Karim et al., 2021). For instance, evapotranspiration is important in dry areas (Wallace et al., 2015) particularly when the model is ran for longer periods such as months or years. In the present case, there will be negligible evapotranspiration in a 10-day model run. However, evapotranspiration might have caused the different pattern in observed and simulated depth at logger 17, which was placed in a depression. Simulated depth remains constant following inundation, while observed depth decreased over time. Adding evapotranspiration data could therefore increase model accuracy in those areas characterised by more complex topography.

The selected model must represent the dominant processes of the study site, which means that end-users of these approaches must, therefore, be careful and understand the selected model's limitations, such as error and uncertainty (Wechsler, 2007), and is within an acceptable limit to answer ecological questions. Based on the objectives of the simulation, different models are selected, and processes need to be added or deleted from the model. For example, groundwater/surface water interaction cannot be modelled in all 2D models. I believe that the approach presented provides a way forward in understanding tidal wetland inundation where there is limited starting data.

2.6.3 UAV-derived DEM

The approach to UAV data collection, image processing, and post-processing implemented in this study derived DEMs with a resolution of 3 cm, and high accuracy (8 cm elevation error) suitable for small scale and detailed hydrodynamic modelling tidal wetlands. The DEM accuracy assessment results are similar to that of studies that have used SfM to derive DEMs, where DEM RMSE range from 3-8 cm (e.g., Gonçalves & Henriques, 2015; Koci et al., 2017; Taddia et al., 2021).

Although studies have developed high resolution UAV-SfM derived DEMs and highlighted their potential uses in water management (Kalacska et al., 2017; Taddia et al., 2021), only a few studies have used UAV-SfM derived DEMs to parametrise 2D hydrodynamic models (Tamminga et al., 2015; Yalcin, 2018; Annis et al., 2020; Li et al., 2021a). To the best of my knowledge, the present study is the first to use a UAV-SfM derived DEM to parametrise a 2D hydrodynamic model of a tidal wetland. Although, UAV-SfM presents advantages to create DEM for the management of tidal wetlands (Table 2.7), the key limitations encountered in the present study remain the same as that of floodplain and rivers, which are attaining ground points in vegetated areas (e.g. Hashemi-Beni et al., 2018), obtaining bathymetric data (Tamminga et al., 2015), and limitations due to GCPs requirements and computing demand.

The elevation errors computed in this study are less, near or higher than those of similar tidal wetland studied with UAV- or LiDAR-DEM. For instance, the UAV-DEM derived by Taddia et al. (2021) (which was not further cleaned after Agisoft Metashape ground-point classification) obtained a RMSE of elevation of 1.5 cm for mudflats from UAV-DEMs, which is coarser to the 5 cm obtained in this study. Their RMSE for saltmarshes (dominated by *Spartina alterniflora*) was 20 cm (compared to 8-12 cm in the present study), which was considered too coarse by the authors to investigate geomorphological changes. Hladik and Alber (2012) obtained a RMSE of 5 cm for *Salicornia virginica* (corrected Lidar-DEM)*,* similar to the RMSE of 8 cm obtained here for succulent saltmarshes dominated by *S. quinquefolia*. Herbaceous saltmarsh elevation errors (dominated by *S. virginicus,* with *C. dactylon* and *Juncus* spp.) were also comparable, although higher (12 cm), to the RMSE of low and medium *S. alterniflora* (5-7 cm) (Fernandez-Nunez et al., 2017) and *Juncus roemarianus* (10 cm) (Hladik & Alber, 2012) derived from corrected Lidar-DEMs.

The performance of in-built ground point filtering algorithms (e.g., geometric algorithms such as the progressive morphological filter (PMF)) available in photogrammetric software remains poor in highly vegetated areas such as herbaceous saltmarsh (Štroner et al., 2021). Studies have attempted to address this by developing more specific algorithms to remove non-ground points such as in mangrove forests (e.g. Navarro et al., 2020; Mohamad et al., 2021). However, trade-offs between study site size (Navarro et al., 2020) and resolution (Mohamad et al., 2021) remains due to the high computing/processing demand when using those techniques. Those difficulties are overcome with Lidar-UAV (Pinton et al., 2020; Pinton et al., 2021; Cao et al., 2021).

Here, the relatively simple approach used to create a DEM from a DSM (Digital Surface Model) might not have been suitable if the site was a mangrove-dominated system with dense vegetation. Indeed, this technique (Agisoft Metashape algorithm to remove non-ground points followed by manual cleaning of the mangrove forest using ArcGIS Pro) led to artefacts and uncertainties in the DEM in vegetated areas and below water (elevation error increases from -1-8 to 8-20 cm in some vegetated areas near the mangrove forest after DEM cleaning). This represents a weakness in the present approach as this area is a critical part of the study site where the system is flooded and drained. Yet uncertainties in the DEM in this area could not be explicitly addressed as the RTK-GPS did not work in the mangrove forest, and accessibility and safety due to crocodiles were impeded along and in the channel. This workflow would also not be suitable for terrain under low-tide level (e.g., seagrasses). In addition, manual classification of land cover makes this technique inappropriate for larger sites. The uses of multi-spectral UAVs for high-resolution mapping of vegetation with similar RGB colour would have helped in the classification of land cover here (Yeo et al., 2020; Nardin et al., 2021) – where complex overlaps of vegetation with similar characteristics (e.g., herbaceous saltmarsh and terrestrial grass; mudflat and succulent saltmarsh) rendered autonomous classification unreliable.

2.6.4 Model validation

The limited availability or difficulty in acquiring accurate validation data is a recognised cause of uncertainty in hydrodynamic modelling studies (Molinari et al., 2017). I advise using water level loggers for validating hydrodynamic modelling results. The water level loggers identified the need to offset the calculated simulated model depths from the observed water depths. Solely comparing simulated inundation extent to inundation extent extracted from Sentinel-2 imagery reinforced that the model was efficient at modelling tidal inundation extent, but would not be able to quantify this offset. Additionally, the satellite imagery resolution (3 m) was also markedly coarser than the resolution of UAV-SfM derived DEM (0.03 m), making it challenging to distinguish the inundation boundary on the satellite imagery. Remotely sensed data from satellites are increasingly used to validate large-scale hydrodynamic modelling (Teng et al., 2017). I suggest, however, that in the context of high-resolution, small scale hydrodynamic modelling such as presented here, on-ground data (e.g., water level loggers) should be collected when possible and used in conjunction with other validation methods (e.g., remotely sensed data, Reid et al. (2014)).

2.6.5 Applications, hydroperiod and future studies

The model quantitatively shows what has been described non-empirically in the literature concerning that saltpan and saltmarsh inundation is infrequent (<10% of simulation time) and shallow (< 0.3 m) in Australia (Thomas & Connolly, 2001). However, the model also highlights that maximum depth and duration of inundation can vary at small spatial (i.e., few centimetres) and temporal (e.g., minutes to lunar month) scales. Accounting for this will be essential for the management and restoration of coastal ecosystems (Sheaves et al., 2021). By showing that micro-topographic differences result in locally changing hydroperiod, the model highlights that these ecosystems are complex, with site-specific nuisances suggesting that even small human interventions such as vehicle uses could have the potential to modify their function as productive coastal habitat. For instance, waterlogged soil resulting from faults in soil elevation caused by vehicle uses promote *A. marina* growth, algal mats formation, and mosquito breeding sites, while considerably reducing saltmarsh habitability to invertebrate populations (Kelleway, 2006).

The workflow presented here is particularly meaningful given increasing interest in restoring blue carbon ecosystems above low tide levels (Macreadie et al., 2021; Lovelock et al., 2022).

Table 2.7 Summary of advantages and limitations of the present UAV-SfM and 2D hydrodynamic modelling workflow, as well as further research and improvements, alternatives, examples of applications, and key outcomes.

	UAV-SfM for hydrodynamic modelling	**HEC-RAS 2D Modelling**
Advantages	• High-resolution DEM (3 cm) • High-resolution (0.02 m) orthomosaic map that can be used for Manning's n Roughness calibration and cover assessments (e.g., vegetation distribution, patch size, road tracks). • Instruments low-cost (<10,000) • User-friendly instruments and photogrammetric software • Practical licences not required for using light quadcopters in research in some countries (e.g., Australia, only a theoretical online test is required).	• Free • User-friendly and highly documented • Highly dependent on DEM resolution and accuracy • Many mapping outputs options are available. • Official tidal gauge data can be used as boundary condition. • Bathymetric, precipitation, and wind data can be added in a 2D grid system. • In-built tools to reconstruct channel structure and bathymetry.
Limitations	• Applications remain limited by vegetation and water. • Not easily applicable in dense mangrove forests or in low-tide terrain (e.g., seagrasses, mudflats). • Study site size needs to remain small (< 100 ha) due to GCPs surveying, short UAV battery life, limited day times at which UAVs can be flown, and data storage, processing, and analyses, which require high computing demands.	• Simulation processing times are principally controlled by computer processor speed. • Simulations might require higher computing demands than other 2D hydrodynamic modelling software such as Delft3D-FM (Muñoz et al., 2021) • Fixed grid modelling • Computational cells have a maximum of 8 sides.
Further research and improvements	• DEM accuracy in vegetated areas • Ground point classification algorithms • Workflows to reduce GPCs uses (e.g., Taddia et al., 2020)	•
Alternatives for potentially higher performances at a higher financial cost	• UAV-borne topo bathymetric LiDAR and UAV-based green LiDAR system (GLS) (TDOT GREEN 2022) for higher DEMs accuracies in vegetated and inundated areas • RTK-UAVs and/or PPK techniques to reduce GCPs (Taddia et al., 2020) • Multi-spectral UAVs for high-resolution mapping of vegetation (Yeo et al., 2020; Nardin et al., 2021)	• 2D/3D modelling software (e.g., TUFLOW, MIKE 21, MIKE 3, Defl3D) for coastal and estuarine modelling that propose both unstructured or fixed structured grid modelling and in which many environmental variables can be added (Karim et al., 2021; Kumbier et al., 2022)
Applications and uses for tidal ecosystems management	• Restoration and protection of hydrological connectivity • Identification of suitable restoration sites • Tidal vegetation replantation projects • High-resolution mapping of tidal wetland vegetation distribution • Evaluation of changes over time (e.g., vegetation loss/grain, connectivity loss/gain; elevation changes) • Modelling sea-level rise or reduction of tidal inundation and their effects on tidal wetland hydroperiod • Identification of local stressors (e.g., vehicle uses on saltmarshes) • Fish and invertebrate habitat management (e.g., nurseries) • Ecological processes related to hydroperiod (e.g., prey-pulses, food webs) • Identification of mosquito breeding sites	
Key outcomes	• Quantitative and visual understanding of critical tidal wetland processes such as hydrological connectivity with minimal expertise and financial resources • Impactful (i.e., visual and high-resolution) and understandable communication of results to stakeholders, practitioners, and investors. • Possibility to quantitatively link hydroperiod to tidal wetland ecological and morphological processes as well as human impacts.	

Financial resources for the restoration and conservation of ecosystems are highly competitive and request measurable outcomes (Vanderklift et al., 2019; Waltham et al., 2021). Concurrently, the lack of quantitative understanding of tidal wetland functioning and hence of potential measurement of restoration success increase dubiety in investing in coastal restoration (Waltham et al., 2020). Achieving a spatial and quantitative understanding of tidal hydrological connectivity, such as provided by the simple workflow presented here, will provide cost-benefit solutions for investors and stakeholders to assist in predicting and measuring restoration and protection outcomes. Indeed, this workflow has many potential applications in tidal ecosystem management (Table 2.7). For instance, it can be used to quantify tidal hydrological connectivity, which can then be associated with information on elevation, tidal vegetation distribution and survival, accretion rates, and carbon storage capacity and how this might change with sea-level rise or reduction of tidal inundation. Such understanding is paramount in identifying, implementing, and evaluating the success of restoration and protection of blue carbon ecosystems. Repetitions of the same workflow overtime can also provide information on morphological evolution of tidal wetlands (Taddia et al., 2021).

2.7 Conclusion

New advances in remote sensing techniques and hydrodynamic modelling software are opening new horizons to understanding tidal wetland hydrodynamic at high spatio-temporal resolution. In this study, I present a case for using UAV-SfM to derive DEMs with a high resolution and accuracy suitable to parametrise small-scale hydrodynamic models of tidal wetlands. With some exceptions in model performance in the mangrove channel, tidal inundation depth and duration were represented with acceptable accuracy between simulated maximum observed and simulated depth and duration of inundation. The DEM derived from UAV-SfM was accurate (7 cm RMSE) but still represented challenges in obtaining ground points in the mangrove forest and in the main channel, which likely caused lower model performance (higher depth and duration inundation error) in those areas. Overall, representation of tidal wetland inundation patterns was importantly improved by using the high-resolution 3-cm UAV-SfM DEM. The approach shows that small changes in elevation such as due to vehicles tracks and water level modify tidal wetland inundation patterns and hydrological connectivity at small temporal and spatial scales. These methods will assist in planning, defining, and implementing practical and measurable restoration and protection projects that consider tidal flooding dynamics and implications in areas with very low elevation. Calibrated hydrodynamic model also can be used to predict future inundation and hydrodynamic levels due to projected climate change scenarios.

Chapter 3:Linking tidal wetland vegetation mosaics to micro-topography and hydroperiod in a tropical estuary

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- Vulliet, C., Koci, J., Sheaves, M. and Waltham, N., Submitted December 2023, In Review. Linking tidal wetland vegetation mosaics to micro-topography and hydroperiod in a tropical estuary.

The submitted manuscript has been modified to fit with the style of the thesis.

Authors contributions: **Vulliet:** Conceptualisation, Methodology, Investigation, Data curation, Formal analyses, Writing-original draft, Visualisation, Funding acquisition, Project administration; **Koci:** Investigation, Formal analyses, Validation, Writing - Review & Editing, Supervision, Resources; **Sheaves**: Review & Editing, Supervision, Resources; **Waltham:** Conceptualisation, Validation, Visualisation, Writing - Review & Editing, Supervision, Resources

3.1 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. 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, elevation and hydroperiod explained only 28% of the variability in tidal wetland cover distribution. These findings underline that simplistic rules in the causality of tidal wetlands need to be applied with caution, because their applicability in management and restoration are likely to vary depending on contexts, as observed in the study site, with varying environmental and biological factors playing important roles in the distribution patterns of tidal wetland components. I also identified strong monthly variability in tidal hydroperiods, and connectivity experienced by each tidal wetland cover, highlighting the importance of integrating temporal dynamics in tidal wetland research and management. Additionally, I explored the potential effects of sea-level rise (SLR) on the tidal hydroperiods and connectivity of the study site, with the results underlining the importance of acquiring detailed spatio-temporally resolved data to enable the development of robust long-term and adaptive saltmarsh management strategies. The results are discussed from a management and

restoration perspective. I highlight the uncertainties and complexities in understanding the processes influencing tidal wetland causality, their functionality, and hence, their management and restoration.

3.2 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 & 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 therefore are a key asset in responding to climate change (Macreadie et al., 2021), while also providing multiple environmental and economical services (Lovelock & Duarte, 2019). Yet, saltmarshes are declining globally (Dixon et al., 2016; Murray et al., 2022), threatened by direct human activities, such as agriculture and urbanisation (Boon et al., 2011; Cherry & 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 efforts, 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 & Faber, 2001; Bayraktarov et al., 2016). Failed tidal wetland restoration projects 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 & 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., 2021b; Rogers &

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 & 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 a 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 boundary (e.g., vegetation type, intertidal zones) and on the conception that these systems are well-segregated and work in isolation (Weinstein & 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., 2014b; 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 (Gesh 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 & Shumway, 1993; Nunes & 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. 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 & Adams, 2009). 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 Chapter 2. 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 the 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 the 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.

3.3 Methods

3.3.1 Study site

This study is located in Blacksoil Creek (19.297867 147.021333; 82.54 ha), northern Australia (Figure 3.1). 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 & 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 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 saltpans 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) (Figure 3.1). This main channel becomes increasingly narrower with higher elevation at the study site.

The extent of urban development and agricultural land within Blacksoil Creek’s catchment is relatively minimal (Mattone & 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 area occur within the vicinity of the study site – a common feature of estuaries in the region (Sheaves & Johnston, 2009). The topography (Chapter 2) and saltmarsh vegetation within the study area have been impacted by 4-wheel drive vehicles that use the area for recreational purposes (Figure 3.1), which is a common problem in the study region (Trave & 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 (Figure 3.1). 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 & Phillips, 2015), which have created barriers to fish, invertebrates, and propagules movement (Sheaves et al., 2014).

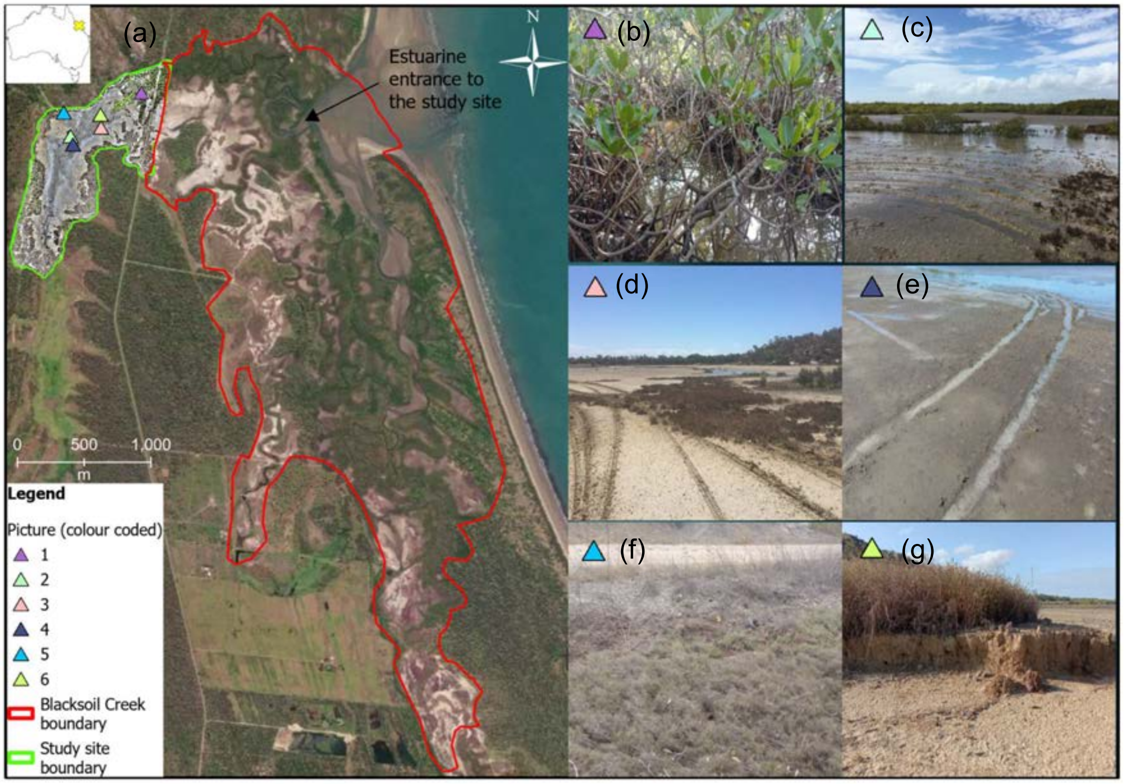

Figure 3.1 (a) Study area map showing the location of the study site (in green) within the larger Blacksoil Creek estuarine complex (in red) and an indication of the estuarine entrance of the tidal creek (the "main channel") leading to the study site. Ground pictures associated to the study site (from left to right) show (b) the main channel surrounded by *Rhizophora stylosa*; (c) inundated saltpans with patches of *Sarcocornia quinqueflora*; (d) drained saltpans with vehicles tracks and patches of *Sarcocornia quinqueflora;* (e) vehicles tracks after inundation; (f) herbaceous saltmarsh dominated by *Sporobolus virginicus* with terrestrial vegetation along a dirt road; (g) saltpans and errored banks of terrestrial grass and shrubs.

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 (2.150 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 remains inundated during neap tide cycles. Tides near 2.95 m (1.36-m elevation AHD) are required to start inundating the mangrove-saltmarsh ecotone in the study area (Chapter 2), while tides greater than 2.6 m (1.01-m elevation AHD) trigger the inundation of mangroves adjacent to the main channel (Chapter 2). The main channel is the principal source of surface tidal water exchange with the study site (Chapter 2). 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 (Figure 3.1). 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 glaucescen*s.; prickly saltwort, *Salsola australis*; and seablite, *Suaeda australis.* The herbaceous saltmarsh community is principally composed of the saltcouch, *Sporobolus virginicus* with some greencouch, *Cynodon dactylon,* and jointed rush, *Juncus kraussii*.

3.3.2 UAV surveys and imagery processing

Details on field and UAV-SfM imagery processing methods are found in Chapter 2. 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 Chapter 2 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 Chapter 2.

3.3.3 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 other than *Ceriops* spp.); *Ceriops* spp. (C); succulent saltmarsh (SS); herbaceous saltmarsh (HS); mudflats/saltpans (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 (Chapter 2).

3.3.4 Data analyses

3.3.4.1 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/saltpans). Note that each land cover had outliers due to high number of data points, DEM inaccuracies, and potential centime-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 scale) of wetland cover elevation values. Detailed summary statistics with and without outliers are provided in Appendix B (Table B1) with a boxplot showing the distribution of the outliers (Appendix B, Figure B1).

3.3.4.2 Tidal wetland inundation characteristics across lunar month and wetland cover

The 2D hydrodynamic model developed in Chapter 2 was used here to measure spatial and temporal variability in tidal inundation and to calculate the mean hydroperiod of each wetland cover class. 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 hours (31.3 days) characterised by lower (low), average (average), and higher (high) than average spring tides using the same hydrodynamic model settings used in Chapter 2. As in Chapter 2, inundation patterns were well presented by the model with RMSE between observed and simulated inundation of 0-0.055 m (Appendix B, Figures B2-B4). Some inundation duration and maximum depth inaccuracies were noted (Appendix B, Figures B2-B4), notably at five loggers near the main mangrove channel and a small drain where inundation and maximum depth were under or overestimated (loggers 1, 6, 7, 15, 19) (Appendix B, Figures B2-B4). These five loggers influenced RMSE in elevation duration (calculated as the root mean square error between the number of observed and simulated 10-minute intervals above 0 m) to 35.67 hours compared to 9.53 hours over the entire simulation periods without these loggers. The model performance is discussed in depth in Chapter 2.

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 & 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). The normalised hydroperiod variables and elevation were used as the environmental variables pooled across simulations.

3.3.4.3 Sea level scenarios

To examine the potential effects of SLR on the hydrological connectivity and tidal inundation characteristics at the study site, 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.

3.4 Results

3.4.1 Distribution of tidal wetland cover with soil elevation

The mean and standard deviation derived from elevation points extracted from the 0.1 m-spaced land cover point features were used to observe zonation across vegetated and unvegetated cover types following Silvestri et al. (2005). Zonation across vegetated and unvegetated covers can be assessed by the differences and overlaps between vegetated and unvegetated cover elevations shown in Figure 3.2. 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. However, the results show that the distribution of all vegetated and unvegetated cover types overlaps to some extent with the elevation range of at least one other wetland category (as shown by the overlapping standard deviations in Figure 3.2).

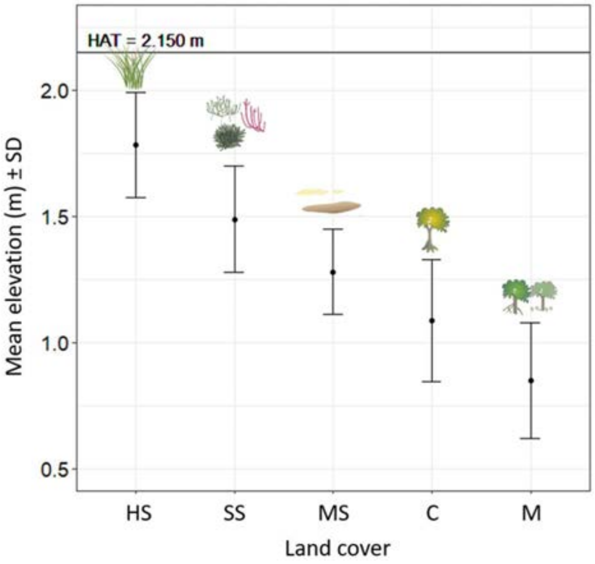

Figure 3.2 Tidal wetland land cover class zonation observed at the study site. Mean elevation of tidal wetland land cover class with their standard deviations (SD). "HAT" = Highest Astronomical Tide at Cape Ferguson, Australia; ""HS" = Herbaceous saltmarsh; "SS" = Succulent saltmarsh; "MS" = Mudflats/Saltpans; "C" = *Ceriops* spp.; "M" = *R. stylosa*/*A. marina* (abbreviated as "M" for mangroves other than *Ceriops* spp.).

Elevation frequency distribution graphs were computed by extracting elevation from the 0.1 m-spaced land cover point features. The graphs revealed there were clear differences in elevation between some covers (e.g., *R. stylosa*/*A. marina* and herbaceous saltmarsh), however, there interestingly were also overlapping elevation distribution among vegetated and unvegetated covers (Figure 3.3). All vegetated and unvegetated cover had non-normal elevation frequency distribution (Kolmogorov–Smirnov statistic: D>0.4;

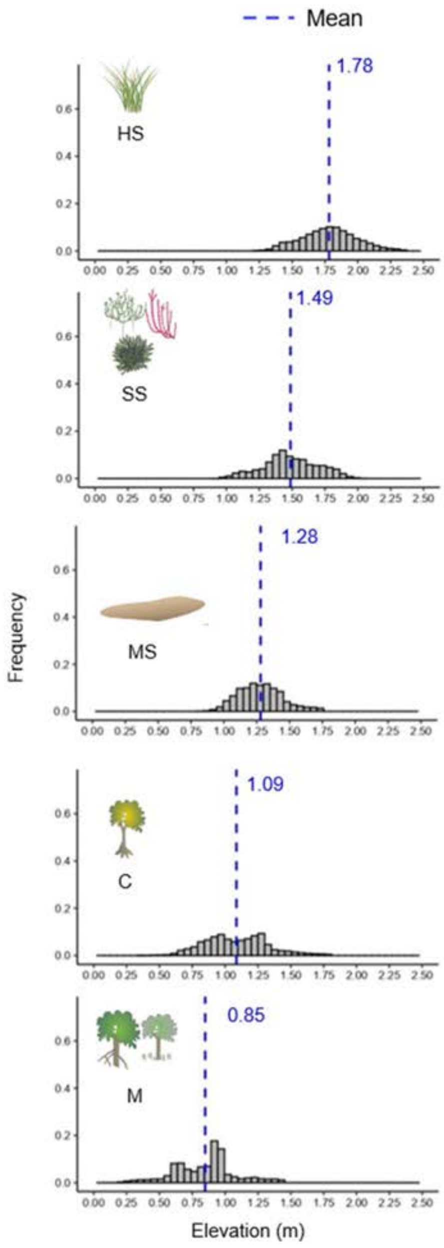

Figure 3.3 Elevation frequency of tidal wetland land cover class. “HS” = Herbaceous saltmarsh; “SS” = Succulent saltmarsh; “MS” = Mudflats/Saltpans; “C” = *Ceriops* spp.; “M” = *R. stylosa*/*A.* marina (abbreviated as “M” for mangroves other than Ceriops spp.).

$P<0.001$ 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/saltpans 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 Appendix B, Table B2.

3.4.2 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/saltpans, succulent saltmarsh, and herbaceous saltmarsh (Figure 3.4). However, large standard deviations (Appendix B, Table B3) suggest that there was variability in the mean tidal hydroperiod of each tidal wetland cover.

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

The BIO-ENV routine determined that elevation and higher-than-average and lower-than-average tide duration of inundation accounted for 28% of the variability of the presence-absence of tidal wetland cover pooled across the three simulations. Elevation alone accounted for 15% of the variability.

3.4.4 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 (Figure 3.5) (Table 3.1). The model revealed that even during higher-than-average tides, which occurred 1-2 times per year in 2019-2021 (Table 3.2) and are shown to inundate 52.04 ha of the study

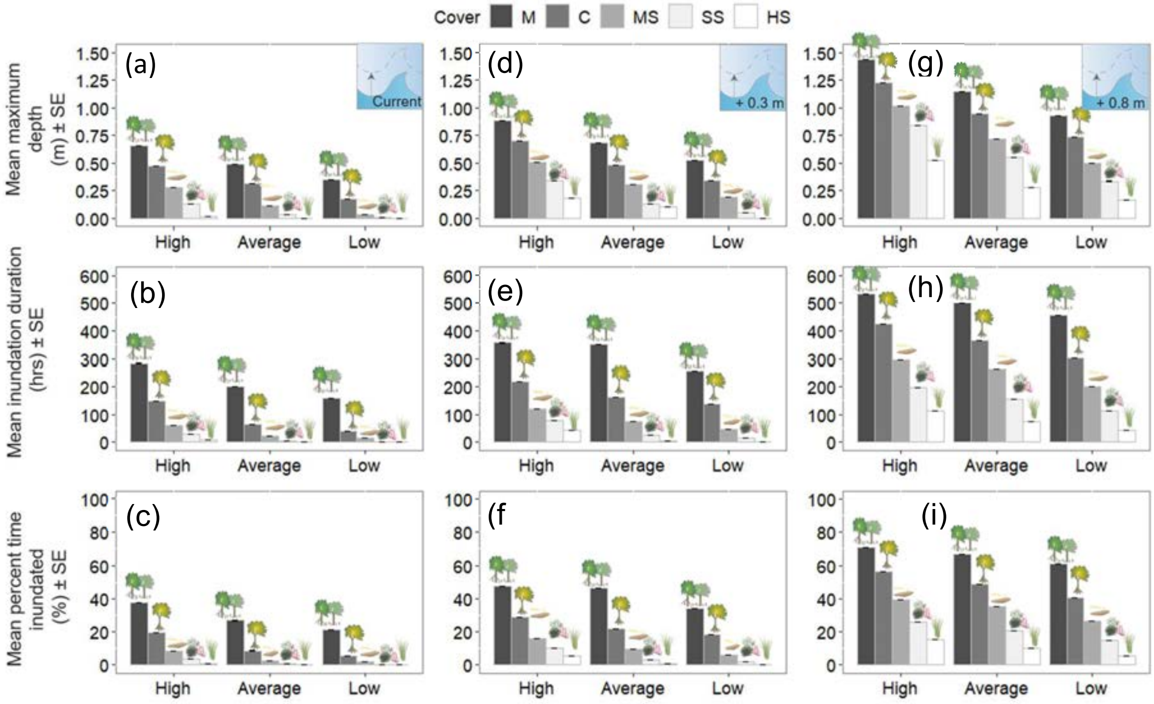

Figure 3.4 Mean maximum depth, duration of inundation (hours) and percent time inundated ± standard error (SE) per tidal wetland land cover for: (a-c) current, (d-f) +0.3 m, and (g-i) +0.8 m sea level rise scenarios for the higher-than-average tide (High), average (Average), and lower-than-average tide (Low) scenarios. "HS" = Herbaceous saltmarsh; "SS" = Succulent saltmarsh; "MS" = Mudflats/Saltpans; "C" = *Ceriops* spp.; "M" = *R. stylosa/A. marina* (abbreviated as "M" for mangroves other than *Ceriops* spp.*)*.

site (Figure 3.5), 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 (Appendix B, Table B3) 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 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.

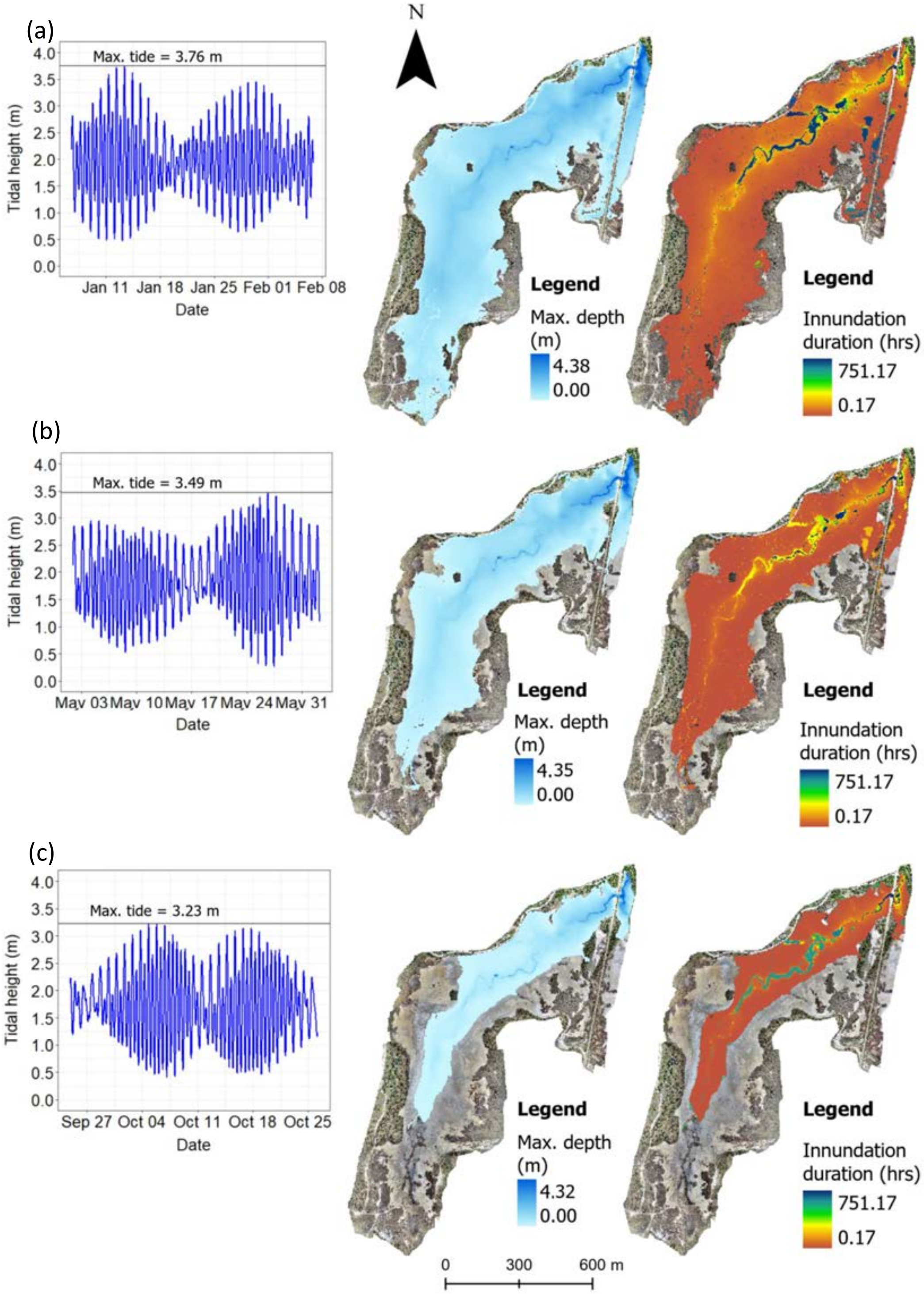

Figure 3.5 Observed tidal height (m) recorded at Cape Ferguson tidal gauge (-19.277208; 147.060908), Australia with associated maps of simulated maximum depth and inundation duration (hours) for each lunar month: (a) Higher-than-average tides observed in January 2021; (b) Average tides observed in June 2022: and (c) Lower-than-average tides observed in September 2021.

Table 3.1 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 SL	0.8 SL	Current	0.3 SL	0.8 SL	Current	0.3 SL	0.8 SL
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

Table 3.2 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": ≥ 3.76 ± 0.1 m	**"Average": ≥ 3.49± 0.1 m**	**"Low": ≥ 3.23± 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%)

3.4.5 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 (Figure 3.6). 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.

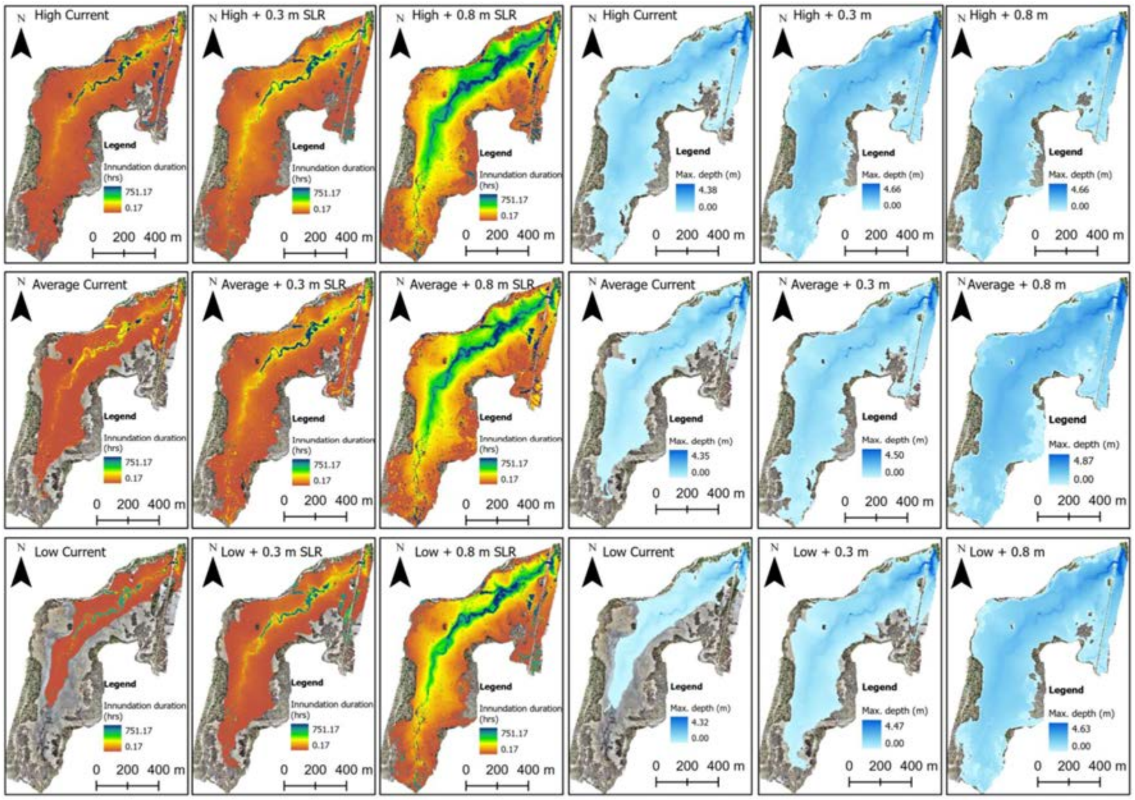

Figure 3.6 Simulations of inundation duration (hrs) and maximum depth (m) under current, +0.3 m and +0.8 m sea level rise for the higher-than-average tide (High), average (Average), and lower-than-average tide (Low) scenarios.

An increase in hydroperiod was observed for each land cover class under the sea level scenarios (Figure 3.5). 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 salt marsh mean inundation duration would be higher than the current *Ceriops* spp. inundation in all tides.

3.4 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; Hagger et al., 2022) 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.

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 & 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. The 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). This supports that research and restoration effects should prioritise a more holistic or system understanding (e.g., "whole-of-catchment strategies", 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, 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., 2014a). 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).

Elevation and hydroperiod as drivers of vegetation patterns

Although each tidal wetland cover had distinct maximum depth, duration of inundation, and percent time inundated, highlighting the important role of tidal inundation in influencing tidal wetland vegetation patterns, 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 the study site. This likely suggests that other factors not studied here (Table 3.3) more strongly contribute to the observed vegetation patterns at the study site (Figure 3.7) 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 & 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 & Heathwaite, 2012; Bayraktarov et al., 2016; Sullivan et al., 2018; Williamson & Gattuso, 2022). The processes determining the successful establishment and development of tidal wetland vegetation at a given location may be more complex (Figure 3.7) than “oversimplistic rules” based on tidal hydroperiod and elevation alone (Bertness & Pennings, 2002; Silvestri et al., 2005; Clarke, 2014; Friess, 2017; Lee & Kim, 2018; Rogers & 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 3.3) 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 the study site which represents high intertidal to subtidal areas punctuated by roads where factors other than surface tidal inundation (Table 3.3) might exert a high control on vegetation patterns (Huckle et al., 2000; Rodríguez et al., 2017; Goodwin & Mudd, 2019).

· **Table 3.3** 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 & Morris, 2012; Xiao et al., 2017; Xin et al., 2013a; 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 proprieties (including salinity) Soil moisture	Oxygen availability Root respiration Germination and seedling growth	González-Alcaraz et al., 2014; Xin et al., 2017 Rogel et al., 2000
	Nutrient availability	Growth limitation (specific responses)	Morris et al., 2013b; Redelstein et al., 2018; Simpson et al., 2013
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.	Rodríguez et al., 2017; Xin et al., 2022
	4WD vehicle uses	Affect cover distribution and composition; influence soil compactness and local hydroperiod;	Kelleway, 2006; Trave & Sheaves, 2014; Chapter 2
Biotic	Competition	Competition of one species over the other	Nunes & Camargo, 2018, 2020; Pennings et al., 2005; Bertness & Shumway, 1993
	Facilitation	Facilitate intra and inter-specific establishment (e.g., soil accretion, salt removal)	Bertness & Shumway, 1993; Ghosh et al., 2022
	Propagule dispersal and establishment	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 & Zedler, 2001
	Crab burrowing activity	Influence porewater and subsurface water exchange	Xin et al., 2009

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. The analyses revealed that it is the non-average tide duration of inundation that was the most significant in determining the presence or absence of tidal wetland cover. This suggests that the most extreme tides and their potential effects on other processes (Armstrong et al., 1985; Goodwin & Mudd, 2019) contribute more to vegetation patterns at the study site than average tides. 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.

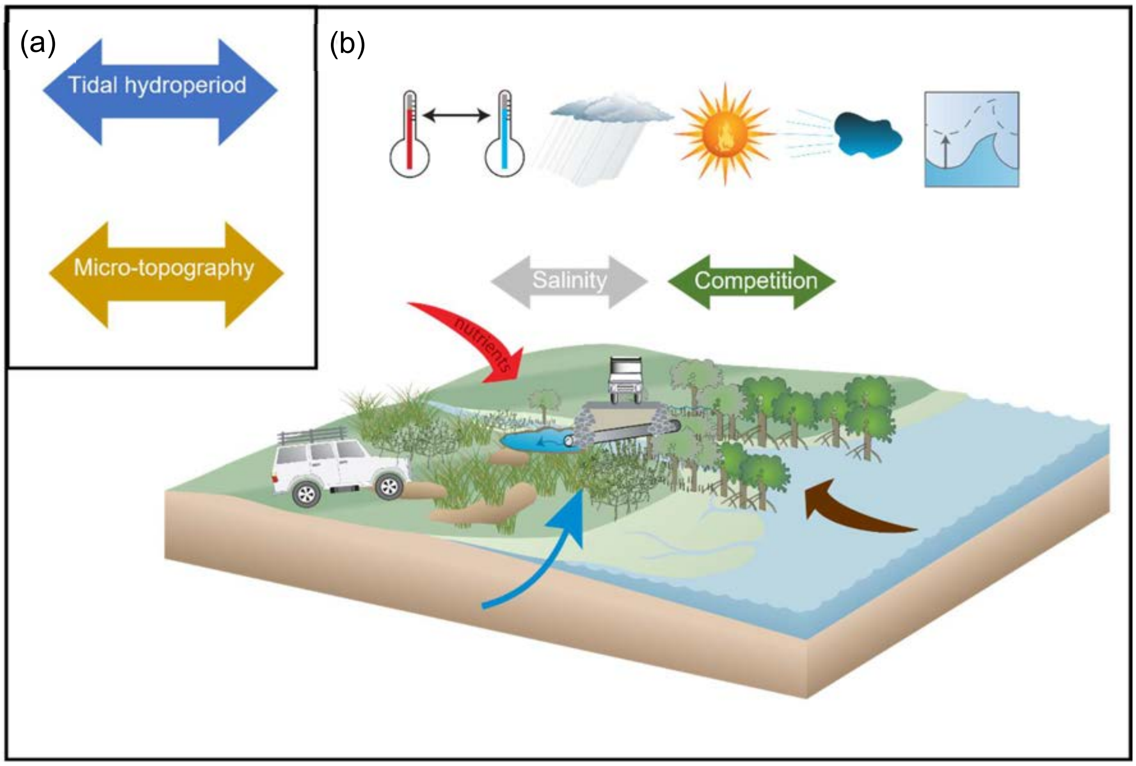

Figure 3.7 Conceptual diagram of (a) the processes studied in the present study by opposition to (b) the likely interacting processes, together with tidal hydroperiod and microtopography, that shape saltmarsh and mangrove zonation patterns in tropical seascapes.

Sea level rise: An additional driver of uncertainty

An important aspect of this study was the demonstration of the further complexities facing managers and long-term restoration success when considering SLR. The 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 & Krauss, 2019), effective management requires strategies that can adapt to new knowledge and changes 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 SLR. 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 & Krauss, 2019). 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).

Limitations of the approach

The present study experienced uncertainties in obtaining information on tidal wetland hydroperiod and elevation that have been discussed in Chapter 2. 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 *Ceriops* 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 Chapter 2 as tidal wetland vegetation cover and soil elevation in saltmarshes can vary seasonally such as in response to tidal dynamics (Olff 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 & 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).

3.5 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. Although restoration and management practices are often based on generalised understandings of mangroves and saltmarshes causality (Rogers & Krauss, 2019), such as that zonation patterns are strongly linked to tidal hydroperiod and soil elevation, the present study has established that, in the context of the 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 3.3) 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 ; Sheaves et al., 2021). However, modelling approaches that consider multiple contextual factors in the distribution of tidal wetland vegetation, including their temporal and spatial variability (Rogers & Krauss, 2019), will ultimately be necessary to develop robust understanding and management of these important but intrinsically complex ecosystems.

Chapter 4: Intertidal crab prey pulse export quantifies importance of tidal wetland connectivity

This chapter has been submitted (17th January 2023) and is in review in *Marine Environmental Research*:

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The submitted manuscript has been modified to fit with the style of the thesis.

Authors contributions: **Vulliet:** Conceptualisation, Methodology, Investigation, Data curation, Formal analyses, Writing-original draft, Visualisation, Funding acquisition, Project administration; **Koci:** Validation, Writing - Review & Editing, Supervision, Resources; **Sheaves**: Review & Editing, Supervision; **Waltham:** Conceptualisation, Validation, Visualisation, Writing - Review & Editing, Supervision, Resources

4.1 Abstract

A key value of saltmarshes is their role in providing trophic subsidies, notably under the form of prey pulses of crab zoeae (CZ). No studies to date, however, have quantitatively investigated the patterns between crab zoeae pulses and saltmarsh connectivity. In this study, CZ densities were examined over successive tides and months using a zooplankton sampling pump to understand the links between tidal fluctuations and pulses of CZ in a tropical Australian estuary composed of tidal saltmarshes, mangroves, and unvegetated flats. CZ densities were linked to spatially explicit information on tidal wetland inundation derived from Unattended-Aerial-Vehicle (UAV) Structure from motion (SfM) photogrammetry and two-dimensional hydrodynamic modelling. The study found that: (1) tidal connectivity is a key trigger to prey pulse export in tropical coastal ecosystems; (2) while tidal connectivity was critical in the export of CZ, not all tidal connections resulted in meaningful ecological connectivity; and (3) succulent saltmarshes was one of the tidal wetland types contributing to the export of CZ. However, not all succulent saltmarshes were uniformly participating in CZ export. The findings highlight the significance of quantitative eco-hydrological approaches to assess saltmarsh and tidal connectivity values. This study supports the need for management and restoration approach that integrate a contextual understanding of the synergies between hydrology, ecology, and habitat heterogeneity. Our data emphasise the need to move beyond generalisations that “similar” habitat type necessarily share similar ecological functions and should be managed equally, and in isolation, from the remaining coastal ecosystem mosaic.

4.2 Introduction

Tidal saltmarshes (hereafter saltmarshes) located on the landward side of mangroves in tropical locations, are ecosystems connected and disconnected with broader coastal ecosystems (mud flats, seagrass, sandy beaches) via tidal flow (Rozas, 1995; Odum, 2000). This connection is known as 'tidal hydroperiod', the duration, depth, and frequency of inundation of which is determined by lunar tides, and meteorological and local factors (Rozas, 1995). The pulsing and dynamic nature of tidal ecosystems in the coastal zone is described by Odum (1968) and Odum et al. (1995) – where wetlands are best considered as "*a frequency modulated radio. For different frequencies of pulsing and hydroperiod, different species may be best adapted to draw useful work. Different frequencies of input energy are different niches for species opportunity"* (p. 554, Odum et al., 1995). This tidal connectivity is therefore an important vector contributing to the services provided by saltmarshes, including the movement of organic matter (well beyond their vegetated boundaries in some cases) in the form of debris (e.g., plant detritus) (Olson et al., 2019), processing of nutrients available in estuaries (Wilson & Morris, 2012), and providing habitat for a range of organisms (fish, migratory birds, crustaceans etc.) (Davis et al., 2012; Olds et al., 2018).

Tidal connectivity mediates pulses that drive ecosystem productivity at complex temporal and spatial scales (Rehage & Loftus, 2007; Matich & Heithaus, 2014) while supporting critical coastal ecosystem functions and services such as maintaining biodiversity (Friess et al., 2012; Granado et al., 2018), and dynamic coastal food webs upon which fisheries rely on (Connolly & Waltham, 2015; Nelson et al., 2015; Taylor et al., 2018b; Abrantes et al., 2019). The causes and consequences of pulsing–from water movement to fish migration and export of trophic subsidies – are a complex network of physical and biological interactions linking diverse ecological units within the coastal ecosystem mosaic or the seascape (i.e., seascape connectivity) (Sheaves et al., 2006; Sheaves, 2009; Litvin et al., 2018).

Saltmarshes in tropical areas, and their connectivity with the broader seascape habitats (e.g. mangroves, seagrass), have been impacted by human development, including land reclamation for agriculture and urbanisation expansion in many places (Bromberg & Bertness, 2005; Hong et al., 2010; Murray et al., 2014; Rogers et al., 2016). These activities are also often associated with engineering structures, such as road culverts, floodgates and levees, that alter tidal wetland connectivity (Burdick & Roman, 2012; Sheaves et al., 2014). Such alterations have detrimental effects on saltmarsh ecosystems (Davis et al., 2017; Dybiec et al., 2023), including associated biota (Kennish, 2001; Mora & Burdick, 2013a; Gehman et al., 2018), the movement of aquatic life (Eberhardt et al., 201), and nutrient dynamics and food webs (Bouwman et al., 2013; Abrantes & Sheaves, 2010). Additionally, sea-level rise (SLR) and the expansion of mangroves to higher elevation (driven by factors like increasing annual temperatures (Whitt et al., 2020) and local SLR (Krauss et al., 2011) also present a major threat to saltmarshes (Saintilan & Rogers, 2013), notably when human land uses and topography preclude their landward migration (Schuerch et al., 2018). Given the ongoing trend of coastal development, ecosystem fragmentation and degradation (Gedan et al., 2009; Waltham and Sheaves, 2015; Henderson et al., 2020; Gilby et al., 2020), understanding how saltmarsh systems work as connected and productive habitats in relation to tidal inundation is particularly important for successful restoration and management.

Management and restoration decisions are thought to be often based on "outdated restoration techniques" (*sensu* Liu et al., 2016) and "pseudoscientific paradigms" (*sensu* Sheaves et al., 2020), which misdirect decisions and lead to economic and ecological loss. Among these restoration techniques are focusing on only one physical attribute, such as restoring tidal hydrology via the removal of barriers (Liu et al., 2016; Abbott et al., 2020), assuming that this will "automatically" restore ecological connectivity and, therefore, the expected values (e.g., fishery values) of a system back. However, studies in both rivers (Fullerton et al., 2010) and coastal ecosystems (Davis et al., 2014b) have highlighted that organisms such as fish and crabs do not respond linearly to hydrological connectivity and that other contextual variables (e.g., reproductive strategies, food availability, type of substrate, plant community structure) (Davis et al., 2012; Davis et al., 2014b; Luk & Zajac, 2013) participate in achieving ecological, or realised connectivity (*sensu* Davis et al., 2014b). The second is that, as postulated by Sheaves (2017) but for mangroves, the values and functions of saltmarshes may also be generalised, assumed to be uniform and transferable across estuaries due to the presence of similar habitat, often defined by broad vegetation categories (e.g., saltmarshes or mangroves). Consequently, it is common to read in non-government and governmental publications generalised and not scientifically proven statements such as "*Saltmarshes* [in Queensland, Australia] *are known to contribute to fisheries productivity by providing direct habitat for juvenile fish and invertebrates*" (Johns, 2019, p.13) or that "*Saltmarshes* [in Queensland, tropical and subtropical Australia] *play a significant role as a feeding and/or nursery area for fish*" Jaensch 2005, p.6). These generalisations and extrapolated paradigms may misdirect management decisions to focus only on one process or habitat, thereby potentially missing central contextual factors that are important in influencing the functionality and values of a system and, hence, restoration success (Sheaves et al. 2021).

Despite their position high in the intertidal zone, on the landward side of mangroves in Australia (Bridgewater & Cresswell, 1999; Saintilan & Adams, 2009; Kumbier et al., 2021), saltmarshes have recognised conservation values for their role as crustacean habitat (Mazumder, 2009; Saintilan & Mazumder, 2017). Saltmarsh crabs are viewed as keystone species, in part due to the monthly mass release of their zoeae (Mazumder et al., 2009; Ricardo et al., 2014). These previous studies show that saltmarsh crabs synchronise their spawning release of zoeae with high spring tide inundation, which can become a major prey pulse for zoo-planktivorous fish in estuaries (Mazumder et al., 2006; Hollingsworth &

Connolly, 2006). Zoo-planktivorous fish can potentially take advantage of this prey pulse by switching their diet to crab zoea during these optimal times (Hollingsworth & Connolly, 2006; McPhee et al., 2015b). This process symbolises the importance of saltmarsh connectivity in supporting prey pulses and ecological productivity through trophic subsidies (Saintilan & Mazumder, 2017). However, these previous saltmarsh studies have occurred in sub-tropical and temperate areas of Australia, which means that applying this pattern to tropical ecosystems need to be tested. In addition, understanding the values of tidal connectivity to upper tidal wetlands such as saltmarshes is particularly important given that tropical coastlines are expected to be particularly jeopardised by human development, climate change and SLR projections in the next few decades (Sale et al., 2014).

Previous temperate studies have provided considerable knowledge on the important role of saltmarsh as the export site of crab zoea, as opposed to mangroves (Mazumder et al., 2009). The mass export of crab zoeae seems to occur almost monthly, with peaks during the coolest month of the year (Mazumder et al., 2009) and during night time high tides (Mazumder et al., 2009; Ricardo et al., 2014). In addition, dietary studies have found that consumed crab zoea by estuarine fish did not coincide with the day of the highest spring tide, but indeed highest occurrence in the fish stomachs occurred following the day of the first tide inundating the marsh (Mazumder et al., 2006; Hollingsworth & Connolly, 2006) – suggesting a crab reproductive strategy to maximise crab zoeae export on successive tides (Hollingsworth & Connolly, 2006). However, to date no studies have quantitatively described the links between the variability in tidal connectivity – measured as the variability in tidal height and the spatial extent of saltmarsh and adjacent wetland inundation – and ecological connectivity – measured as the variability in patterns of prey pulse export. This contextual and quantitative understanding of both hydrological and ecological connectivity is, nevertheless, necessary to move towards a more holistic, process and pattern-based understanding of the values of tropical saltmarshes (Weinstein et al., 2014).

The present study aims to develop a contextual understanding of the value of saltmarshes and connectivity in the export of crab zoea from a tropical estuary composed of mangroves, unvegetated flats and saltmarshes. Specifically, this study investigated: (1) the relationships between crab zoea export, tidal height, and the extent of tidal wetland inundation (consisting of saltmarsh, mangrove, and unvegetated flats); and (2) the effects of other potential drivers of pulse variability, such as diel period, the number of days before and after the highest spring tide, and the sampling month. By investigating these research questions, I explored the importance of integrating both hydrological and ecological connectivity in assessing the value of saltmarshes and tidal connectivity. In addition, I discussed the need for management and restoration actions to reflect tidal wetland habitat values from a more holistic, process-based (e.g., hydrological and ecological connectivity) perspective rather than an individual habitat or vegetation-focused approach. Together, this study presents an innovative method that integrates information on prey pulses, tidal data, land cover, and spatial inundation data derived from unattended aerial vehicle structure from motion (SfM) photogrammetry (hereafter UAV-SfM) and hydrodynamic modelling, which I consider important for coastal managers in developing a contextual understanding of the value and function of saltmarsh resources.

4.3 Methods

4.3.1 Study Area

This study was conducted at Blacksoil Creek (-19.297867, 147.021333), a saltmarsh-mangrove-saltpan complex typically observed in the dry tropics of north Queensland, Australia (Figure 4.1). The study area (82.5 ha) is the upstream area of the larger Blacksoil

Creek system (>300 ha). The site has been split from the remaining system by a concrete road, which has a multi-pipe culvert (1-m in diameter) as well as smaller culverts along its southern side. Tidal exchanges between the study site and the downstream portion of the system are via the main tidal creek, (the main channel) that connects the site to the coastal waters. The tidal regime is meso-tidal with semi-diurnal tides, with two sets of spring tides during the month, one having higher amplitudes than the other (Chapters 2 and 3).

The tidal wetland cover consists of 63.9% of saltpans and mudflats, 15.8% of herbaceous saltmarsh, 9.2% of succulent saltmarsh, 7.4% of *Ceriops* spp. (yellow mangrove, *Ceriops tagal* and *Ceriops australis*) (which are mangrove species that generally dominate high intertidal zones in tropical northern Australia, Robert et al., 2015), 3.1% of other mangroves (principally the grey mangrove, *Avicennia marina*), and 0.6% of main channel (the main tidal creek which drains the study site) (Chapter 3). The main channel is bordered by the red mangrove, *Rhizophora stylosa,* transitioning to *A. marina* and *Ceriops* spp. at the highest elevation (Chapter 3). 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;* the pigweed, *Portulaca* spp.; the pigface, *Carpobrotus glaucescen*s.; the prickly saltwort, *Salsola australis*; and the 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*. Although there is an overall transition from mangroves to succulent saltmarsh and herbaceous saltmarsh with increasing elevation, mosaic distribution patterns characterised by overlapping distribution of different wetland types across similar elevations were also identified (Chapter 3). Further details on the study site vegetation, configuration and hydrology can be found in Chapters 2 and 3.

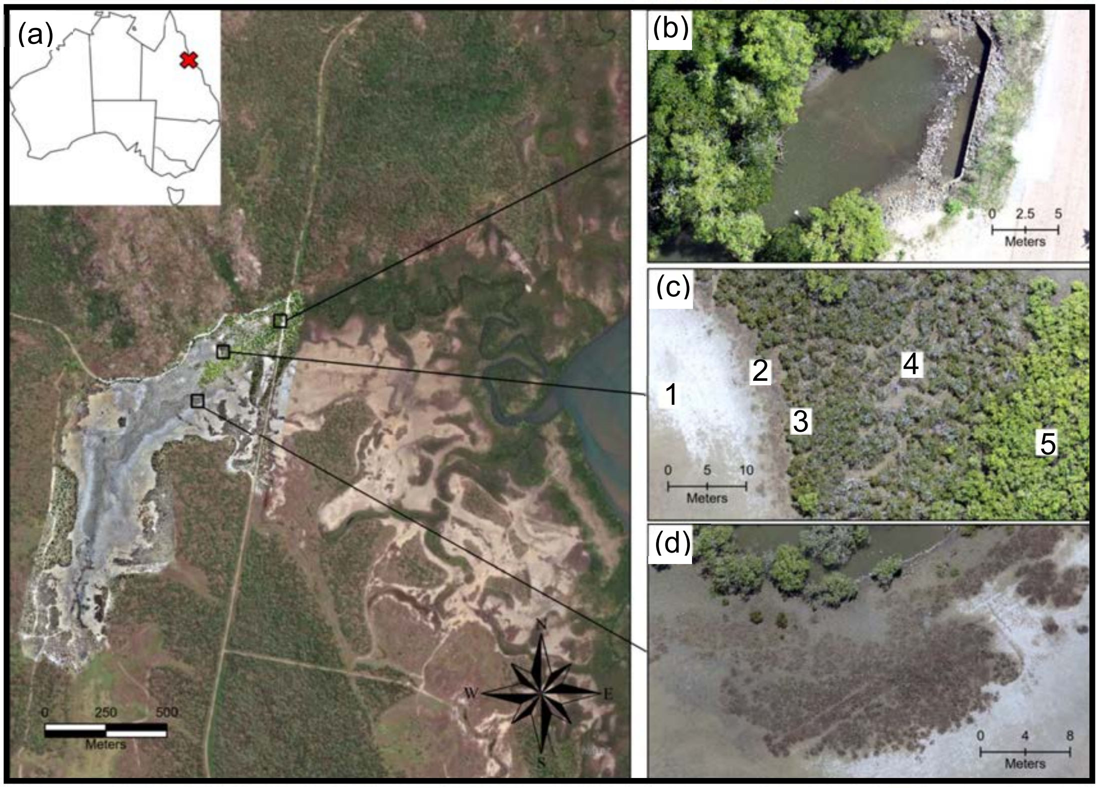


Figure 4.1 Map of the study area showing (a) the study site (UAV-SfM-derived orthophoto map) within the estuarine complex of Blacksoil Creek (Landsat Imagery) in Queensland, Australia. The boxes show: (b) the location of the zooplankton sampling system upstream of the road culvert (the white float in which the bilge pump is lodged is apparent on the bottom left part of the box); (c) the mosaic structure of tidal wetland habitats characterised by (1) saltpans; (2) patches of succulent saltmarshes along (3) the *Ceriops* spp. forest; (4) patches of mudflat within the *Ceriops* spp. forest; and (5) mangrove forest dominated by *Avicennia marina*; (d): patches of succulent saltmarshes bordering the main channel with mudflats. The destructive effects of 4-wheel driving on the saltmarsh is noticeable. Cape Ferguson Tidal Gauge is not shown in this figure but is shown in Chapter 2, Figure 2.1. Note that the scale bar differ in each boxes.

Pilot studies were conducted to identify and quantify crab species occurring on the saltmarsh areas. Underwater cameras were trialed without success due to high turbidity. Deploying fyke nets (1-mm mesh panels, 5-m opening) placed across draining channels and directly on the saltmarsh were more successful – I was able to identify *Metograspus latifrons* (Graspidae), *Paracleistostoma wardi* (Graspidae), *Parasesarma erythrodactyla* (Graspidae), *Australoplax tridenta* (Ocypodidae), and *Uca signata* (Ocypodidae). There are likely other species found at the study site (e.g., Vermeiren & Sheaves, 2014a, 2015), the catch therefore is a subset of the total species possible in the study area.

4.3.2 Sample collection and processing

Traditional zooplankton sampling methods (e.g., zooplankton nets, Mazumder et al., 2009) could not be used due to the high risk of saltwater crocodile (*Crocodylus porosus*) encounters at the study site. I therefore had to design a zooplankton pumping system that was operated using a programmed timer switch (Figure 4.2), which meant that I did not have to enter the water or be near the creek edge at night during high tides. The sampling system consisted of a 1000L intermediate bulk container (IBC) tank linked to a 750 GPH bilge pump attached to a float at the end of a 4-m-length swimming pool telescope pole (Figure 4.2c). The bilge pump was linked to a 12V battery and activated by a timer switch (Figure 4.2e) programmed to power the battery when the study site starts draining. The IBC tank had a float switch to stop the pump when the tank was full. The end of the pole near the float was attached via two ropes extended at two extremities to prevent the pole from retracting toward the bank edge during ebbing and flooding tides (Figure 4.2d). The battery was placed in a toolbox to prevent damage from rain or tidal water. The timer switch was placed in a small container to prevent additional damage from humidity, rain, and rodent damage.

Pilot tests revealed that the tank was filled after 200 minutes. To sample crab zoea export over the entire ebbing tide draining the study site (which was estimated from visual observations during pilot surveys to take approximately 5-7 hours), pumping was divided into five sessions of 40 minutes, starting 2 hours after the predicted high water (HW, referring to the time at which tide is at its height point) at Cape Ferguson tidal gauge (19.277208; 147.060908). The tank was positioned directly upstream of the main culvert (i.e., the downstream boundary of the study area) (Figure 4.1b and Figure 4.2b). This was a strategic placement to explicitly sample the export pulse of crab zoea from the upstream wetland area.

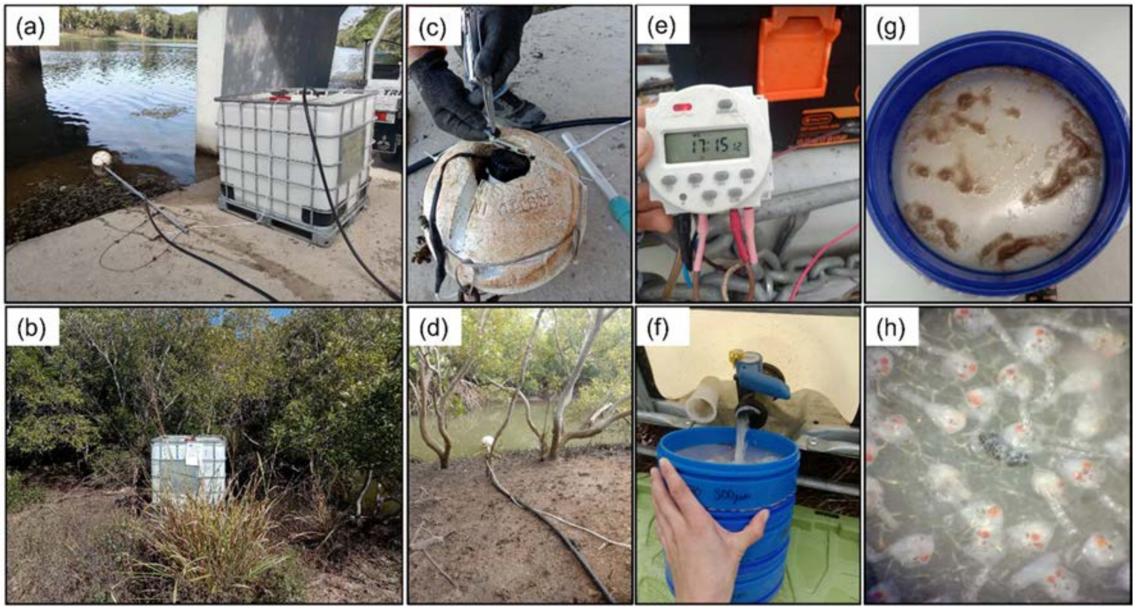


Figure 4.2 Description of the pumping sampling system showing: (a) the intermediate bulk container (IBC) linked to the hose with the telescope pole and the float where the bilge pump is attached; (b) the sampling system deployed at the study site; (c) close viewed of the 750 GPH bilge pump attached to the pole and the float; (d) the pump deployed at the study site, with the pole attached to two ropes; (e) the timer switch linked to the 12V battery in the tool box; (f) example of sampling where the water from the IBC is released through a 500 μm and 250 μm sieve at the sampling site; (g) pulse of crab zoeae on the 250 μm sieve (after cleaning) in the laboratory; (h) stereo-microscope view of crab zoeae.

The system successfully sampled ebbing tides over 90 days, totaling 490 hours of pumping. Timer switch issues (rain and timer switch failure) and a rodent damaging the wiring caused unsuccessful sampling days in September, January, and February-March. Previous fish dietary studies in temperate and subtropical saltmarshes have suggested that tides which first inundate saltmarshes, rather than necessarily the highest spring tide, trigger crab spawning (Hollingsworth & Connolly, 2006; Mazumder et al., 2006). Therefore, I sampled the neap and spring tides over several consecutive days to decipher the crab zoea pattern between tidal height and export. The first deployments were over 21 nights in August 2021 and 23 nights in September, and 24 days in December 2021. Subsequently, due to consistently negligible crab zoea densities during neap tides (presumably because the wider vegetated study area had not been inundated by tidal flow connection), the sampling system was deployed over ten days in

January 2022, six days in February-March 2022, and seven nights in June 2022 to coincide for several days before and after the spring tide.

The IBC tank was emptied at low tide every morning (austral winter) or every afternoon (austral summer) after the high tide had flooded the site area, by filtering the water through a 500 µm (to remove larger debris and prevent damage from water pressure on crab zoea and copepods) and 250 µm filter sieves (Figure 4.2f). The material remaining on both sieves was transferred into a flask with water and ethanol until processing in the laboratory. The filtered content (Figure 4.2g) was cleaned and transferred into a beaker in the laboratory. Copepods (consisting principally of calanoid copepod *Acartia sinjiensis*) and crab zoea were counted in five replicates on a Bogorov tray under a stereomicroscope following subsampling and enumeration procedures (Alden III et al. 1982; Wiebe et al. 2017). The densities of copepods and crab zoea in 1000 L (full IBC tank) (individual/m^3) were computed by calculating the number of individuals counted in 6 ml of subsample multiplied by the volume of water used to subsample the samples (150-1000 ml) divided by 6 ml. Copepods were included in this research as this taxa was the dominant zooplankton in the samples and could be used as a sampling control (i.e., whether the sampling system was successful at pumping zooplanktonic organisms). Additionally, copepods can provide important information on the functioning and variability of seascape connectivity due to copepods being “sink organisms” (coming from estuarine, open waters) in opposition to “pulsed organisms” (i.e., crab zoea, coming from upper tidal systems) (Mazumder et al., 2009; Qin et al., 2015).

4.3.3 UAV land cover and hydrodynamic modelling data

The two-dimensional hydrodynamic model developed in Chapter 2, utilising digital terrain and land cover information derived from an unoccupied aerial vehicle (UAV) survey, was used to report the export of crab zoea as a proportion of the tidal wetland inundated area following each inundation. The same land cover and tidal wetlands classification described in Chapters 2 and 3 were used, where land cover was categorised as Main Channel (MC), *Ceriops* spp. (C); *A. marina/R. stylosa* (abbreviated as M for other mangroves than *Ceriops* spp.) Mudflat/Saltpan (MS); Succulent Saltmarsh (SS); and Herbaceous Saltmarsh (HS). Inundation simulations were set to cover each sampling period following the same procedure and parameters described in Chapter 2. The categories Woodland/Terrestrial and Manmade as well as the land cover area downstream of the main concrete road (Figure 4.1) were not included in the analysis.

To quantify the extent of inundation of tidal wetland type when the pump was deployed, simulations were run for each inundation time surveyed. To obtain the extent of inundation for each night/day of sampling, mapping outputs were computed every 10 minutes and added to cover the time the pump commenced until it had stopped. This technique allowed the calculation of the maximum boundary extent over the study site per sampling night/day rather than over the entire simulation period. The raster mapping outputs were exported to ArcGIS Pro 2.8.6 (Esri) and overlaid with the raster land cover layer to obtain a spatial dataset with tidal wetland type inundation area for each sample collection.

The final environmental multivariate datasets also contained: 1) the maximum observed tidal height (m) recorded at Cape Ferguson tidal gauge; 2) whether sampling was conducted at day or night; and 3) the number of tides preceding and succeeding the highest spring tide of the spring tide cycle (DayNum). The latter consisted of denoting HW by T0, previous day by -T1, -T2, -T3, and subsequent days by T1, T2, and T3. The length and high amplitude of the spring tides occurring in January 2022 led to adding a T4 tide. The remaining sampling days were denoted as neap tides (N) (Figure 4.3c).

4.3.4 Data analyses

Crab zoea and copepod density data were $\log_{10}(x+1)$ transformed to reduce skewness (due to zeros and extreme values) and decrease non-normality (see Figures C1-C2 in the Appendix C for residual normality plots and Table C1 for Shapiro-Wilk tests). Univariate classification and regression trees (CARTs) (De'Ath, 2002) (see Davis et al. (2014a) for an application of CARTs in ecological studies) were used to observe the influence of the extent of tidal wetland inundation, diel period (i.e., day or night sampling), days before/after HW, and observed HW (HWobs) on crab zoea density. Multivariate CARTs (or MRTs) were then used to assess the influence of the variables on crab zoea and copepod density. CARTs and regression trees are a robust and unbiased constrained multivariate technique used to investigate relationships between explanatory and response variables in ecology (De'ath & Fabricius, 2000). CART uses a binary algorithm that grows the tree by splitting data into distinct homogenous groups according to thresholds in the explanatory variables (Ouellette et al., 2012). The splitting process continues separately on each node (i.e. homogenous group), forming distinct community composition responding to a given threshold of environmental variables at each tree leaf (De'ath & Fabricius, 2000). The tree cross-validated (CV) error represents the average test error over the k cross-validations. A CV error ≥ 1 means that the selected tree has no predictive power, while a CV error $= 0$ means that the selected tree has a perfect predictive power (De’ath and Fabricus, 2000). The selected tree should have a CV relative error within 1 SE of the minimum relative error (De’ath and Fabricus, 2000). The “mvpart” function (De'ath, 2014) was used to create CARTs using the function default settings (downloaded from the devtool package, formerly in the CRAN package), applied in RStudio Desktop Version 2022.12 (Integrated Development Environment for R, Bostion, MA. Available at: http://www.rstudio.com/).

The distribution of copepods and crab zoea across all sampling periods was analysed using non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarities of $\log_{10}(x+1)$ of crab zoea and copepods densities. The BIO-ENV function (vegan package in Rstudio (Oksanen et al., 2013)) was used to find the subset of environmental variables that best correlates with the community data by calculating the Spearman rank correlation between the Euclidian distance (environmental variables) and the Bray-Curtis dissimilarity (community data) matrices. Following Clarke and Gorley (2015), environmental data were first individually normalised using the sqrt(x) function (see Appendix C, Figures C3-C4 for residual normality plots and Table C2 for Shapiro-Wilk tests). No transformation was conducted on the variables Observed High Water (HWObs), *A. marina/R. stylosa*, *Ceriops* spp., and Main Channel as transformations increased homoscedasticity. Variables that were highly auto-correlated ($R^2>0.95$) were removed for the analyses (Appendix C, Table C3) (i.e., only Total boundary inundation area was removed). Permutational multivariate analysis of variance (PERMANOVA, non-parametric MANOVA) was used to observe statistically significant differences in the community composition among DayNum (i.e., neap tides and days before and after HW) and diel period. The function adonis available in the R vegan package (Oksanen et al., 2013) was used. The pairwise adonis function (devtoools package, pmartinezarbizu/pairwiseAdonis/pairwiseAdonis) was used as a post-hoc test on the factors identified as statistically significant by adonis. In addition, individual Kruskal-Wallis tests (non-parametric alternative to ANOVA) were conducted to observe whether there were statistically significant differences in crab zoea and copepod density respectively between DayNum, months (average of T3 to T4 tides – not including N tides as these were not consistently sampled across months), and the diel periods (Night, Day, Day/Night (Down) and Night/Day (Dusk). Note that when two high spring tides of the same month were sampled, such as in September, the month was denoted as SeptP1 and SeptP2, referring to the first and second spring tides, respectively). Multiple pairwise comparisons were run using the Wilcoxon rank Sum Test (using the Benjamini-Hochberg Procedure (false discovery rate) as the p-adjustment method) to observe statistically significant groups. Unless otherwise stated, all density data are given in $\log_{10}(x+1)$ transformed.

4.4 Results

4.4.1 Patterns of crab zoea density in relation to tidal fluctuations, timing, and diel period

The greatest crab zoea density sampled over the entire study period was in August at T-1 (4.17 ± 0.01 individuals (ind.) m^{-3} ($\log_{10}$ x+ 1 transformed) or 15060 ± 479.98 ind. m^{-3} (untransformed)) (Figure 4.3) where HW was 3.50 m – which was not the highest tide recorded over the sampling period (3.71 m in January) (Figure 4.4). The lowest densities were recorded during neap tides and when observed HW did not exceed 3.16 m (Figure 4.4), such as in the second spring tides of December.

There was a strong correlation between the crab zoea density and tidal fluctuations (Figures 4.3-4.5). This was characterised by a primary split in the univariate CART of crab zoea density (Figure 4.6). The split was determined by mean observed high water (MeanHWobs) of 3.16 m, where observed HW $\geq$ 3.16 m resulted in mean $\log_{10}$ (crab zoea density + 1) of 2.45 ind. m^{-3} compared to 0.49 ind. m^{-3} ($\log_{10}$ x +1) in HW $\leq$ 3.16 m (Figure 4.6). The secondary split shows that crab zoea density was not only related with HW height, but also with the variable DayNum (i.e., neap tides and day before and after the highest spring tide of the spring tide cycle), where the highest densities were recorded before HW (T-3 to T-1) and at the highest spring tide (T0) rather than days after T0. Over the sampling period, the greatest mean crab zoea density (3.14 ± 0.25 (SE) ind. m^{-3} ($\log_{10}$ x+ 1 transformed) or 3383 ± 1734 ind. m^{-3} (untransformed)) was observed at T-1, followed by T0 (2.82 ± 0.24 ind. m-3 or

1343 ± 484 ind. m-3 untransformed)), and T-2 (2.71 ± 0.29 ind. m-3 or 1342 ± 529 ind. m-3 (untransformed)) (Figure 4.7a).

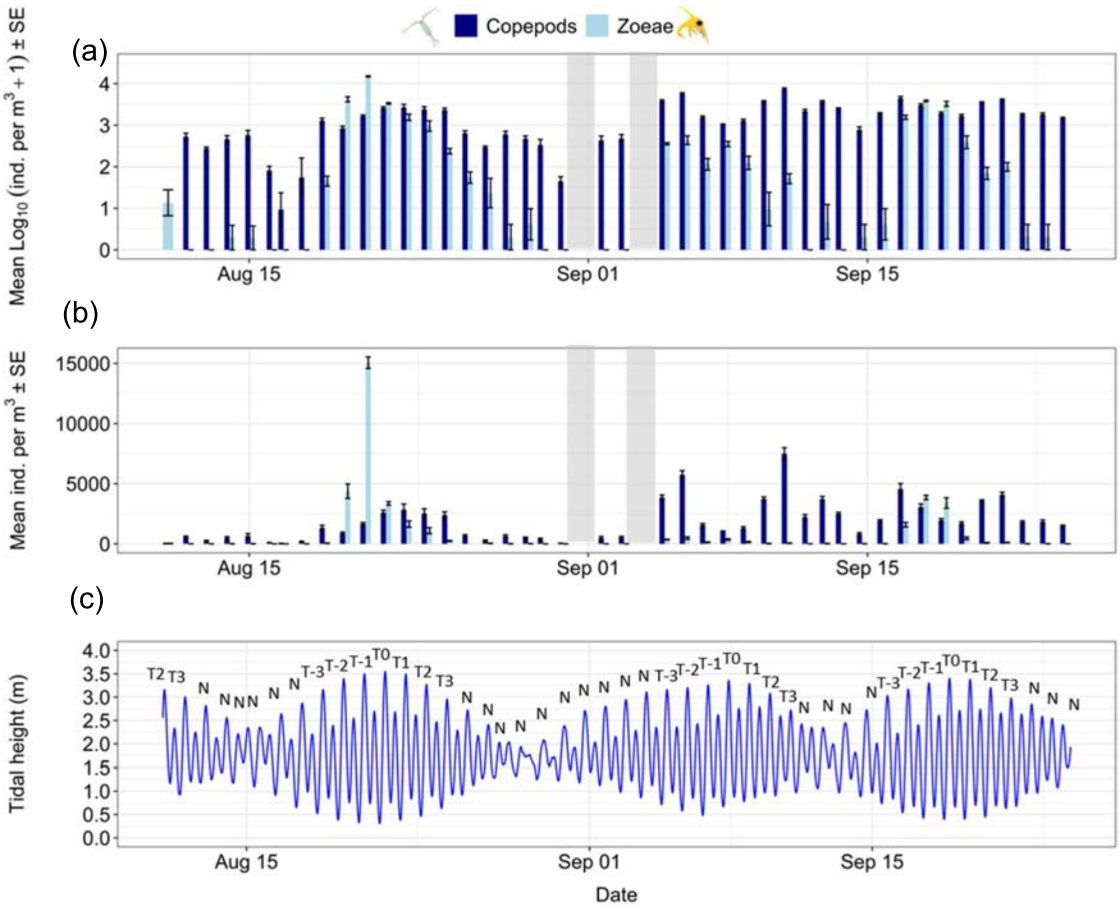


Figure 4.3 Crab zoea and copepod densities per sampling day (i.e., per samples of 5 replicates of 6 ml where the mean and standard error (SE) are the sample mean and standard error) over August and September 2021 showing (a) mean $\log_{10}$(individual per m^3+1) ± SE, (b) mean count of individuals per m^3 ± SE, and (c) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge). "DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring tide); T1; T2; T3; T4, and N (Neap Tide). The shaded areas were not sampled (planned or sampling issues).

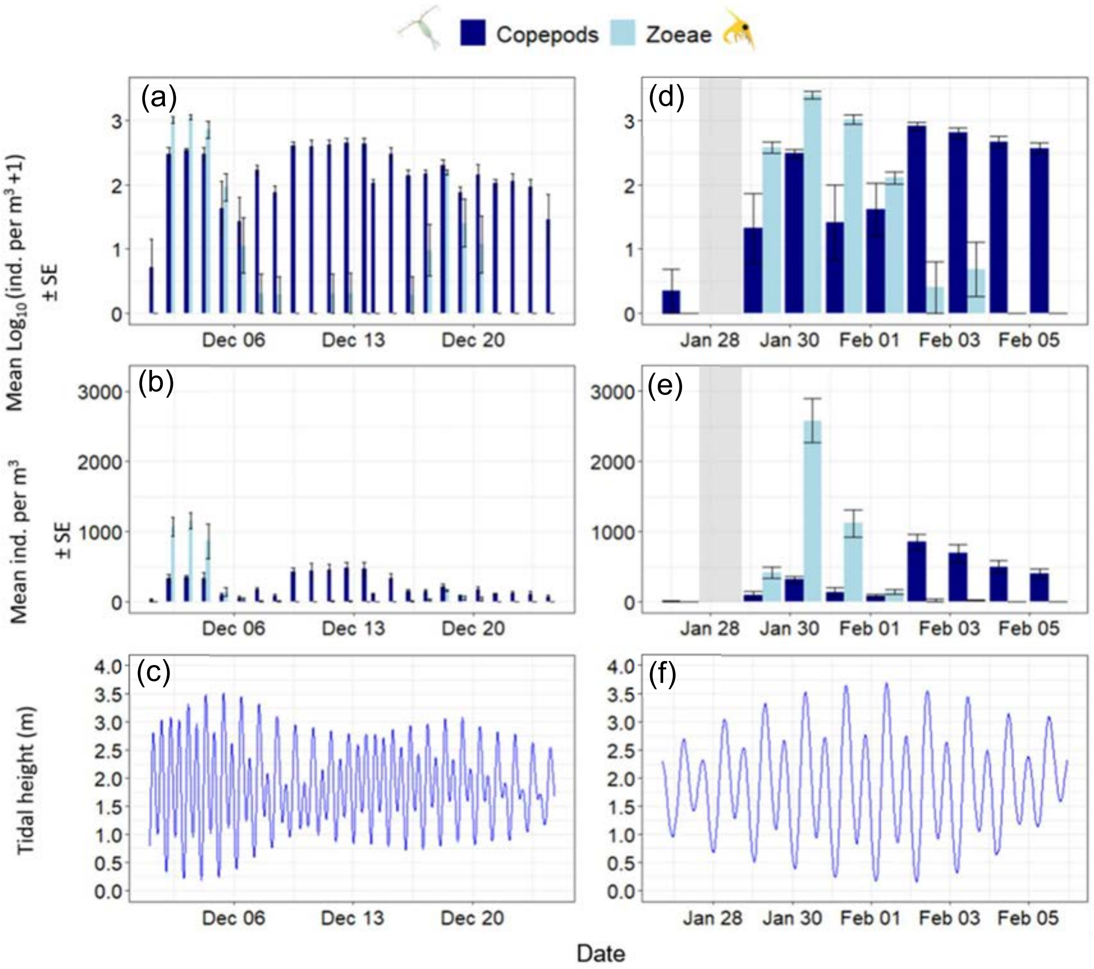


Figure 4.4 Crab zoea and copepod densities per sampling day (i.e., per samples of 5 replicates of 6 ml where the mean and standard error (SE) are the sample mean and standard error) showing (a) mean $\log_{10}$(individual per m^3+1) ± SE, (b) mean count of individuals per m^3 ± SE, and (c) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge for (a-c) December 2021 and (d-f) January 2022.

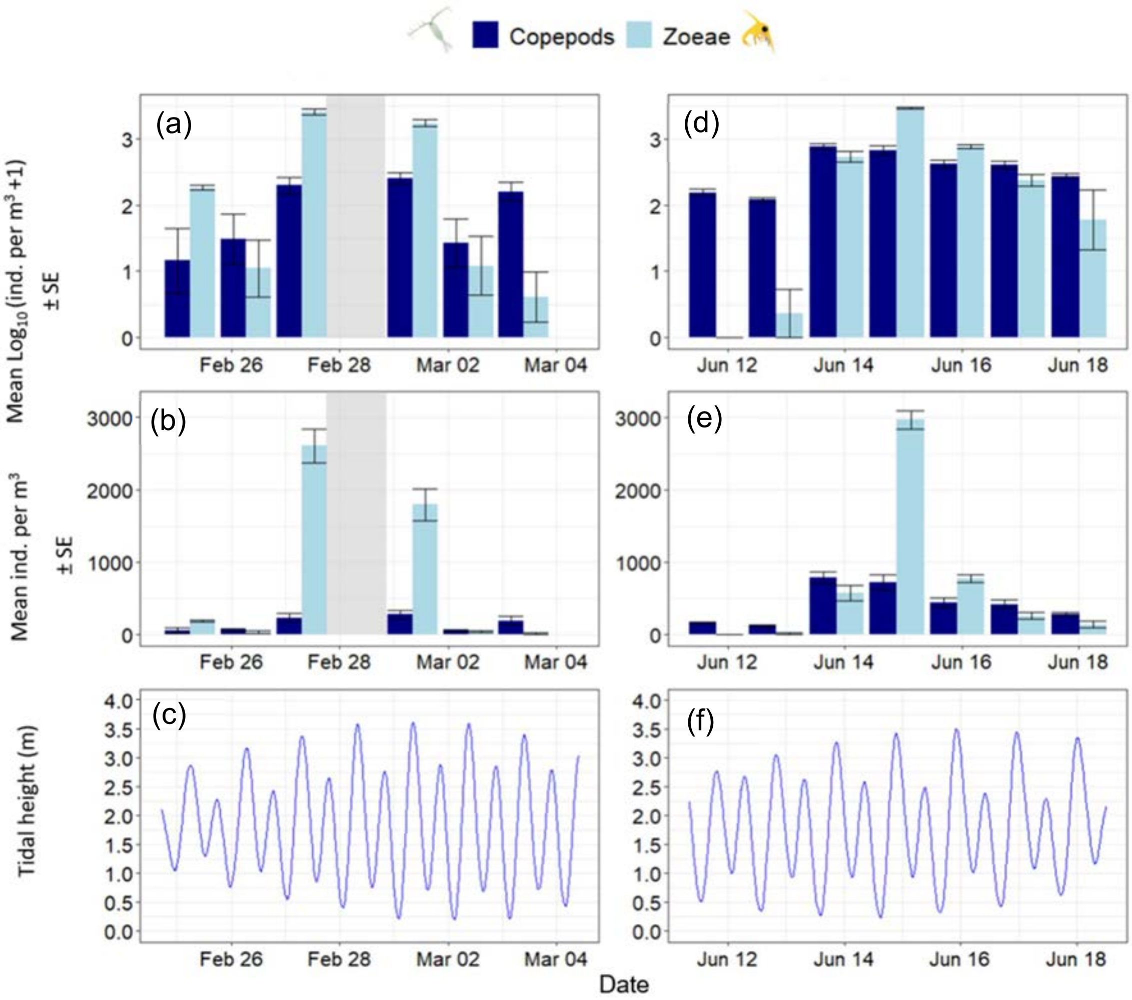


Figure 4.5 Crab zoea and copepod densities per sampling day (i.e., per samples of 5 replicates of 6 ml where the mean and standard error (SE) are the sample mean and standard error) showing (a) mean log10(individual per m3+1) ± SE, (b) mean count of individuals per m3 ± SE, and (c) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge for (a-c) February-March 2022 and (d-f) June 2022. The shaded areas were not sampled (sampling issues).

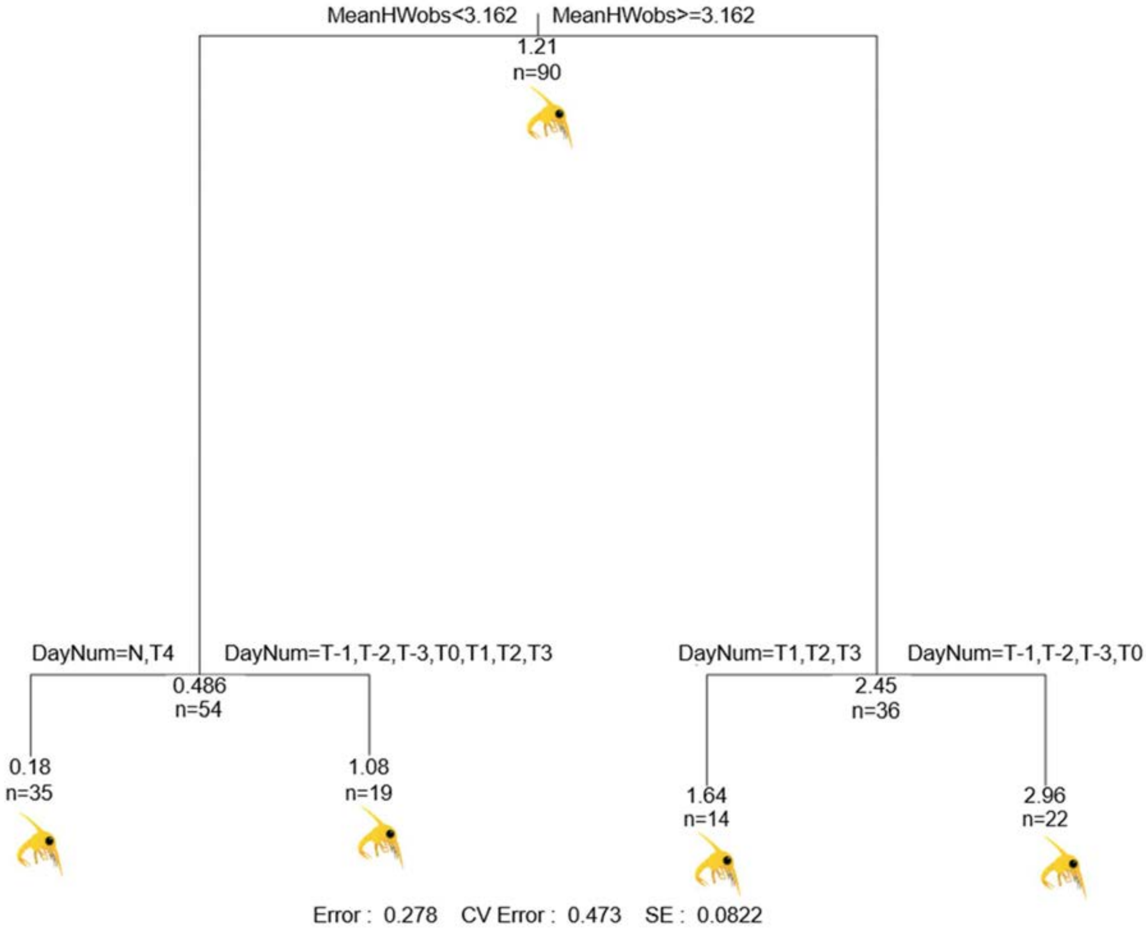


Figure 4.6 Univariate classification and regression tree representing the distribution of crab zoea densities, based on log10(Individuals per m3 +1). Mean densities are shown at each terminal node with the sample size in bracket. Each node represents the split based on the environmental variables that best explained variability in crab zoeae densities across samples. “MeanHWobs”: MeanHigh Water observed at Cape Ferguson tidal gauge; “DayNum” = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide). “Error”: The total relative error of the tree, where R2 of the model is 1. “CV error”: Cross-validation error of the tree; “SE”: Standard error of the cross-validation statistic (i.e., cross-validation error).

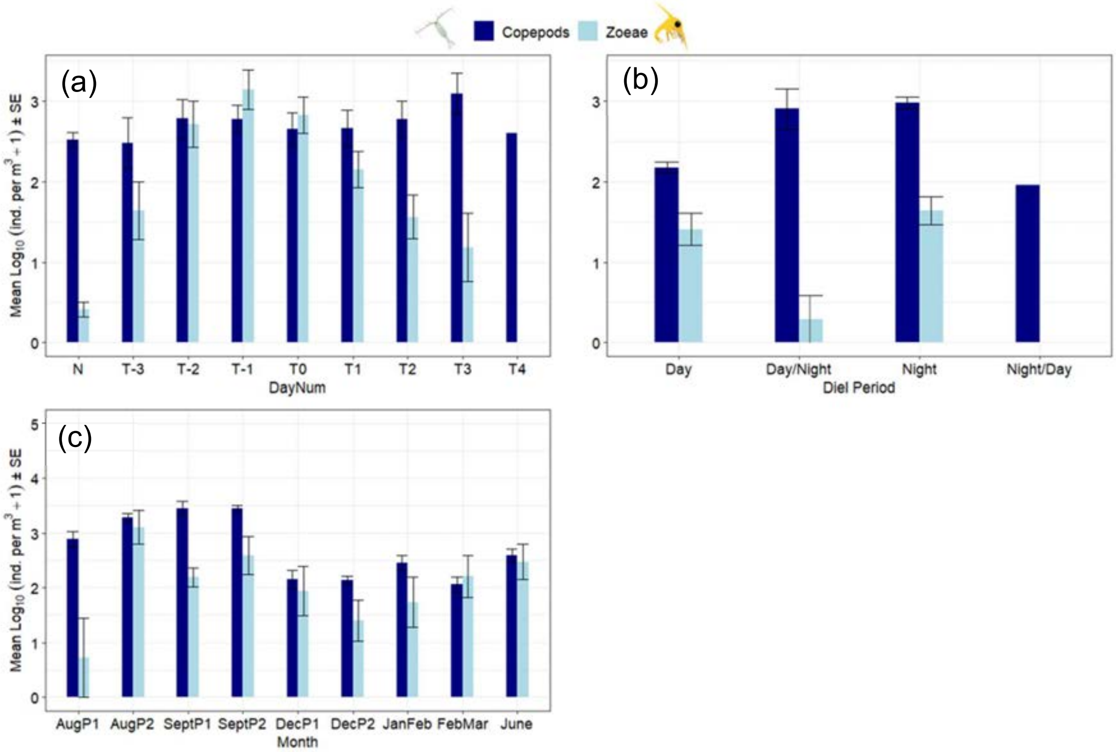


Figure 4.7 Mean copepod and crab zoea densities (log10(individual per m3 + 1) ± standard error (SE) grouped by (a) DayNum = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide) and (b) diel period at which HW occurred; and (c) months (i.e., all samples of the spring tide phase without neap tide samples).

While the variables DayNum and HWobs were important attributes determining crab zoea density, the density of copepods was unrelated to the number of days preceding and succeeding the highest spring tide of the spring tide cycle (i.e., DayNum). The effects of HWobs were also negligible on copepod densities, as observed by similar density (although lower ≤ 3.16 m) at the primary split of CART (Figure 4.8). Instead, copepod density was influenced by the diel period (Figure 4.8), where greater densities of copepods were observed during night tides compared with day tides (Figure 4.7b).

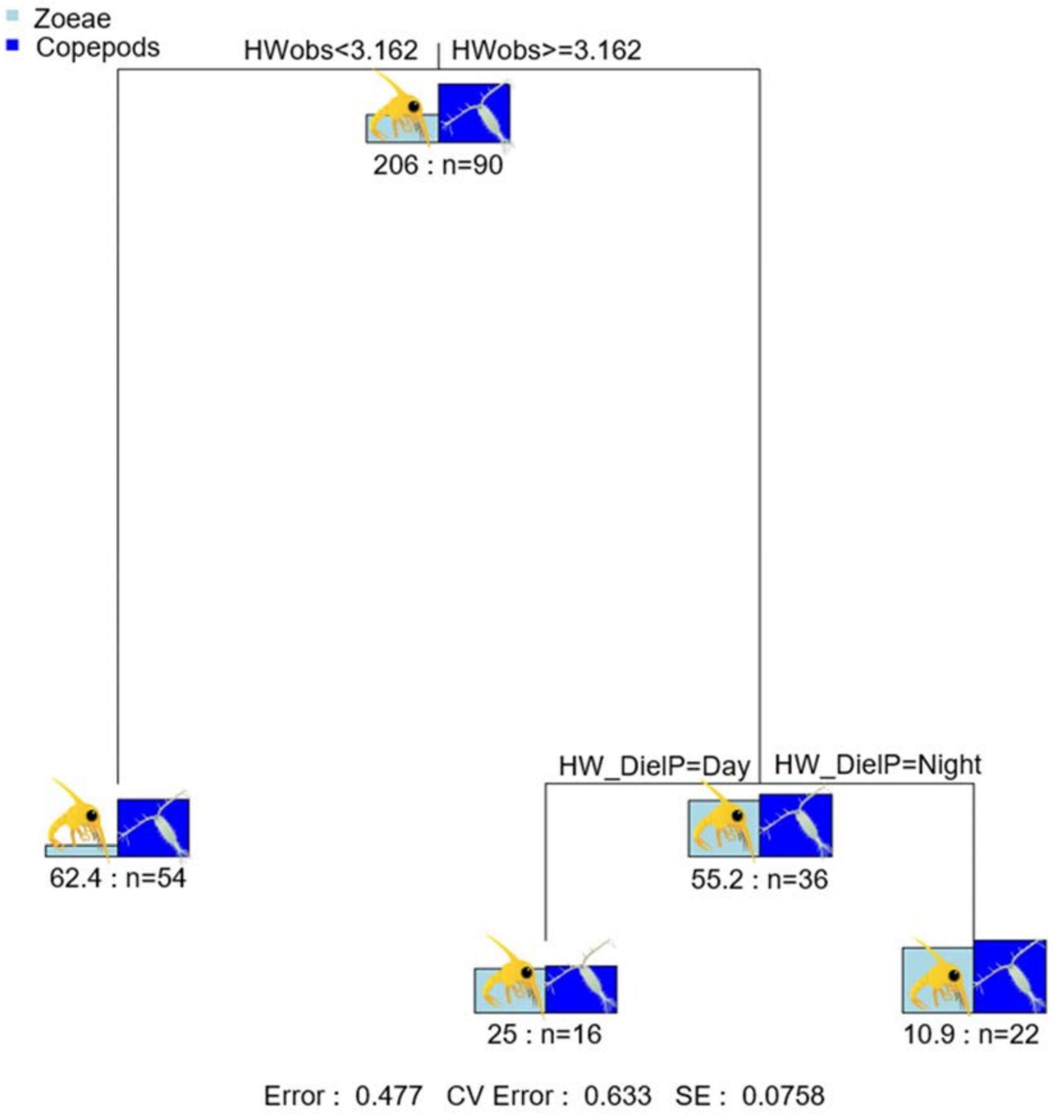


Figure 4.8 Multivariate classification and regression tree of the crab zoea and copepod densities distribution, based on $\log_{10}$(individual per m^3+1). Each node represents the split based on the environmental variables that best explained variability in the zooplankton community across samples. The relative density of crab zoeae and copepods are shown in the histogram below each branch. The first value below the histogram is the sum of the squares for the branch or group (SS_{gr} statistic), while *n* represents the number of samples in each branch. "HWobs": High Water observed at Cape Ferguson tidal gauge; "HW-Diel period": Diel period at which high water (HW) occur (Day; Night). "Error": The total relative error of the tree, where R^2 of the model is 1. "CV error": Cross-validation error of the tree; "SE": Standard error of the cross-validation statistic (i.e., cross-validation error).

The relative statistical importance of DayNum and diel period to crab zoeae and copepods densities were further tested using the Kruskal-Wallis tests, which showed no statistically significant difference in densities of crab zoeae between day, night, dawn (transition from day to night: day/night), and dusk (transition from night to day: night/day) (Kruskal-Wallis χ^2 = 5.33, df = 3, p = 0.149), but significant difference in copepod density (Kruskal-Wallis χ^2 = 40.98, df = 3, p = 0.001). By opposition, copepods densities were not statistically significant different between DayNum (Kruskal-Wallis χ^2 = 5.75, df = 8, p = 0.70). However, this term was statistically significant for crab zoea (Kruskal-Wallis χ^2 = 62.52, df = 8, $p < 0.001$). Post-hoc pairwise comparisons using the Wilcoxon rank Sum Test showed that the location of median densities between DayNum was statistically significant between neap tides and T-3 (p = 0.006), T-2 ($p < 0.001$), T-1 ($p < 0.001$, T-0 ($p < 0.001$), T1 ($p < 0.001$) and T2 ($p < 0.001$,). Neap tides were not statistically different compared with T3 (p = 0.117) and T4 (p = 0.519).

Although no significant differences in crab zoea densities were revealed among diel periods, mean crab zoea densities were higher during the night (1.64 ± 0.18 (ind. m^{-3} ($\log_{10} x+1$ transformed) compared to the day (1.41 ± 0.20 ind. m^{-3}); and at dawn (day/night) (0.30 ± 0.30 ind. m^{-3}) compared to dusk (night/day) (0 ind. m^{-3}) (Figure 4.7b). This difference was higher when adding night/day to the day (1.37 ± 0.20 ind. m^{-3}) and day/night to the night category (1.56 ± 0.17 ind. m^{-3}). Diel differences remained not statistically significant for crab zoea even when pooling those terms (Kruskal-Wallis χ^2 = 0.52, df = 1; p = 0.471).

There were also statistically significant differences in densities among months in the data here (without the N tides samples) for both crab zoea (Kruskal-Wallis χ^2 = 21.28, df = 9; p = 0.0114) and copepod populations (Kruskal-Wallis χ^2 = 47.40, df = 9; $p < 0.001$) (Figure 4.7c). Although the post-hoc pairwise comparisons using the Wilcoxon rank Sum Test identified not statistically significant groups.

4.4.2 Ordination of crab zoeae and copepods densities

Ordination of the samples based on Bray-Curtis dissimilarities of crab zoea and copepod densities (Figure 4.9) indicated a distinct pattern in sample structure. Samples principally characterised by spring tides, notably T-3 to T0 tides, were situated in the left part of the ordination space, with which crab zoea was highly correlated. By opposition, copepods were correlated to the right part of the ordination space, where mostly N and T2-T3 samples were ordered. This part of the ordination space was also opposed to the upper left part, where many day samples were situated. The patterns observed in the ordination space were reflected by the two-way PERMANOVA, which revealed significant differences in assemblage structure due to DayNum (driven by crab zoea) and HW Diel Period (driven by copepods) (Table 4.1).

4.4.3 Relationships with tidal wetland inundation

The BIO-ENV routine identified succulent saltmarsh, mudflats and *Ceriops spp* inundation area as environmental variables explaining 45% of the variability in the zooplankton structure. The vectors referring to the inundation extent of succulent saltmarsh, mudflat/saltpan, and *Ceriops spp.* were correlated with the upper left part of the ordination space in the same direction as the crab zoeae vector and in the opposite direction of copepods (Figure 4.9). These results are consistent with the relationships between HWobs and the extent of upper tidal wetland inundation (Figure 4.10a), where the inundation above *A. marina/R. stylosa* and *Ceriops* spp. (i.e., mangrove-saltmarsh ecotone) is predominately triggered with tides above 3 m (Figure 4.10a).

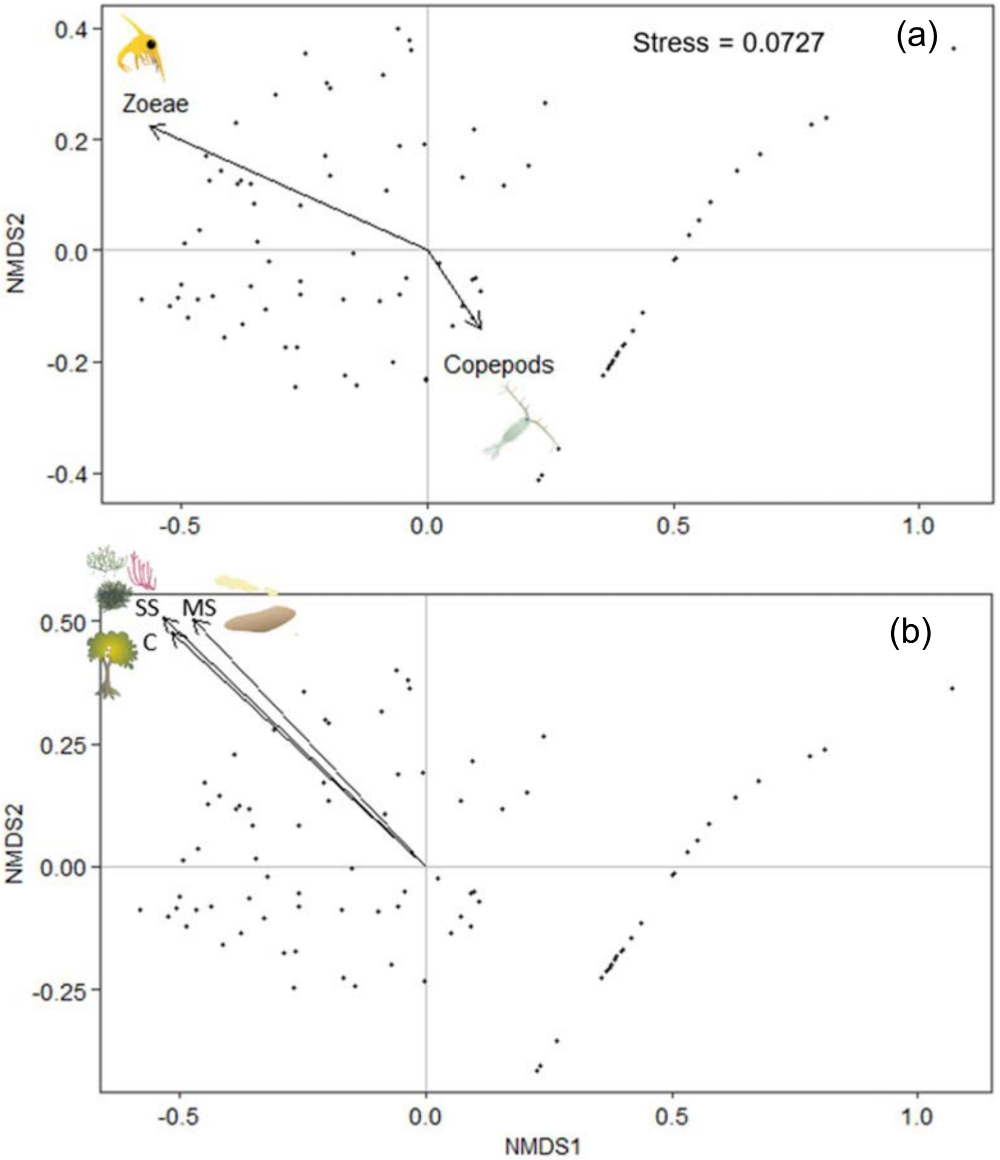


Figure 4.9 Non-metric multidimensional scaling (nMDS) ordination of the samples based on Bray-Curtis dissimilarities of zooplankton density data (log$_{10}$(individual per m^3 +1)). The vectors in (a) show the direction in the ordination space to which the zoeae and copepods are the most correlated. The environmental variables identified by the BIO-ENV routine are also shown in (b) ("SS" = Succulent saltmarsh; "MS" = Mudflats/Saltpan; "C" = *Ceriops* spp.). The direction and length of the vector is proportional to the strength of the correlation with the ordination space.

Table 4.1 PERMANOVA table showing the relationships between the Bray-Curtis dissimilarity matrix of the community data (i.e. copepods and crab zoeae densities, with $\log_{10}(x+1)$ transformation) and the DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide succession, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide); T1; T2; T3; T4, and N (Neap tide)) and diel period variables.

Treatment	**Degree of freedom**	**SS**	**R^2**	**Pseudo-F**	**p**
DayNum	8	1.94	0.48	12.32	0.001
Diel period	1	0.66	0.16	33.81	0.001
DayNum:Diel period	7	0.019	0.0046	0.14	0.999
Residual	73	1.44	0.353		
Total	89	4.059	1.00		

Mudflat/saltpans, succulent saltmarsh, and herbaceous saltmarsh remain dry during neap tides in opposition to some expanses of *A. marina/R. stylosa* (<50% of total area) and *Ceriops* spp. (<25% of total area) (Fig 10b). The extent of their inundation increases from T-3 to T0 and decreases after T0 (Fig 9b). During the study period, no more than 56% of the succulent saltmarsh became inundated, corresponding to 3.55 ha (Figure 4.10c) of succulent saltmarsh. The mean percentage of inundation of succulent saltmarsh at T-1 (when the highest export of crab zoea was usually observed) was 20.6 ± 5.20 %, corresponding to a mean of 1.31 ± 0.33 ha of succulent saltmarsh inundated. Very few herbaceous saltmarshes became inundated during the study periods (<12.5% at maximum tidal height in January) (Figure 4.10a).

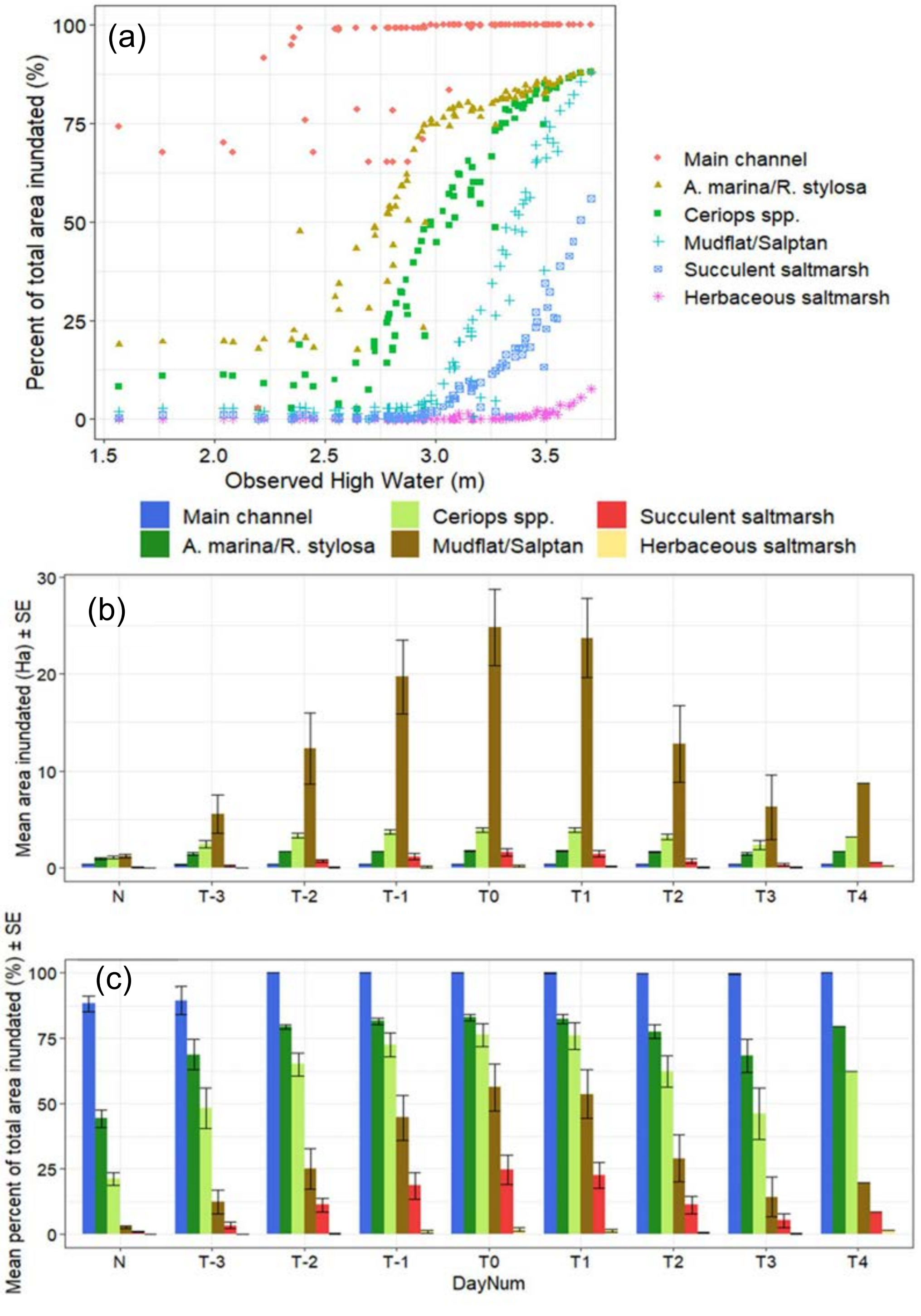


Figure 4.10 (a) Relationships between the maximum percentage of wetland inundation and the observed High Water corresponding to the day of zooplankton sampling; (b) Mean area inundated (hectares) and (c) Mean percentage of total wetland area inundated (± standard error) pooled by DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide).

4.5 Discussion

4.5.1) Tidal connectivity triggers prey pulse export

The findings demonstrate the key role of tidal connectivity in regulating the transfer of upper tidal tropical wetland habitat production to wider coastal ecosystems – probably in much the same way as they are importantly connected in temperate and sub-tropical regions. Specifically, for this study, crab zoeae pulse exports were triggered by tides exceeding 3.2 meters, corresponding to the inundation threshold above the mangrove-marsh ecotone. This study adds more evidence to support existing eco-hydrological models that emphasise the importance of tidal connectivity patterns in driving the ecological values of upper tidal wetland habitats such as saltmarshes (Odum, 1980; Thomas & Connolly, 2001; Minello et al., 2012; Baker et al., 2013). In addition, the data supports that tidal connection to upper tidal wetlands, and the export of crab zoeae, is a vector of carbon (energy) export away from tidal saltmarsh areas, and could be supporting fisheries production more broadly, aligning to studies in temperate and subtropical saltmarshes (Saintilan & Mazumder, 2017; Raoult et al., 2018).

4.5.2) Tidal connectivity is critical for ecological connectivity

Tidal connectivity patterns undoubtedly play a key role in mediating prey pulse export, but the synchrony among suitable hydrological, biological and environmental factors and conditions must also be considered (Baker & Sheaves, 2007; Davis et al., 2014b). The model showed that once the threshold in tidal height of 3.2 m was reached, the amplitude of the peaks in prey pulse export was not proportional to tidal height or the extent of tidal inundation to upper tidal habitats. Rather, the distinct peaks in prey pulse aligned with the reproductive strategies of intertidal crabs, a notion reported in previous studies elsewhere (Christy & Stancyk, 1982; Mazumder et al., 2009). Crab reproductive behaviour has been shown to be influenced by additional contextual environmental and biological factors beyond tidal connectivity (Christy, 1978; Christy, 1986; D'Incao et al., 1992; Ituarte et al., 2006). For example, many crab species coordinate their spawning during the coolest month of the year (August in the present study) to avoid extreme environmental conditions (e.g., high summer temperatures) (Mazumder et al., 2009). They also often spawn at dusk and night to avoid diurnal predators (Christy, 1986; Ricardo et al., 2014). The data also indicates that synchronising spawning the day before the highest spring tide may be a key reproductive strategy, likely to maximise crab zoeae export by subsequent tides (Christy and Stancyk, 1982; Hollingsworth and Connolly, 2006). Therefore, the data supports the theory that the relationship between tidal connectivity and positive ecological outcomes is not linear (Montalto & Steenhuis, 2004; Yin et al., 2020) and contradicts a commonly applied restoration paradigm which suggests that tidal connectivity equals ecological connectivity (Hilderbrand et al., 2005; Liu et al., 2016). Consequently, in addition to maintaining tidal connectivity patterns, recognising contextual processes and patterns beyond tidal connectivity, such as life cycle histories and species requirements, should be an integrated part of coastal wetland management or restoration campaign (Weinstein et al., 2014; Nagelkerken et al., 2015).

4.5.3) Similar "habitat types" do not imply similar ecological values

The importance of considering contextual processes and patterns to determine the values of saltmarshes was apparent from the data. Specifically, the inundation of succulent saltmarshes, along with unvegetated flats (mudflats and saltpans) and *Ceriops* spp. inundation, was identified as a contributing component to the export of crab zoeae. However, an average of only approximately 25% of succulent saltmarshes were tidally connected when the highest peaks in prey pulse export were recorded (in T-1 tides). This suggests that the remaining succulent saltmarshes were unlikely to be important contributors to prey pulse export, unlike the most connected saltmarshes that are slightly lower in the elevation gradient. This result emphasises that "similar" habitat types may indeed have different habitat functions due to contextual variability in factors such as tidal connectivity, spatial arrangements and anthropogenic disturbances that operate at even small spatial scales (Rogers & Krauss, 2019; Bradley et al., 2020; Ziegler et al., 2021), such as within the same location (Davis et al., 2012). Therefore, this finding highlights the importance of avoiding generalisations on the values of saltmarshes based on a vegetation-focused approach or "basic structural criteria" (*sensu* Weinstein et al., 2014). Instead, the study suggests that saltmarsh values should be defined by considering the physical and ecological contexts that influence their functions rather than generalisations and extrapolation of broader models. This shift towards a context-driven understanding of saltmarsh values should enable management and restoration strategies to align more effectively with the specific characteristics of each location (Bradley et al., 2020; Ziegler et al., 2021), which would ultimately increase the much needed overall success of restoration and management efforts (Waltham et al., 2021).

4.5.4) Challenges and future directions

While previous temperate and subtropical studies have associated crab zoeae export from saltmarshes (Hollingsworth & Connolly, 2006; Mazumder et al., 2009), the mosaic distribution patterns and the tidal connectivity of succulent saltmarsh, mudflats, and *Ceriops* spp. made it challenging to isolate succulent saltmarsh from the inundation of these other high intertidal vegetated and unvegetated covers in the present study. Nevertheless, as highlighted by Sheaves et al. (2012), it is possible that the complex physical and ecological interactions that link tidal wetland components make efforts to isolate the importance of individual components in supporting critical functions not necessarily informative. Correlative studies isolating a process to a single habitat may potentially misdirect restoration efforts to focus on this particular habitat or ecosystem (e.g., saltmarshes) without considering broader contextual functioning (Sheaves et al., 2021). For instance, this may motivate increasing the area of targeted habitats without considering additional factors that may lead to restoration success (Peng et al., 2016). Consequently, in the context of whole-of-system management, it may be more relevant to understand how the patterns in the configuration of tidal wetland components (Connolly et al., 2005) and their synergies (Sheaves et al., 2012) support prey pulse export rather than attempting to assign a specific process to a specific habitat type using correlational approaches. These observations do not intend to underestimate the role of saltmarshes in providing crab habitats (Mazumder, 2009) but rather highlight the importance of considering the integrity of the coastal ecosystem mosaic and the ecological and physical (e.g., tidal connectivity) interactions among different components (Sheaves et al., 2012; da Silva et al., 2022) in our understanding of the values of saltmarsh to crabs and the export of crab zoeae.

4.5.5 Implications for management and restoration

Overall, the findings add further evidence of the importance of managing saltmarshes from a whole-of-system approach (Queensland, 2016; Weinstein & Litvin, 2016; Waltham et al., 2020) and not in isolation to the remaining coastal ecosystem mosaic (Weinstein & Litvin, 2016). Recognising the ecological linkages within the coastal ecosystem mosaic is a key aspect of coastal ecosystem resilience and productivity (Bernhardt & Leslie, 2013; Carr et al., 2017; O'Leary et al., 2017; Scapin et al., 2022). Understanding current linkages (e.g., hydrological and ecological) within the coastal ecosystem mosaic is also important to improve our ability to predict tidal wetland responses to climate change and anthropogenic modification of the coastal landscape (Sheaves, 2009). Changes in the current patterns of the coastal ecosystem mosaic and its tidal connectivity patterns due to SLR, such as a shift from shallower saltmarsh and mudflats habitats to deeper mangrove-dominated systems (Kelleway et al., 2017), are likely to have important effects on current connectivity patterns, which may alter predator-prey dynamics (Davis et al., 2022). In addition, human adaptation strategies to climate change, often involving barriers to connectivity such as seawalls, have the potential to alter physical and ecological linkages among habitats (Sheaves et al., 2016), which may negatively impact the overall ecological functioning of tidal wetlands (Gilby et al., 2021). Therefore, management approaches should take into consideration the many ecological linkages that interconnected tidal wetland components hold, including prey pulses from tidal wetland habitat occurring much higher in the intertidal zone.

The results add evidence that saltmarsh habitats should not be managed following a "one-size-fits-all" approach (Neal et al., 2018; Waltham et al., 2021). Scientists now widely accept that the context in which habitats occur is more important in defining the functions and values of tidal wetland habitats than the presence of "a type of habitat" (Bradley et al., 2020; Ziegler et al., 2021). Consequently, efforts to understand and define environmental contexts, such as tidal connectivity, should be prioritised over habitat-based management actions. The eco-hydrological workflow used in this study may be useful for coastal managers elsewhere, to assist with monitoring key contextual aspects of tidal wetland functioning, such as tidal connectivity and prey pulse exports.

4.5 Conclusion

The results not only highlight the importance of maintaining tidal connectivity patterns within a burgeoning modified coastal seascape (Waltham et al., 2021), but also underscore the need to consider how organisms interact with and respond to variability in their environment when planning tidal wetland restoration projects (Weinstein & Litvin, 2016). This suggests that evaluating restoration success goes beyond monitoring tidal connectivity and should include a comprehensive understanding of additional physical and ecological processes and patterns underpinning ecological functioning (Sheaves et al., 2021), such as the prey pulses described here. This is particularly important because the multifaceted and pervasive nature of connectivity (Sheaves, 2009) suggests that not incorporating less conspicuous aspects (e.g., prey pulses and trophic links) of ecological connectivity may potentially have unforeseen consequences on wider faunal community structures (Yang et al., 2008; Weinstein & Litvin, 2016). Not including this may ultimately negatively affect key coastal ecosystem values such as fishery productivity (Weinstein et al., 2014).

Chapter 5: Contrasting effects in tidal inundation under varying sea levels on the ecological structure and functions of tropical wetland ecosystems

5.1 Abstract

Coastal managers continue to be confronted with making management decisions with few data available and insight of the outcomes. Simple tools that can be used to inform on the potential effects of different scenarios of changes (e.g., climate change, management decisions) are therefore particularly important to assist decision-making. This study used a Bayesian Belief Network (BBN) to investigate the contrasting effects of SLR scenarios and a reduction in tidal inundation on a tropical tidal wetland complex that includes a mosaic of transitional habitats including saltmarshes, mangroves, and intertidal mudflats. In this study I investigated: 1) the habitability of the study site for tidal vegetation under different scenarios associated with changes in inundation; and 2) the probability that the ecological values of export of crab zoea and blue carbon be supported under the different scenarios. The study highlights that, without the ability to adjust to future SLR scenarios, saltmarshes in the study region, for example, are likely to be lost at the expense of mangroves and open water under a scenario of 0.8 m SLR, likely by the end of this century. Tidal inundation reduction decreased mangrove cover but increased habitability for terrestrial vegetation and subtidal herbaceous saltmarshes. SLR is likely to positively affect the blue carbon value but decreases the likelihood of the site holding high crab zoeae export values. In contrast, a reduction of tidal inundation declined the likelihood of the site holding both high blue carbon and crab zoeae export values. The findings highlight the importance of "whole-of-system" approach to assessing the effects of different scenario changes in tidal inundation. Focusing only on one tidal wetland habitat (e.g., mangrove) and a single targeted value may affect the structure and

functions of other components of the coastal ecosystem mosaic. BBNs are a useful tool to summarise preliminary assessments of the potential effects of SLR and reduction in tidal inundation on tidal wetland ecosystems, which may assist managers to make the most informed decision with respect to conservation of coastal transitional areas.

5.2 Introduction

The direct effects of human activities on ecosystems are exacerbated by rapidly changing climate and sea-level rise (SLR) (Boon et al., 2018). Those changes particularly threaten coastal ecosystems (He & Silliman, 2019), such as saltmarshes (Simas et al., 2001; Hartig et al., 2002; Saintilan & Rogers, 2013; Adams, 2020). Their position along coastlines, the most prized geographic areas in the world by humans (Kron, 2013) for living, recreational activities, tourism, and commerce (Martínez et al., 2007), makes them particularly vulnerable to human exploitation (Gedan et al., 2009; Sandi et al., 2018). Shifts in their distribution are already visible (Saintilan & Hashimoto, 1999; Armitage et al., 2015; Raposa et al., 2017). This pattern is likely to continue to increase across this century (Langston et al., 2021), requiring careful management of coastlines (Harty, 2004; Boateng, 2008; Raposa et al., 2016; Schuerch et al., 2018; Nguyen et al., 2022).

Tidal wetlands such as saltmarshes provide incredible biodiversity, economical, cultural, and recreational values in many places (Barbier et al., 2011). For instance, they provide nursery and feeding grounds for fish (Beck et al., 2001; Litvin et al., 2018; Whitfield, 2017), support coastal fisheries by providing primary and secondary productions to coastal water (Hollingsworth & Connolly, 2006; Raoult et al., 2018; Taylor et al., 2018b), protect coastlines from erosion (Finotello et al., 2022), and improve water quality by processing nutrients (Sousa et al., 2010). Tropical saltmarshes have been the subject of few investigations compared to other coastal wetland habitats like mangroves, but in the few studies available they are described as providing basal sources for coastal food web productivity (Sheaves et al., 2007) and providing habitat for benthic macrofauna (Reis et al., 2019; Reis & Barros, 2020). In addition, tidal connections to upper tropical tidal habitats where saltmarshes occur have been shown to export considerable quantities of crab zoea (Chapter 4) in a similar way to subtropical and temperate Australian saltmarshes (Saintilan and Mazumder 2017). The synchronised release of substantial densities of crab zoeae by crabs has been seen as an important prey-pulse that links together high intertidal habitats with the remaining seascape, symbolising the importance of land-seascape connectivity (Saintilan & Mazumder, 2017; Chapter 4).

One of the most discussed values of tidal wetlands is the ability to assimilate carbon at higher rates and quantities than primary terrestrial forests, hence tidal wetland ecosystems are referred as “blue carbon ecosystems” (Alongi, 2020a; Lovelock & Duarte, 2019; Macreadie et al., 2021). The blue carbon value of coastal ecosystems makes them particularly attractive to mitigate climate change (Macreadie et al., 2021), while providing other critical services such as fisheries and storm protection (i.e., “the multifaceted nature of blue carbon ecosystems”, Macreadie et al., 2019). Consequently, blue carbon ecosystems are at the centre of discussions in carbon offsets and credits (Crooks et al., 2011; Ullman et al., 2013). Mangroves are often reported as having a high above-ground and below-ground carbon stock compared to saltmarshes and seagrasses (Kelleway et al., 2016; Alongi, 2020a, 2020b). For instance, reviews of carbon stocks within the first meter below the surface of mangroves found a mean of 255 Mg C ha^{-1} and a maximum of 683 Mg C ha^{-1} compared to a mean of 162 Mg C ha^{-1} and maximum of 259 Mg C ha^{-1} in saltmarsh soils (Duarte et al., 2013).

The intrinsic link between tidal hydroperiod (duration, depth and frequency of tidal inundation) and intertidal wetland distribution and connectivity patterns (Crase et al., 2013; Rozas, 1995; Baker et al., 2013; Minello et al., 2012), makes increased tidal flooding associated with accelerating SLR potentially a major positive service that is offered by tidal wetlands (Craft et al., 2009; Saintilan & Rogers, 2013; Cahoon et al., 2006; Raposa et al., 2016; Macreadie et al., 2017). For example, an increase in SLR may lead to the upland migration of saltmarshes at the expense of terrestrial woodland species (Donnelly & Bertness, 2001). Nevertheless, in the tropics and subtropics mangroves are encroaching into saltmarshes in response to SLR (Rogers et al., 2014a; Saintilan et al., 2014), leading to a landward squeeze of saltmarshes to mangroves (Oliver et al., 2012). Without elevation space and sediment availability for upland transgression, saltmarshes might be casualties of coastal squeeze (Leo et al., 2019; Torio & Chmura, 2013) and becoming lost at the expense of mangroves or open waters.

Barriers to tidal inundation, such as culverts, have important consequences on tidal wetland vegetation distribution and extent (Mora & Burdick, 2013b). For instance, bund walls can increase the proliferation of, on the landward side of the wall, freshwater or terrestrial invasive weeds to the detriment of tidal wetland vegetation such as saltmarshes (Abbott et al., 2020; Karim et al., 2021). Artificial barriers can also change the wetting and drying of upper tidal wetland habitat (Rodríguez et al., 2017), hence changing groundwater and drainage dynamics and soil properties (Mora & Burdick, 2013b), which can negatively affect saltmarsh and mangrove vegetation. Engineered barriers such as dams can also reduce sediment availability, which is necessary for saltmarsh accretion (Lovelock et al., 2011) and coastal erosion prevention (Wolanski & Hopper, 2022). The effects of man-made barriers can decrease the resilience of tidal wetlands to other anthropogenic stressors such as climate change (Rodríguez et al., 2017), further threatening the values and services provided by tidal wetlands.

Given intensifying degradation of coastal ecosystems, there have been developing interest in restoring tidal wetland connectivity and vegetation so that tidal wetland values and services are maintained or increased (Sheaves et al., 2021; Hagger et al., 2022; Raw et al., 2021; Waltham et al., 2021; Waltham et al., 2020). Simultaneously, growing interests in carbon offsets have raised public and political motivations in restoring or enhancing tidal wetland habitats to improve the blue carbon values of coastal areas. Nevertheless, managers are increasingly challenged to predict management and restoration outcomes with little quantitative data (Mishra & Farooq, 2022), and examples of successful restoration outcomes are few and far between (Bayraktarov et al., 2016; Primavera & Esteban, 2008; Suding, 2011).

The notion that restoring one value or habitat does not necessarily improve another creates trade-offs and contradictions in coastal ecosystem restoration and management (Yang et al., 2018; Yang et al., 2021; Choi et al., 2022). For instance, removal of bund walls to restore tidal connectivity and tidal wetlands so as to enhance the blue carbon values of coastal areas or to restore historical tidal vegetation (Karim et al., 2021) might be done to the detriment of freshwater habitats with nesting and bird habitat values. Conversely, while a detriment for freshwater species, this mitigation might enhance habitat values for mangrove bird species specialists (Canales-Delgadillo et al., 2019). Similarly, mangrove afforestation on bare tidal flats to enhance blue carbon sequestration and shoreline protection (Jia et al., 2018) can be performed at the expense of bare tidal flats values (Erftemeijer & In, 2000), such as decreasing the extent of critical foraging areas for threatened shorebirds (Choi et al., 2022). Another example is that an increase in mangrove encroachment due to SLR might improve the blue carbon value of coastal areas including mangroves which have a higher carbon reserve compared to saltmarshes (Kelleway et al., 2016). Yet, the effects of this encroachment are poorly understood (Kelleway et al., 2017) and might negatively affect the floristic and faunal diversity, and conservation values held by saltmarshes such as the provision of foraging grounds for threatened bats (Saintilan & Rogers, 2013) or the export of large quantities of crab zoea (Mazumder et al., 2009).

Developing simple tools to assist scientists and practitioners observe these trade-offs and assess whether restoration measures achieve multiple outcomes while maximising ecological benefits is needed (Yang et al., 2021; Waltham et al., 2021). Bayesian Belief Networks (BBNs) are used increasingly in ecosystem management and conservation due to their ability to deal with complex systems with high degrees of uncertainty (McCann et al., 2006). The "concise representation" (Coupé & Van der Gaag, 2002) of BBN and the user-friendly interface make them highly attractive for managers to inform decision-making on the outcomes and effectiveness of management or restoration measures. Examples of BBN application in coastal ecosystems include environmental risk level assessments (Jäger et al., 2018; Malekmohammadi et al., 2023), prediction of erosion due to SLR and assessment of SLR prevention measures efficiencies (Sahin et al., 2019), and the evaluation of tidal wetland values based on management strategies such as feral pig exclusion by fencing (Waltham et al. 2020).

The aim of this study was to use the BBN platform to illustrate the contrasting effects of SLR and a reduction in tidal inundation on a tropical tidal wetland complex that has a mosaic of habitats including saltmarshes, mangroves, and mudflats. More specifically, we investigate the potential impacts of sea level rise scenarios (+0.3 m and +0.8 m) and reduction in tidal inundation (-0.3 m) on the habitability of the study site to tidal wetland vegetation (i.e., "habitability" from Cockell et al. (2016) which refers to the probability or ability of an environment to support or not support an organism). In addition, we observed how these changes may affect the blue carbon prospects of the site and its value in providing for trophic subsidies in estuaries via the export of crab zoea. The main objectives were to assess: 1) the habitability of the study site for tidal wetland vegetation under different scenarios of change inferred by maximum inundation depth and duration of inundation; 2) the probability that the values of export of crab zoea and blue carbon be supported under the different scenarios computed in (1); and 3) the potential of BBN to identify trade-offs or contrasting outcomes of hydrological changes such as SLR.

5.3 Methods

5.3.1 Case study area

The case study site is in the north part of Blacksoil Creek (Site A) in north Queensland, Australia (-19.297, 147.021) (Figure 5.1). The site is within the Bowling Green Bay National Park, a Ramsar internationally important wetland complex adjacent to the Great Barrier Reef. Detailed descriptions of the site are found Chapters 2-4. Briefly, the site represents a dry tropical wetland complex composed of mangroves dominated by the red mangrove, *Rhizophora stylosa,* at low elevation near channels and seaward edge of the site followed by the grey mangrove, *Avicennia marina* and the yellow mangrove, *Ceriops tagal* and *Ceriops australis* at higher elevations. The site is then composed of mudflats and saltpans including succulent saltmarshes (including the bead weed *Sarcocornia quinqueflora*) and herbaceous saltmarsh (dominated by the saltcouch, *Sporobolus virginicus)* below and near the highest astronomical tide (HAT). Additional details on this study site and vegetation are found in Chapters 2 and 3.

Two other sites were used to obtain data on crab zoea export and to inform the values of tidal wetlands in the BBN (Figure 5.1). The Jerona site (Site B) (-19.450, 147.228, 89.21 ha) is found south of Site A and has the same climate and tidal characteristics as Site A. This site also lies within the Bowling Green Bay National Park and is listed under the Ramsar Wetland Convention. The site also has an intersecting road with a small (1 m) 1-pipe culvert. The mangrove community is dominated by *A. marina,* along the channel and at the saltmarsh-landward margin. The Blind-Your-Eye Mangrove, *Excoecaria agallocha*, is another species found at the terrestrial margin at Site B. The site is mostly dominated by saltmarsh vegetation. The saltmarsh vegetation community is dominated by succulent marsh, notably the bead weed, *Sarcocornia quinqueflora*, with isolated patches of the glasswort, *Tectinoria* spp., the grey samphire; *Tecticornia australasica,* the pigweed; *Portulaca* spp., the pigface; *Carpobrotus glaucescen*s, the prickly saltwort; *Salsola australis*; and the seablite; *Suaeda australis.* The herbaceous saltmarsh community is composed of the salt couch, *Sporobolus virginicus* with green couch, *Cynodon dactylon,* and jointed rush, *Juncus kraussi.* The saltmarsh vegetation at Site B is less visibly affected by human activities than at Site A, although vehicle damage is apparent at some locations. In addition, there are signs of erosion of herbaceous saltmarsh at tidal-terrestrial margin.

The Lucinda Site (Site C) (-18.542, 146.330) is mangrove-dominated (Table 5.1). The site is located in the Wet Tropics near the Lucinda township. The site is mostly dominated by mangrove vegetation, although some small patches of succulent saltmarshes were found in areas on the landward side of mangroves (pers. observations). The site has a mesotidal and semi-diurnal regime. The highest astronomical tide is 1.15 m above AHD (Boswood et al., 2007). The site is also bisected with a road with a large multi-pipe culvert. The culvert was where crab zoea sampling was conducted (see below for details on crab zoea sampling).

Table 5.1 Wetland cover at the case study site (Site A), Site B, and Site C used to inform the crab zoea value node in the BBN. The land covers at Site A and Site B were calculated using the UAV-derived orthophotos whose methods are described in Chapters 2 and 3. Land cover at Site C was estimated to be predominately mangroves (based on on-site visual and satellite imagery assessments) with some saltmarsh patches (on-site observations as the patches could not be seen via satellite imagery)

Land cover	**Site A Per cent of total wetland area (%)**	**Site B Per cent of total wetland area (%)**	**Site C Per cent of total wetland area (%)**
Mudflat/Saltpan	65.87	61.01	5
Herbaceous saltmarsh	16.41	9.28	0.1
Succulent saltmarsh	8.56	29.17	0.1
Ceriops *spp.*	6.24	0	0
Mangroves	2.53	0.31	93.25
Main channel	0.37	0.22	0.75

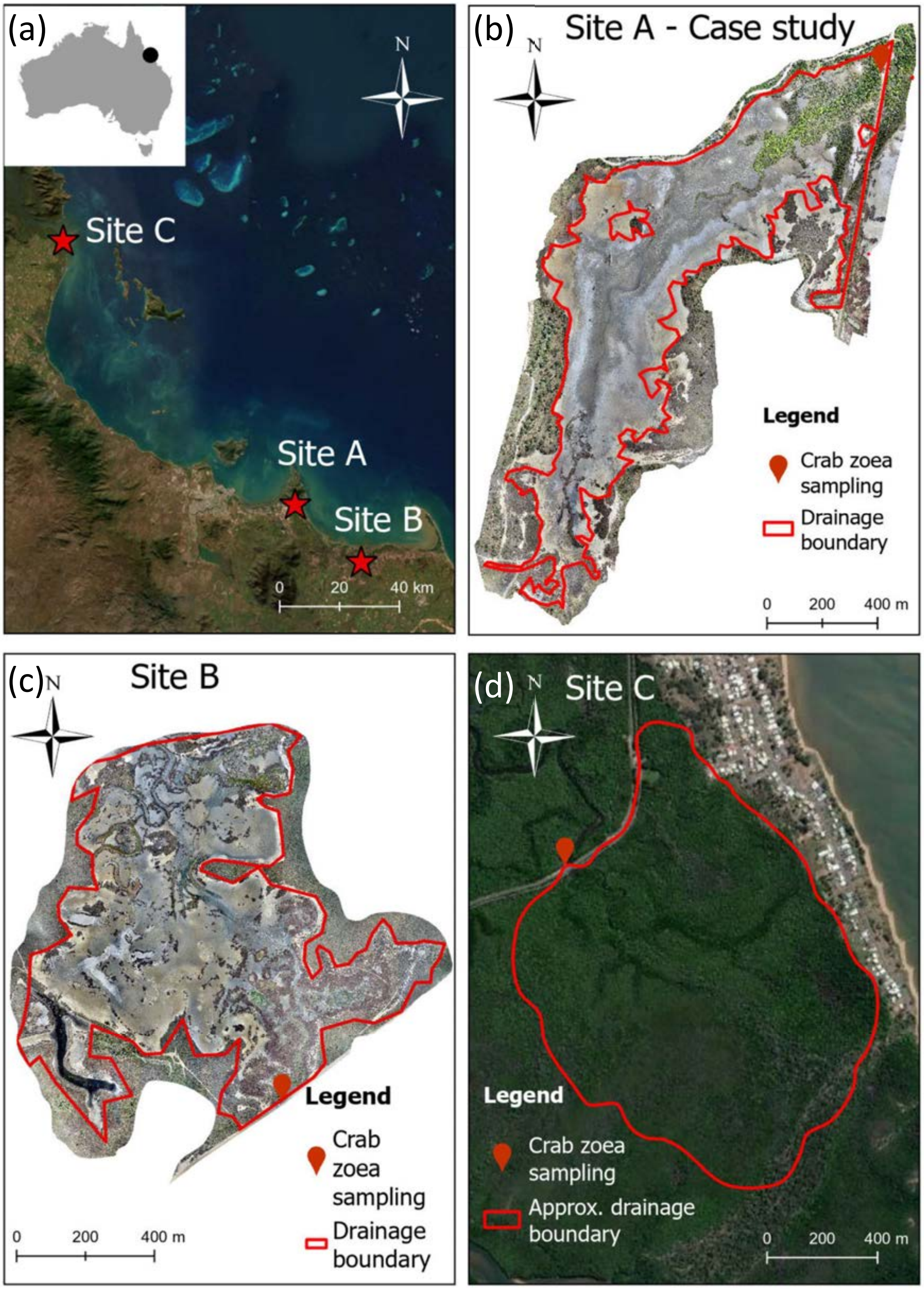


Figure 5.1 Map of the study area showing (a) the geographic locations of the case study site (Study Site A) and of the two study sites where crab zoea were sampled (Site B – saltmarsh-dominated site and Site C-mangrove-dominated site) along the eastern Australian coast; (b) the orthophoto of Site A derived from UAV-SfM showing the position of the sampling of crab zoea; (c) the UAV-SfM orthophoto of Site B with the position of the sampling of crab zoea; and (d) satellite imagery of Site C showing the position of crab zoea sampling and the approximate drainage area of the site

5.3.2 Bayesian Belief Network

5.3.2.1 Development

Bayesian Belief Networks (BBN) are a graphical modelling framework (represented by a directed acyclic graph-DAG) that illustrates causal relationships between variables based on probabilities computed using the Theorem of Bayees (for detailed methods, description and examples of applications of BBNs, see Jensen and Nielsen (2007), Henriksen and Barlebo (2008), Dlamini (2010), and Loftin et al. (2018)).

A BBN is first built qualitatively by listing all the variables potentially influencing the targeted study system (Marcot et al., 2006). In the case of the effects of different sea levels on tidal wetland vegetation distribution, these variables are summarised in Figure 5.2. and include the complex feedback and interactions of surface hydrology, local tidal dynamics, topography, microtopography, temperature, accretion rates, vegetation type, estuarine and coastal geomorphology, meteorological conditions, climatic events, edaphic variables, nutrients inputs and underwater hydrology, as well as biological interactions such as predation, facilitation, competition and diseases (see reviews from Friess et al., 2012; Saintilan et al., 2019; Rogers & Krauss, 2019). Here, the study has used field and modelled data only based on the hydrodynamic model computed for Site A (Chapters 2 and 3) to inform the BBN on the habitability of the site under different SLR scenarios and reduction of tidal inundation. Hence, the model consisted of only two parent nodes: inundation maximum depth and inundation duration that were informed using field data. The BBN was built with Netica 6.09 (Norsys Software Corporation 2021).

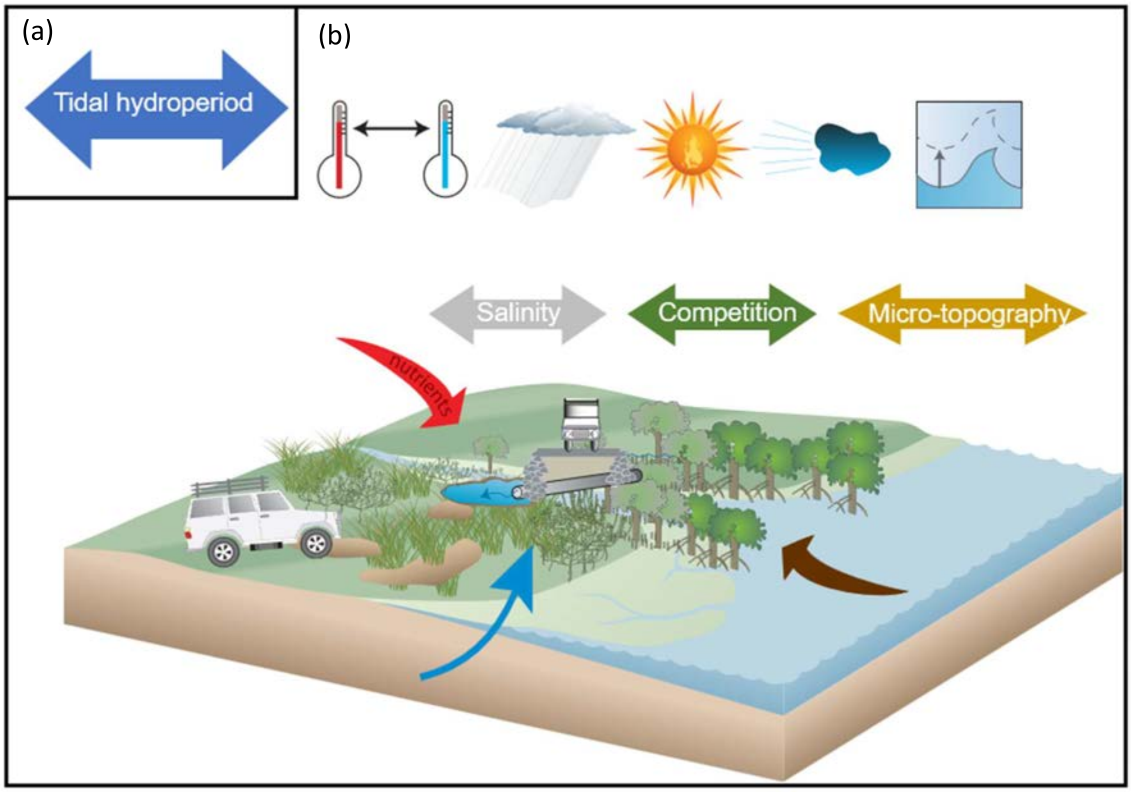


Figure 5.2 Conceptual diagram of (a) the processes considered in the present study by opposition to (b) the likely interacting processes, together with tidal hydroperiod (b) that shape saltmarsh and mangrove dynamics in tropical seascapes and influence their vulnerability to sea-level rise and human interventions.

5.3.2.2 Cases and data inputs

5.3.2.2.1 Duration of inundation and maximum depth

Outputs from a hydrodynamic model of average-tide scenarios computed in Chapter 3 were used to inform the BBN on the duration of inundation and maximum inundation depth at the study site (only the area above the main concrete road was included here to represent the area drained by the zooplankton sampling pump, see section 5.3.2.2.3). The rasters were reclassified to obtain discrete states for the duration of inundation and maximum depth (Table 5.2) to populate the probability tables. The outputs rasters were discretised into six states from no inundation (or depth) to very long duration of inundation (or very deep maximum depth) (Table 5.2). Following Loftin et al. (2018), the rasters were resampled to 0.1 m resolution and converted to points. The value to point was extracted to create a database with the number of pixels (calculated from the points) for each state. The percent probability fed into the tables was calculated by dividing the number of pixels for each state by the total number of pixels of the study site. This was repeated for the SLR scenarios of 0.03 m and 0.08 m, and a reduction in inundation of 0.03 m.

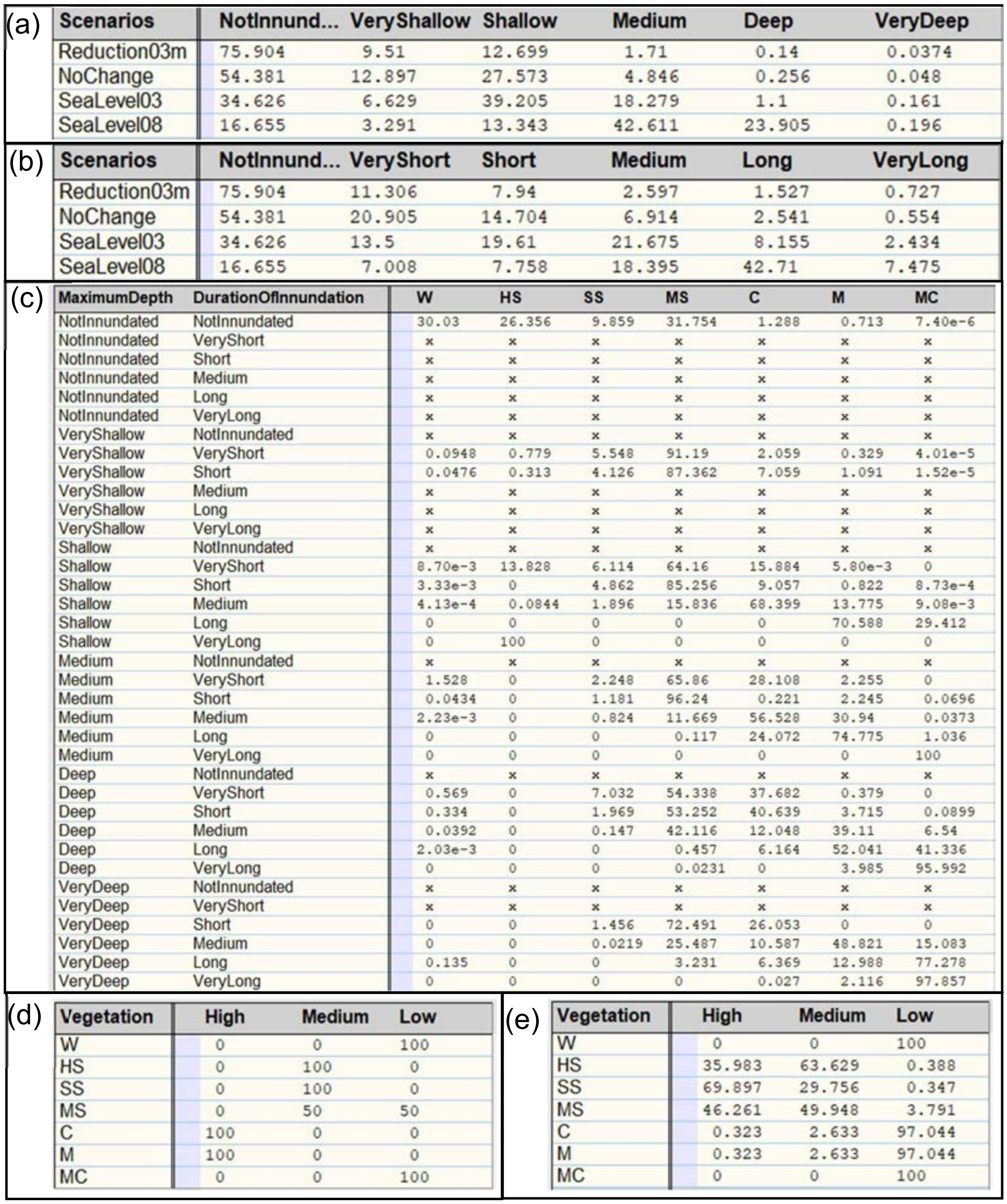
Table 5.2 Discretisation of the hydroperiod continuous values (maximum inundation depth and duration of inundation) used to inform the parent nodes in the BBN.

Parent node	Range of values	Discrete state
Duration of Inundation (hours)	None=0	Not Inundated
	]0;12[	Very Short
	[12;48[	Short
	[48;163[	Medium
	[163;560[	Long
	≥560	Very long
Maximum Inundation Depth (m)		
	None=0	Not Inundated
	]0;0.1[	Very Shallow
	[0.1;0.4[	Shallow
	[0.4;0.8[	Medium
	[0.8; 1.5[	Deep
	≥1.5	Very Deep

5.3.2.2.2 Case study 1: Habitability of the site for tidal wetland vegetation type

In this case, the probability of finding a wetland type based on tidal inundation conditions (described in section 5.3.2.2.1) influenced by scenarios of changes was assessed. The probability was considered as a measure of habitability. The child node “Vegetation” was divided into seven states representing land cover type (W= woodland/Grassland; HS = herbaceous saltmarsh; SS = succulent saltmarsh; C = Ceriops mangrove species (*Ceriops tagal and Ceriops australis)*; M= *A. marina/R. stylosa* (abbreviated as “M” for other mangroves than *Ceriops* spp.); MS = mudflat/saltpans; and MC=main channel).

The 3-cm resolution land cover data derived in Chapters 2 and 3 using unattended-aerial-vehicle structure-from-motion (UAV-SfM) photogrammetry was used to obtain information



(a)

Scenarios	NotInnund...	VeryShallow	Shallow	Medium	Deep	VeryDeep
Reduction03m	75.904	9.51	12.699	1.71	0.14	0.0374
NoChange	54.381	12.897	27.573	4.846	0.256	0.048
SeaLevel03	34.626	6.629	39.205	18.279	1.1	0.161
SeaLevel08	16.655	3.291	13.343	42.611	23.905	0.196

(b)

Scenarios	NotInnund...	VeryShort	Short	Medium	Long	VeryLong
Reduction03m	75.904	11.306	7.94	2.597	1.527	0.727
NoChange	54.381	20.905	14.704	6.914	2.541	0.554
SeaLevel03	34.626	13.5	19.61	21.675	8.155	2.434
SeaLevel08	16.655	7.008	7.758	18.395	42.71	7.475

(c)

MaximumDepth	DurationOfInnundation	W	HS	SS	MS	C	M	MC
NotInnundated	NotInnundated	30.03	26.356	9.859	31.754	1.288	0.713	7.40e-6
NotInnundated	VeryShort	×	×	×	×	×	×	×
NotInnundated	Short	×	×	×	×	×	×	×
NotInnundated	Medium	×	×	×	×	×	×	×
NotInnundated	Long	×	×	×	×	×	×	×
NotInnundated	VeryLong	×	×	×	×	×	×	×
VeryShallow	NotInnundated	×	×	×	×	×	×	×
VeryShallow	VeryShort	0.0948	0.779	5.548	91.19	2.059	0.329	4.01e-5
VeryShallow	Short	0.0476	0.313	4.126	87.362	7.059	1.091	1.52e-5
VeryShallow	Medium	×	×	×	×	×	×	×
VeryShallow	Long	×	×	×	×	×	×	×
VeryShallow	VeryLong	×	×	×	×	×	×	×
Shallow	NotInnundated	×	×	×	×	×	×	×
Shallow	VeryShort	8.70e-3	13.828	6.114	64.16	15.884	5.80e-3	0
Shallow	Short	3.33e-3	0	4.862	85.256	9.057	0.822	8.73e-4
Shallow	Medium	4.13e-4	0.0844	1.896	15.836	68.399	13.775	9.08e-3
Shallow	Long	0	0	0	0	0	70.588	29.412
Shallow	VeryLong	0	100	0	0	0	0	0
Medium	NotInnundated	×	×	×	×	×	×	×
Medium	VeryShort	1.528	0	2.248	65.86	28.108	2.255	0
Medium	Short	0.0434	0	1.181	96.24	0.221	2.245	0.0696
Medium	Medium	2.23e-3	0	0.824	11.669	56.528	30.94	0.0373
Medium	Long	0	0	0	0.117	24.072	74.775	1.036
Medium	VeryLong	0	0	0	0	0	0	100
Deep	NotInnundated	×	×	×	×	×	×	×
Deep	VeryShort	0.569	0	7.032	54.338	37.682	0.379	0
Deep	Short	0.334	0	1.969	53.252	40.639	3.715	0.0899
Deep	Medium	0.0392	0	0.147	42.116	12.048	39.11	6.54
Deep	Long	2.03e-3	0	0	0.457	6.164	52.041	41.336
Deep	VeryLong	0	0	0	0.0231	0	3.985	95.992
VeryDeep	NotInnundated	×	×	×	×	×	×	×
VeryDeep	VeryShort	×	×	×	×	×	×	×
VeryDeep	Short	0	0	1.456	72.491	26.053	0	0
VeryDeep	Medium	0	0	0.0219	25.487	10.587	48.821	15.083
VeryDeep	Long	0.135	0	0	3.231	6.369	12.988	77.278
VeryDeep	VeryLong	0	0	0	0	0.027	2.116	97.857

(d)

Vegetation	High	Medium	Low
W	0	0	100
HS	0	100	0
SS	0	100	0
MS	0	50	50
C	100	0	0
M	100	0	0
MC	0	0	100

(e)

Vegetation	High	Medium	Low
W	0	0	100
HS	35.983	63.629	0.388
SS	69.897	29.756	0.347
MS	46.261	49.948	3.791
C	0.323	2.633	97.044
M	0.323	2.633	97.044
MC	0	0	100

Figure 5.3 Computational probability tables (CPTs) of (a) the parent nodes “Duration of inundation” and (b) Maximum depth; (c) the child node “Vegetation” showing the cominations of the states of the parent nodes; (d) the child node “Blue carbon value”; and (e) the child node “Crab zoea export value”

on the distribution of tidal wetland vegetation (herbaceous saltmarsh, succulent saltmarsh, Ceriops, and other mangroves), unvegetated flats (mudflats/saltpans), and terrestrial vegetation (Woodland/Grass). Their distribution was expressed by the number of pixels per parent node state combinations (i.e., inundation duration and maximum inundation depth) (using the same geoprocessing workflow for the hydroperiod variables above) (Figure 5.3). To populate the computational probability tables (CPTs), percent probabilities were calculated by dividing the number of pixels extracted for the land cover type and for the combination of parent node states (e.g., number of pixels with succulent saltmarsh having very short inundation and shallow maximum depth) by the sum of pixels of the given combination of the parent nodes across all land cover type (Figure 5.3).

5.3.2.2.4 Case study 2 - Values and outcomes: Likely probability of crab zoea export

The export of crab zoea by saltmarsh crab's is seen as a key value supporting the need to ensure, frequent, inundation of saltmarshes in temperate (Mazumder et al., 2009) and subtropical Australia (Hollingsworth & Connolly, 2006). By sampling zooplankton outputs in relation to tidal height over multiple days, Chapter 4 described a predictable pattern in the export of crab zoea in relation to tidal height at the case study site (Site A). This study was the first to describe the same patterns in crab zoea export in relation to tidal hydroperiod in tropical tidal wetlands than that of temperate and subtropical saltmarshes (Mazumder et al., 2009; Saintilan & Mazumder, 2017). Nevertheless, although crab zoea export was related to the extent of succulent saltmarsh inundation it was also related to the extent of *Ceriops* spp. and saltpan/mudflats inundation. This makes it difficult to clearly associate crab zoea export as a value that is more importantly attributed to saltmarshes compared to values presented for temperate and subtropical Australian saltmarshes (Mazumder et al., 2009; Saintilan & Mazumder, 2017). Therefore, additional unpublished data was used to further inform the BBN on the crab zoea export values of tidal wetlands.

The same method and sampling apparatus deployed at Site A were used at Site B (dominated by succulent saltmarshes) (over one week in February-March and one week in June 2022, simultaneously sampled with Site A) and Site C (dominated by mangroves, over one week in July 2022 as geographic constraint prevented simultaneous deployment with Sites A and B (Figure 5.1)). By using the same sample processing methods described in Chapter 4, it was found that the succulent saltmarsh-dominated site (Site B) provided the highest densities of crab zoea per m^3 (Figure 5.4).

This information was used to inform the child node "Export of Crab Zoea Value" (Figure 5.5). The states of the BBN node "Export of Crab Zoea Value" were divided into High, Medium and Low. According to the field data (Figure 5.4), each of the states were assigned one of the values: Site B (saltmarsh-dominated site) had the highest value as export of crab zoea and was therefore qualified as "High", while Site A (case study site) was assigned to "Medium", and Site C ("mangrove- dominated site) to "Low". To populate the probability table, we related the crab zoea value to the percentage of land cover found at each site (Table 5.1). For instance, succulent saltmarsh at Site B was 20.1% compared to 9.2% at Site A, and 0.1% at Site C. Therefore, the row of succulent saltmarsh in the CPT was set to 68.3 for High, 31.3% for Medium, and 0.3% for Low (Figure 5.3) (calculated as the percentage of the given land cover at the given site (e.g., 20.1% for Site B) divided by total percentage of cover for the given land cover category across the three sites (here 29.4% for succulent saltmarsh).

For Sites A and B, the proportion of each land cover was derived from the 3-cm UAV-SfM orthomosaic maps created for each site following the methods described in Chapters 2 and 3. As no UAV-SfM orthomosaic map was derived for Site C, the land cover type at Site C was broadly estimated using GoogleEarth and was assigned as predominantly mangroves (Table 5.1).

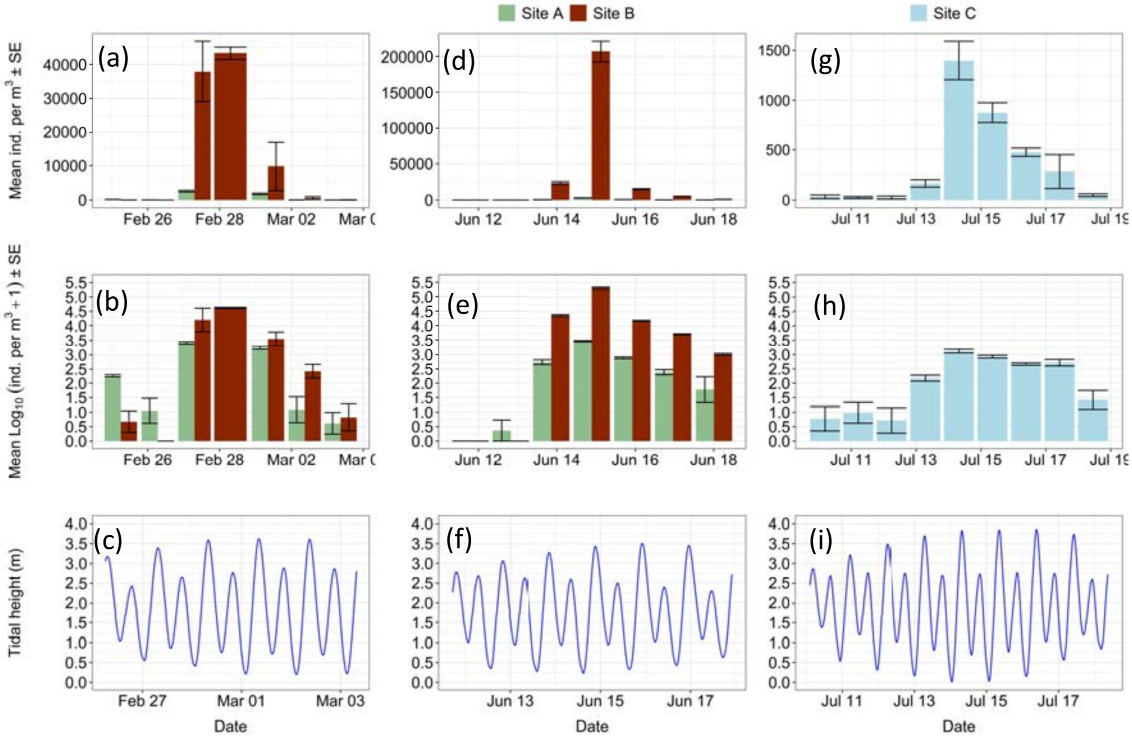


Figure 5.4 Mean crab zoea densities per sampling day (i.e., per samples of 5 replicates of 6 ml – the mean and standard error (SE) are the sample mean and standard error) sampled at Site A (Blacksoil Creek, the case study site site), Site B (Jerona, the saltmarsh-dominated site), and Site C (Lucinda Site, the mangrove-dominated site) showing (a, d, g) mean log10(individual per m3+1) ± SE, (b, e, h) mean individual per m3 ± SE, and (c, f, i) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge for Site A and Site B and at the Cardwell tidal gauge for Site C. Note that for visualisation purposes, the scale of the y-axis of a,d,g are different on each graph.

5.3.2.2.4 Case study 3 - Values and outcomes: likely probability of blue carbon value

The values of blue carbon between tidal wetland types were investigated in the literature to inform the BBN. The carbon storage capacity was used as a proxy to inform the blue carbon value node, although it is acknowledged that saltmarsh and mangrove contribution to carbon flow is known to vary substantially (Alongi, 2020a). For instance, mangroves have a higher carbon storage capacity compared to saltmarshes, but rates of C_{org} burial is greater in saltmarsh soils (although not statistically significantly greater) (Alongi, 2020a, 2020b). Nevertheless, carbon storage was used here to simplify the BBN.

Based on the literature examined (Table 5.3), mangroves had an overall higher blue carbon value compared to saltmarshes. In addition, several studies have highlighted the likely potential positive effects of SLR on coastal blue carbon capacities as mangroves encroachment becomes more important (Kelleway et al., 2016). Hence, mangroves and Ceriops were assigned as having high value ("High"), while succulent and herbaceous saltmarsh were assigned a medium value ("Medium"). Mudflats/saltpans were assigned to both "Medium" and "Low", and woodland/terrestrial and main channel was set to "Low".

5.3.2.2.5 Sensitivity analysis and model validation assessments

Sensitivity analyses are commonly used in the validation process of BBN (Coupé & Van der Gaag, 2002). Sensitivity analyses test how much a finding in one variable influences the beliefs of another variable. The sensitivity analysis allows the user to observe which variables are influencing model outputs and which variables are least sensitive to variability in the model. Sensitivity analysis results can then be used to refine or obtain more accurate information on targeted input parameters (Rohmer & Gehl, 2020). It is also used as a measure of model output robustness. Model sensitivity was analysed using the in-built function "Sensitivity to Findings" in the Netica software. Sensitivity was calculated on the vegetation, crab zoea value, and blue carbon value node for each scenario. In addition, the root mean square of error (RMSE), mean error, and coefficient of correlation R^2 were calculated between the observed (calculated from the land cover) and simulated (calculated by the BBN in the child node "Vegetation") land cover percentage to assess the accuracy of the BBN in predicting vegetation cover from the parent nodes.

5.4 Results

5.4.1 Effects of scenarios on the duration of inundation and maximum depth

At the current sea level, the hydrological conditions of the study site were principally characterised by no inundation (54.4% of the 0.1 m pixels) (Figure 5.3). Inundation duration and maximum depth were predominantly very short (0 to 12 hours during the entire simulation time (i.e., one month) (20.9% of the pixels) and shallow (0.1-0.4 m) (27.6% of the pixels). An increase in sea level of 0.3 m shifted the tidal hydrological conditions of the site towards medium (48-163 hours, 21.7% of the pixels) and short inundation (12-48 hours, 19.6% of the pixels), but shallow maximum depth (0.1-0.4 m, 39.2% of the pixels). Longer inundation times (163-560 hours) became notably more predominant (42.7% of the pixels) under a 0.8 m SLR scenario, while the probability of deep maximum depth (0.8-1.5 m) increases (23.9% of the pixels), although medium depth (0.4-0.8 m) was the most likely maximum depth condition (42.6% of the pixels). A reduction in inundation of 0.3 m from the current scenario shifted the study site to a smaller inundation area (with 75.9% of the pixels being not inundated).

5.4.2 Effects of scenarios on site habitability to tidal wetland vegetation

Under the current scenario, mudflat/saltpans were the dominant land cover (45.7% of pixels), followed by woodland (18.1%), herbaceous saltmarsh (17.9%), succulent saltmarsh (7.7%), and *Ceriops* spp. (7.5%). *A. marina/R. stylosa* represent 2.6% of the pixels (Figure 5.5). With an increase in SLR of 0.3 m, the system will likely shift towards a mangrove-dominated system with an increasing habitability of 21.1% for *Ceriops* spp., and 11.9% for mangroves. The extent of the main channel also increases from 0.5% of the pixels under the current situation to 2.9% under SLR +0.3 m. The habitability for saltmarsh vegetation decreased to 4.4% for succulent saltmarsh and to 9.2% for herbaceous saltmarsh. The site habitability for saltmarsh vegetation is predicted to be negligible under 0.8 m SLR with 1.12% for succulent saltmarsh and 2.7% for herbaceous saltmarsh. Habitability for *A. marina/R. stylosa* increased to 39.7%, although its habitability for *Ceriops* spp. decrease slightly from the 0.3 SLR scenario (20.3%). The main channel is predicted to occupy a considerably larger extent of the site, with 16.2% of pixels predicted to be the main channel under the 0.8 m SLR, which is 6 times and 33 times, respectively, greater than in the 0.3 m SLR and current scenario.

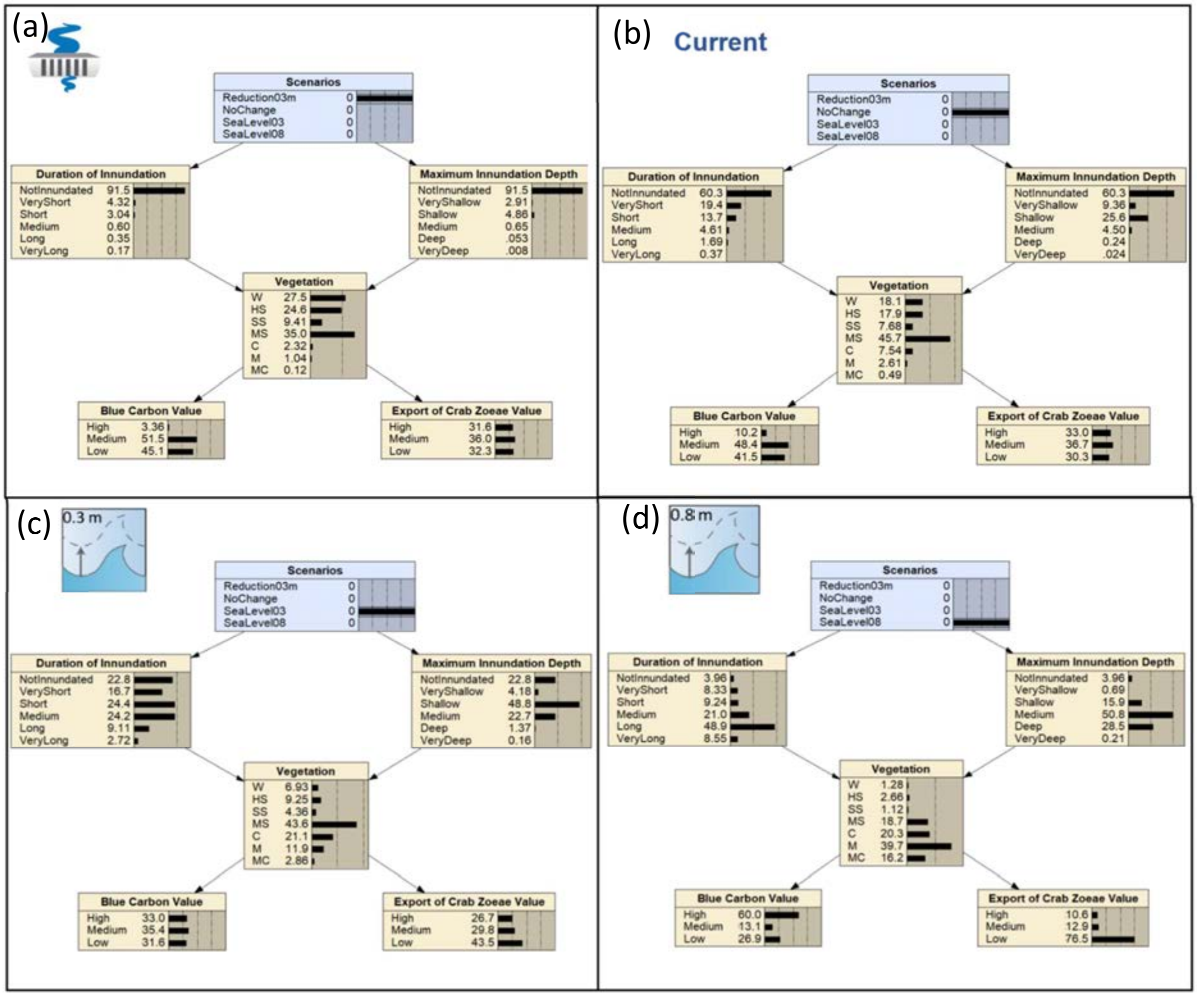


Figure 5.5 Bayesian belief networks predicting changes in the habitability of the study site to vegetation, and to hold blue carbon and crab zoea export value under (a) a reduction of 0.3 m in tidal inundation from the current average tide scenario; (b) current average tidal inundation conditions expressed as duration of inundation and maximum duration depth (see table 1 for explanation of the discrete states); (c) 0.3 m sea-level rise (SLR) scenario; and (d) 0.8 m SLR. "HS" = Herbaceous saltmarsh; "SS" = Succulent saltmarsh; "MS" = Mudflats/Saltpans; "C" = *Ceriops* spp.; "M" = *R. stylosa/A. marina* (abbreviated as "M" for mangroves other than *Ceriops* spp.*)*.

A reduction in inundation of 0.3 m from the current scenario will likely result in woodland/terrestrial vegetation increasing from 17.9% to 27.5%. Herbaceous saltmarsh remains the dominant vegetated tidal wetland (24.6%) and the habitability for succulent saltmarsh increases slightly (9.4%). The habitability for *A. marina/R. stylosa* and *Ceriops spp* decreased sharply to 1.04% and 2.3%, respectively.

5.4.3 Effects of scenarios on crab zoeae export and blue carbon values

Under current conditions, the likely probabilities of the site holding the export of crab zoea and blue carbon values are 36.7% and 48.4% respectively, charaterising a medium value (Figure 5.5). Under a 0.3 m SLR scenario, the probability of the site holding crab zoeae value decreases (low, 40.9%). Conversely, the probability of having a high blue carbon value increases from 10.2% to 33.0%. The 0.8 m SLR has important consequences for the ability of the site to hold a high crab zoea export value (10.6%), which becomes more likely low category (76.5%). On the other hand, the blue carbon value of the site becomes mainly high (60.0%) under a 0.8 m SLR.

A reduction of inundation of 0.3 m is predicted to be slightly less favourable for holding high crab export zoea value (31.6%), with a slight increase in the probability (low category, 32.3%) from the current conditions. A reduction in inundation markedly decrease the probability of having a high blue carbon value (3.4%).

5.4.4 Sensitivity analysis and model assessment

Sensitivity analyses were run separately on each child node for the current scenario. Vegetation was most sensitive to duration of inundation (23.1%) and maximum depth (16.4%). Blue carbon value was sensitive to vegetation (66.6%) but least sensitive to duration of inundation (13.2%) and maximum depth (7.6%). The export of crab zoea was most sensitive to vegetation (48.7%) and only slightly to duration of inundation (6.2%) and maximum inundation depth (1.4%).

The model reliably predicted the land cover percentage according to duration of inundation and maximum depth, with a RMSE between observed and simulated land cover percentage for the current scenario of 0.87%, a mean error between observed and simulated cover of 0.0043% and a coefficient of correlation R^2 of 0.99.

5.5 Discussion

5.5.1 Habitability to tidal wetland vegetation under likely SLR scenarios

The study predicts a decline in herbaceous and succulent saltmarsh with the expansion of mangroves and an increased main channel area, with near total loss of saltmarshes under the projected 0.8 m SLR scenario likely to eventuate by 2100 in the study region (Queensland, 2019). These predictions align with studies reporting losses in saltmarsh cover in response to mangrove encroachment associated with SLR (Krauss et al., 2011; Oliver et al., 2012; Saintilan & Rogers, 2013; Sandi et al., 2018). However, the present results contradict other studies that highlight that SLR may not lead to the disappearance of saltmarsh when local factors such as sediment dynamics and availability of space for saltmarsh retreat landward as well as tidal range, local topography, geomorphology, and vegetation type allow for saltmarsh adaptation (Alizad et al., 2018; Schuerch et al., 2018). For instance, Kumbier et al. (2022) identified mangrove encroachment into saltmarshes in a micro-tidal south-eastern Australian estuary under a 0.4-m and 0.9-m SLR scenario using an eco-morphodynamics model, but saltmarshes were able to extend landward and their cover increased slightly. Here, the approach only considered tidal wetland duration and inundation as predictors of the site habitability to tidal wetland vegetation under SLR and did not consider contextual and dynamic eco-geomorphological feedbacks (Kirwan et al., 2016), and the possibility for saltmarshes and terrestrial vegetation to migrate landward (Schuerch et al., 2018). Therefore, the modelled scenarios here are likely more representative of a "coastal squeeze" situation, where saltmarshes cannot migrate further inland (up elevation, horizontal migration) and adjust their elevation by sediment and biological accretion (vertical migration) (e.g., Borchert et al., 2018).

The present findings are important because they highlight that saltmarshes will be almost totally lost at the study site by the end of the century without the ability to adapt to SLR. This suggests that management efforts need to address the potential adaptation strategies (e.g., Sheaves et al., 2016; Wigand et al., 2017; Leo et al., 2019), that need to be implemented to alleviate the loss of saltmarsh ecosystems to SLR. If passive responses are chosen (e.g., no action, self-adaption, or abandon, Sheaves et al., 2016), it is important to carefully address the trade-offs associated with an increase in the likelihood of a shift to a mangrove-dominated system (see section 5.5.3), so that potential social, economical, and ecological consequences are anticipated.

5.5.2 Habitability to tidal wetland vegetation under a reduction in tidal inundation

A reduction in tidal height of 0.3 m has slightly positive effects on the habitability of the study site to saltmarsh, which were likely to expand at the expense of unvegetated flats and mangroves. This finding aligns with previous studies that indicate an increase in saltmarsh cover and reduced mangrove encroachment when using automated controlled tidal gates to counteract SLR and preserve saltmarshes in Australian tidal wetlands (Sadat-Noori et al., 2021; Rankin et al., 2023). Nevertheless, the type of saltmarsh vegetation advantaged by a reduction in inundation here contrasted with those studies. Specifically, the habitability of the site to *S. virginicus* increased more importantly (7%) compared to succulent saltmarsh (2%), contrasting with Rankin et al. (2023) where those authors observed an increase in succulent saltmarsh (*S. quinqueflora*) in the medium and high marsh, with little increase in herbaceous saltmarsh cover (*S. virginicus*) under a 0.45 m tidal height reduction. In addition, the BBN predictions suggest a 10% increase in the habitability of the study site to terrestrial vegetation under a 0.3 m decrease in tidal height, while Rankin et al. (2023) observed minimal changes in terrestrial vegetation cover. These contrasting results highlight that apparently “similar” habitats may respond differently to a reduction in tidal inundation across different locations. This highlights the need for careful consideration of site-specific nuances in saltmarsh areas (Waltham et al., 2021), including the extent and distribution of tidal wetland vegetation and their tidal inundation characteristics, when planning management strategies or urban development that involve altering tidal inundation, such as roads and culverts.

5.5.3 Probability of holding blue carbon and crab zoeae export values under SLR scenarios

The findings demonstrate that the impacts of SLR have contrasting effects depending on the components and values of the coastal ecosystem mosaic considered. The BBN predictions indicate that SLR scenarios and associated expansion in mangrove cover strongly enhanced the blue carbon value of the site, aligning with global trends that show expending mangrove cover has positive effects on carbon storage at the expense of saltmarsh loss (Kelleway et al., 2016; Rogers et al., 2019; Simpson et al., 2019). The increase in the probability of the site holding a high blue carbon value in the 0.3 m SLR scenario (21%) is notably similar to the measured increase in the carbon storage capacity (22%) of a Floridian mangrove-saltmarsh ecotone after ten years of encroachment (Doughty et al., 2016). By contrast, SLR negatively impacted the ability of the site to maintain a high crab zoea export value, especially under the 0.8 m SLR scenario where succulent saltmarsh loss considerably reduced the probability of the site holding a high crab zoea export value.

The decline in crab zoea export value under SLR scenarios raises concerns about the potential negative consequences of losing this functional process on coastal ecosystem productivity and intertidal biodiversity (e.g., saltmarsh crab diversity, Mazumder, 2009). The export of crab zoeae from saltmarshes is a unique feeding opportunity for small zooplanktivorous fish (Hollingsworth & Connolly, 2006; McPhee et al., 2015a), and the trophic relay that exists between saltmarsh production and coastal food webs (Mazumder et al., 2011). In addition, coastal productivity and functions are usually not linked to a segregated, unique component of the coastal ecosystem mosaic (Weinstein & Litvin, 2016). Rather, it is the synergies within the diverse components of the coastal ecosystem mosaic and their heterogeneity that support key coastal ecosystem functions and values, from supporting commercially important species (Meynecke et al., 2008; Taylor et al., 2018b; Scapin et al., 2022) to enhancing carbon and nitrogen sequestration (Saavedra-Hortua et al., 2023) and coastal protection (Koch et al., 2009). Therefore, it is possible that the predicted reduction in the heterogeneity of the coastal ecosystem mosaic under rising sea levels may negatively impact overall coastal productivity, with consequences such as a reduction in the provision of coastal ecosystem services (Gilby et al., 2021) and resilience to climate and anthropogenic changes (Bernhardt & Leslie, 2013; Aguilera et al., 2020; Li et al., 2021b; Wang et al., 2021b). It is therefore important that coastal management strategies consider future SLR projections and direct anthropogenic alterations in tidal inundation on these less “obvious” synergies within the coastal ecosystem mosaic - such as marsh trophic subsidies (Weinstein et al., 2014) and prey pulses (Chapter 4) - so that unexpected management and restoration outcomes can also be anticipated (Sheaves et al., 2021).

5.5.3 Probability of holding blue carbon and crab zoeae export values under a reduction in tidal inundation

The findings show the negative effects of a reduction in tidal inundation on both the crab export and blue carbon values, underlining the importance of maintaining tidal connectivity to support critical tidal wetland ecosystem functions and processes. Even what may appear as small reductions in tidal inundation (0.3 m reduction in tidal height and 25% of the study site being less inundated), could lead to important shifts in the ecological structure of tidal wetlands (e.g., loss of mangrove vegetation), which may subsequently alter the values and functions of tidal wetlands (Hyland, 2002; Abbott et al., 2020; Gilby et al., 2021). Coastal development and management decisions need to assess these broader implications when implementing barriers to tidal flow. By contrast, the increase in blue carbon and crab export values from the reduction in tidal inundation scenario and current scenario support that removing barriers to tidal flow may increase the blue carbon propositions (Kelleway et al. 2017a) and fisheries value (Abbott et al. 2020) of tidal wetlands under future SLR projections.

5.5.4 Implications for management and future studies

This study illustrates that a “whole-of-system” approach to understanding the components and processes in coastal ecosystems is necessary when considering the potential outcomes of direct (e.g. human disturbances) and indirect changes (e.g. climate change and hydrology changes). The study illustrates that looking at a particular component of a system (e.g., mangroves) separately from the others could lead to unforeseen consequences on other system components and their functions (Choi et al., 2022). Management and restoration strategies will therefore need a holistic approach that evaluate (and test the sensitivity) the potential outcomes of different scenarios and management strategies on multiple ecological values, such as those developed here or elsewhere, rather than focusing on one targeted ecosystem or outcome (e.g., planting mangroves over mudflats to increase carbon sequestration) (Choi et al., 2022). For instance, in the case of the study site, balancing multiple ecological benefits (e.g., fisheries and blue carbon) may require maintaining current tidal inundation patterns or allocating space for saltmarsh upward migration. This would result in keeping principally medium and high probabilities of holding both crab zoeae export and blue carbon values at the study site without considerably reducing one or the other. While we have illustrated this juxtaposition using SLR and a reduction in tidal inundation, this approach could be applied with other scenarios, such as planting mangroves over mudflats (e.g, Erftemeijer & In, 2000; Choi et al., 2022) or reconverting freshwater wetlands to intertidal ecosystems (Karim et al., 2021). In addition, adding information on other key values provided by tidal wetland ecosystems, such as bird breeding and foraging grounds (e.g., Spencer et al., 2009), and fish nursery value (e.g., Whitfield, 2017), would provide a more holistic understanding of the trade-offs and variability in outcomes given different scenarios of changes on key processes and patterns.

This study adds to the knowledge that simple BBNs are useful for preliminary assessments of the dilemmas and directions that may need to be taken when elaborating management or restoration strategies (McCann et al., 2006). This is important because one of the "proposed activities" under objective 1.3, "*Wetlands and other coastal ecosystems are managed from a "whole-of-catchment perspective*", of the "Wetlands in the Great Barrier Reef Catchments Management Strategy 2016-21" (Queensland, 2016) highlights the need to "*redevelop and encourage use of a decision support tool to improve management decisions and prioritization*" (p. 13, Queensland, 2016). BBNs are also useful for identifying thresholds and where more research should be allocated at a targeted study site. For instance, in the case of the study site, there is a need to obtain a better understanding of the additional potential important drivers of the observed vegetation patterns (e.g., groundwater flow, nutrient availability) (Chapter 3) as well as whether local topography and anthropogenic context enable landward migration (e.g., Borchert et al., 2018) and sediment supply and subsurface processes (e.g., plant growth, decomposition, subsistence) (Lovelock et al., 2011; Beckett et al., 2016) enable saltmarshes to keep up with the vertical pace of SLR. Applying a similar BBN workflow using these additional variables in the responses of tidal wetland vegetation to SLR would be necessary to decrease uncertainties in the predictions.

Contextual variably in site structure (e.g., proportion of saltmarsh and mangrove cover) and functions (e.g., Bradley et al., 2020; Ziegler et al., 2021) also imply that each site may have unique trade-offs and dilemmas. Different sites may require different management responses (Waltham et al., 2021), and some sites (e.g., Ramsar wetlands, Sadat-Noori et al., 2021; Rankin et al., 2023) may be prioritised for management actions over other sites. For instance, in the case of the three study sites, the site with the highest saltmarsh cover and crab zoeae export value (i.e., Jerona, Site B) may be prioritised for saltmarsh management over the main study site (Site A), whose saltmarsh cover was lower and affected by 4-wheel vehicle driving (Chapter 2). Managers could use similar BBN approaches to identify sites that should be prioritised for management and restoration programs.

5.6 Conclusion

Predicting future changes in the values of coastal ecosystems is challenging due to the important complexity of interacting factors shaping coastal processes together with the high uncertainties in those processes. Concurrently, managers are increasingly challenged to make management decisions with little understanding of how these decisions benefit non-targeted values. The present study has demonstrated the potential of BBN in identifying how different tidal wetland values (e.g., habitability for a certain type of vegetation) might shift due to changes in tidal wetland inundation due to SLR or human interventions. In addition, this study advocates for BBN as a decision tool that may be useful for managers to identify trade-offs when considering management strategies in response to increasing SLR over other scenarios of changes in tidal inundation and tidal wetland vegetation.

Chapter 6:General Discussion

6.1 Synthesis of key findings implications for scientific advancement and effective management

This thesis investigated the extent to which tidal hydrological connectivity (expressed as tidal hydroperiod and the extent of tidal wetland inundation) mediate important ecological patterns (i.e., vegetation distribution) and processes (i.e., prey pulses) within a tropical estuarine complex composed of saltmarshes, mangroves and unvegetated flats. The spatially explicit eco-hydrological approach applied here provided important insights into the connectivity, distribution patterns, and ecological values of saltmarshes in a tropical context. This thesis addressed key knowledge gaps identified in the systematic review conducted in Chapter 1. Specifically, this thesis examined: 1) the uses of novel technologies in tropical saltmarshes hydrology and ecology (Chapter 2); 2) tropical saltmarsh vegetation distribution patterns in relation to tidal hydroperiod and elevation (Chapter 3); 3) the potential effects of sea-level rise (SLR scenarios) on tropical tidal wetland vegetated and unvegetated cover hydroperiod and inundation patterns (Chapter 3); 4) the role of tropical saltmarshes as producers of trophic subsidies via the export of crab zoeae and the influence of tidal connectivity on this process (Chapter 4); and finally, 5) the contrasting effects of varying sea levels due to climate change and anthropogenic modifications on tidal wetland structure and functions (Chapter 5). Notably, this thesis has found that: 1) High-resolution topographic and land cover data can be derived from Unattended Aerial Vehicle (UAV)-Structure from Motion photogrammetry (SfM) workflow to derive a high-resolution tidal inundation hydrodynamic model and are important to understand low-relief topographic terrains and tidal wetland inundation patterns and hydroperiods (Chapter 2); 2) Tidal hydroperiod and elevation influence tidal wetland vegetated and unvegetated cover distribution, although these variables did not fully explain distribution patterns (Chapter 3); 3) Patterns in crab zoea prey pulse export from tropical tidal wetlands align with observations from temperate and subtropical saltmarshes and are importantly mediated by tidal connectivity (Chapter 4); and 4) Changes in tidal inundation patterns due to SLR reduced saltmarsh cover and the probability of the site in holding crab zoea export value while increasing mangrove cover and blue carbon value. Conversely, reducing tidal inundation decreases both crab zoea export and blue carbon values (Chapter 5).

Overall, the findings of the thesis can be summarised into six main points: 1) The importance of tidal connectivity; 2) Beyond tidal connectivity, 3) Understanding contexts and avoiding generalisations on saltmarshes functioning and ecological value; 4) Viewing saltmarsh as integrated components of the remaining coastal ecosystem mosaic; 5) Anticipating future changes; and 6) The importance of novel technologies. The methods and knowledge developed in this thesis should contribute to a more comprehensive understanding of saltmarsh functioning (Figure 6.1) and the management and restoration of tropical coastal seascapes.

6.2 The importance of tidal connectivity

This thesis highlights the important role of tidal connectivity in mediating tropical intertidal vegetation distribution patterns and ecological processes (Chapters 1-5). Tidal hydrological connectivity patterns influence the distribution of tidal wetland vegetation (Chapter 3) and prey pulse export under the form of crab zoeae (Chapter 4). Overall, the findings support previous evidence of the importance of maintaining tidal connectivity within the coastal ecosystem mosaics and placing a central role to tidal connectivity in saltmarsh studies, restoration and management (Ziegler et al. 2021; Waltham et al., 2021; Chapter 1). Yet, this thesis emphasises that understanding tidal hydrological patterns of saltmarshes is complex (Chassereau et al., 2011; Moffett et al., 2012; Ziegler et al., 2021, Chapter 1). Tidal connectivity in low-lying terrain such as saltmarshes is influenced by seemingly slight micro-

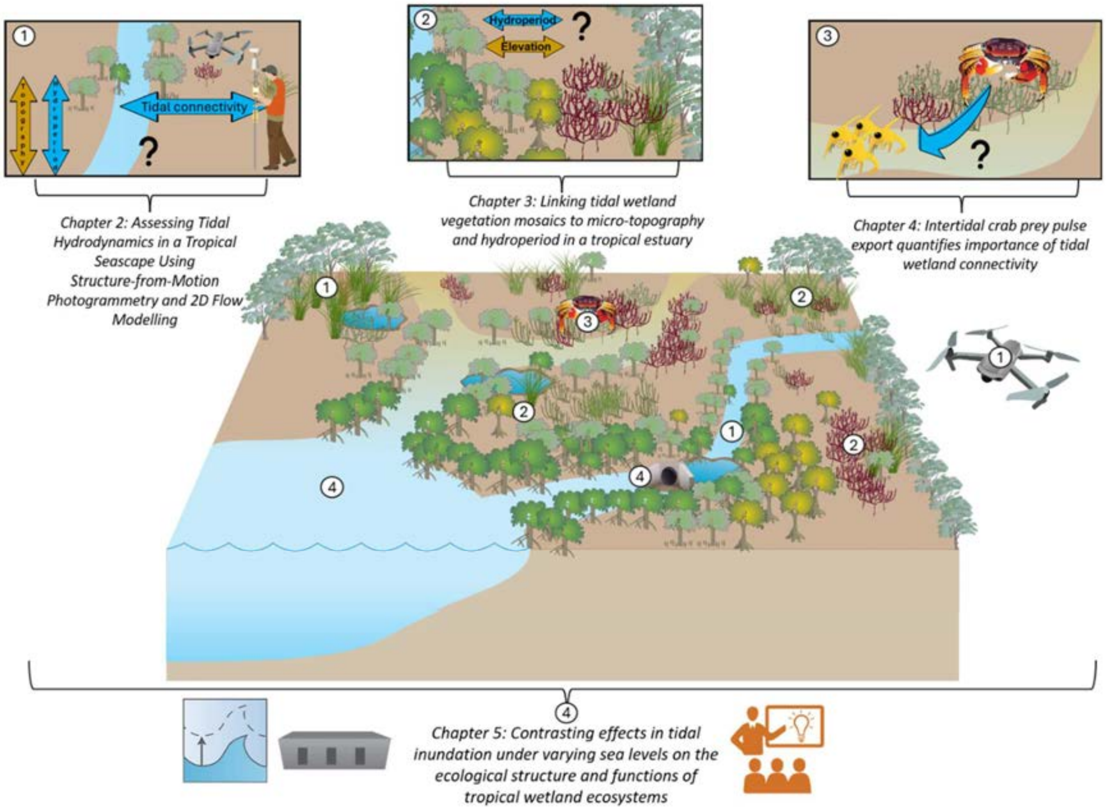


Figure 6.1 Summary of the contributions and key findings of the thesis where: (1) novel technologies were used to derive high-resolution digital elevation model and land cover data. These data were used to parameterise a two-dimensional hydromodel of saltmarsh tidal inundation; (2) the models developed in (1) were applied to assess the distribution of tidal wetland vegetated and unvegetated cover in relation to hydroperiod and elevation; 3) the information developed in (1) and (2) were related to the export of prey pulses from intertidal crab to understand the extent to which this value of temperate and subtropical saltmarsh is also held in tropical seascapes and to what extent it is influenced by tidal inundation patterns and the extent of tidal connectivity; and (4) A decision tool (Bayesian Belief Network) was used to assess the potential effects of sea-level rise and a reduction in tidal inundation on the habitability of the site to tidal wetland vegetation and the probability of the site in holding crab zoea export and blue carbon value. Overall, the thesis highlights the importance of a whole-of-system approach when developing ecological and hydrological studies on saltmarshes, as well as strategies for their management and restoration.

topographic features such as small drains (Chassereau et al., 2011) and vehicle tracks (Chapter 2). Tidal connectivity is also highly variable, displaying variability according to small changes in tidal height (Chapter 2) and across lunar months characterised by average and non-average spring tides (Chapter 3). Therefore, a comprehensive understanding of tidal wetland inundation patterns requires accurate, high-resolution topographic data and careful parameterisation and calibration of two-dimensional (Chapter 2) or three-dimensional hydromodels (Kumbier et al., 2022). The Unattended Aerial Vehicle (UAV)-Structure from Motion photogrammetry (SfM) workflow developed in Chapter 2 represents an accurate and affordable workflow that may be particularly useful for coastal managers to develop a contextual understanding of tidal connectivity patterns and hydroperiod (Chapters 2, 3, and 4) at targeted sites.

6.2 Beyond tidal connectivity

While tidal inundation patterns considerably influenced the distribution patterns of tidal wetland vegetation and the export of crab zoeae at the study site, the findings also highlight that understanding the dynamics and ecological functions of tidal wetlands should not be limited to understanding tidal hydroperiod and tidal connectivity. Specifically, the study revealed that hydroperiod and elevation did not fully explain tidal vegetation distribution patterns (Chapter 3). In addition, not all tidal connections resulted in prey pulse export (Chapter 4). This suggests that other factors beyond the tidal hydroperiod (e.g., groundwater dynamics, crab requirements, and reproductive strategies) also contributed in the observed patterns and processes. These findings are important because management and restoration strategies often apply outdated restoration paradigms, such as that tidal connectivity equals ecological connectivity (Liu et al., 2016), and that the management or restoration of tidal connectivity will guarantee "ecological recovery" (*sensu* Hilderbrand et al., 2005). However, while monitoring and managing tidal connectivity should be central to saltmarsh ecological studies (Ziegler 2021, Chapter 1), as well as management and restoration, it is important that restoration success goes beyond restoring and monitoring tidal connectivity to include an appraisal of additional physical and ecological processes and patterns that support saltmarsh functions (Figure 6.2) (Weinstein et al., 2014; Ziegler et al. 2021; Chapter 1).

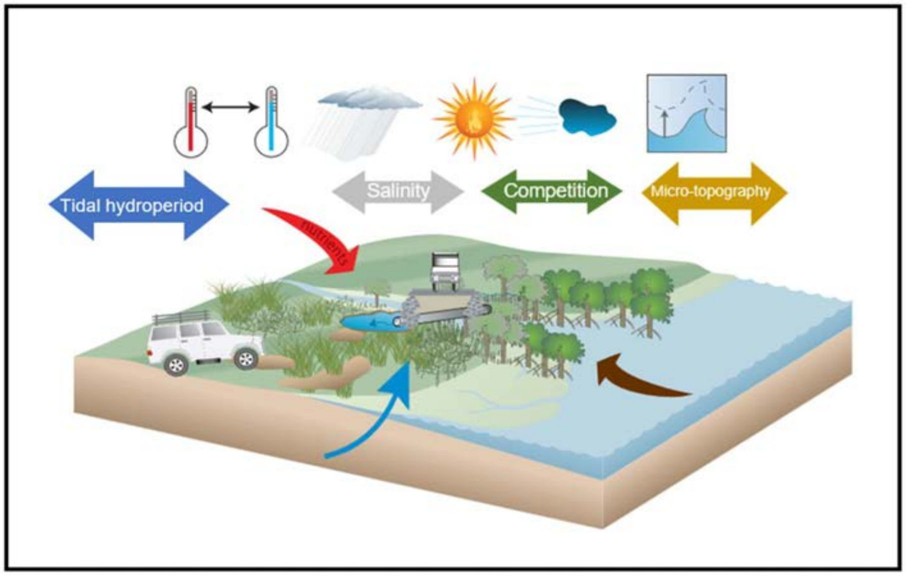


Figure 6.2 Conceptual representation of the potential contextual factors, in addition to tidal connectivity, that may influence the distribution of tidal wetland vegetation and tidal wetland functions in a tropical landscape. An explanation of the factors linked to tidal wetland vegetation distribution and references studies are found in Chapter 3, Table 3.3

6.3 Understanding contexts and avoiding generalisations on saltmarshes functioning and ecological value

The importance of determining saltmarsh functioning and functions according to the specific contexts in which saltmarsh occurs (Ziegler et al. 2021; Chapter 1) was highlighted throughout this study. Specifically, the investigations of crab zoeae export in Chapter 4 identified that the inundation of succulent saltmarshes, *Ceriops* spp., and unvegetated flats was correlated with the export of crab zoeae (Chapter 4). However, this study found that: 1) 30% of succulent saltmarsh found appeared not to be connected to tidal flow even during the higher-than-average tides of the year (Chapter 3), and 2) an average of only 25% of succulent saltmarsh were connected when the highest densities of crab zoeae were recorded (Chapter 4), suggesting that not all succulent and herbaceous saltmarshes were uniformly functioning and supporting prey pulse export. These findings highlight that the presence of saltmarsh vegetation does not necessarily imply that one location necessarily shares the same functioning and values as another location (Figure 6.3). This finding is particularly important because management and restoration strategies are usually based on the concept that the values and functions of saltmarshes (and mangroves) are uniform, generalisable and transferable across estuaries due to the presence of a “similar type of habitat” (e.g., saltmarshes or mangroves- “vegetation-based” or “habitat-based” approaches) (Figure 6.3) (Zhao et al., 2016; Sheaves, 2017). However, anthropogenic, biological and physical contexts (Figure 6.3) may influence the functioning and functions of ostensibly “similar habitats” (Bradley et al., 2020; Ziegler et al., 2021, Chapter 1) and, therefore, the ways saltmarsh should be managed, restored, or prioritised for management (Sheaves et al., 2021; Waltham et al., 2021). Therefore, management and restoration strategies must move beyond a “vegetation-based” or “habitat-based” management approach (Bradley et al., 2020), and place a stronger emphasis on the contextual patterns and processes that shape saltmarsh functions and values (context-based management approaches).

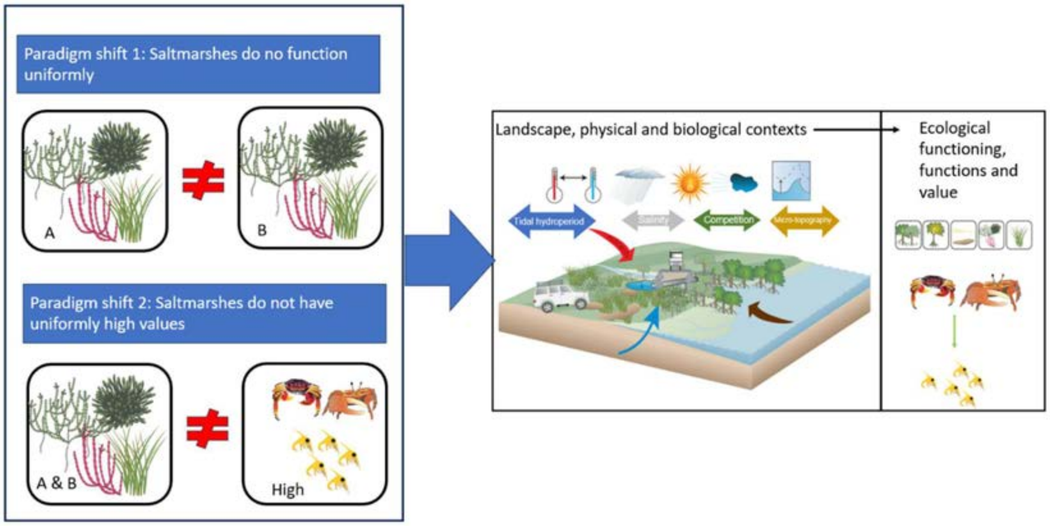


Figure 6.3 Management and restoration strategies should move beyond decisions motivated by generalised paradigms to a deeper contextual understanding of the landscape, physical and biological factors that may influence saltmarsh functioning, functions and value - and therefore how their management or restoration should be approached.

6.4 Viewing saltmarsh as integrated components of the remaining coastal ecosystem mosaic

This thesis outlines that saltmarsh should not be considered an isolated component of the coastal mosaic (Weinstein et al., 2014). Saltmarsh functioning and values are influenced by processes extending beyond their boundaries, such as tidal fluctuations (Chapters 2 and 3), crab reproductive strategies, and related prey pulse export (Chapter 4). The mosaic and overlapping patterns in tidal wetland vegetated and unvegetated covers (Chapter 2) also suggest that the distribution of saltmarshes is not well-segregated or isolated from the other components of the coastal ecosystem mosaic, but rather spatially interconnected within it. In addition, Chapter 5 illustrated that assessing the effects of potential changes in inundation on a single component of the coastal ecosystem mosaic, or a single value, such as blue carbon storage, may overlook broader impacts on other aspects of the coastal ecosystem mosaic. These findings are important because legislation, management, and restoration approaches often target individual habitats or ecosystems (Figure 6.4) without addressing broader connectivity patterns (Weinstein et al., 2014; Elphick et al., 2015; Yang et al., 2018; Waltham et al., 2019). However, the life cycle strategy of estuarine organisms rarely relies on a single habitat (e.g., nekton and crab ontogenetic migrations) (Nagelkerken et al., 2015; Whitfield, 2017). In addition, even at the patch scale, facilitating relationships between mangroves and saltmarshes (Silliman et al., 2015; Ghosh et al., 2022) highlights the complex interconnectivity among seemingly different tidal wetland components. This interconnectivity among system components suggests that altering one or the other may have unforeseen consequences on the overall ecological functioning and value of coastal ecosystems (Weinstein & Litvin, 2016). Overall, these observations outline the importance of ecological studies as well as management and restoration efforts that integrate broader linkages among multiple components of the coastal ecosystem mosaic (e.g., fish migration, prey pulses, trophic linkages) (Weinstein et al., 2005; Sheaves, 2009; Jonsson et al., 2021; da Silva et al., 2022. Therefore, assessing potential effects of management strategies or scenarios of future changes (e.g., climate, anthropogenic) on the whole system rather than on individual, isolated components requires careful consideration by managers (Figure 6.4) (Elphick et al., 2015; Yang et al., 2018; Yang et al., 2021).

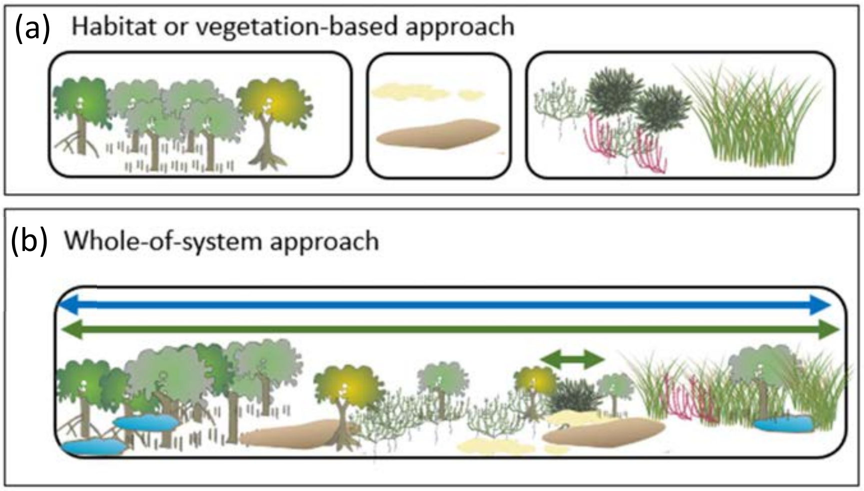


Figure 6.4 Traditional “habitat-based” or “vegetation-based” management approach (a) by opposition to a whole-of-system approach that considers heterogeneity and synergies among components at the patch to system scale

6.5 Anticipating future changes

This study has provided supporting evidence that sea-level rise (SLR) may change current connectivity patterns at the study site (Chapter 3), influencing the site habitability for saltmarsh vegetation and its ecological values (Chapter 5). Therefore, anticipating that current tidal connectivity, and saltmarsh and mangrove distribution, may change in the foreseeable future due to climate change and direct human uses of the coastal landscape (Ury et al., 2021; Chapter 3; Chapter 5) should be central to management and restoration strategies (Duke et al., 2017; Sheaves et al., 2016; Sheaves et al., 2021). Decision tools such as

Bayesian Belief Networks offer an efficient means to identify possible future challenges related to climate change or coastal urbanisation (Chapter 5). They may be particularly useful in guiding the decision-making process in developing efficient restoration and management strategies (Choi et al., 2022) and evaluating environmental risk (Malekmohammadi et al., 2023) in the face of climate change.

6.6 The importance of novel technologies

This study demonstrated the potential of novel technology (UAV-SfM) to advance our understanding of saltmarsh tidal connectivity (Chapters 2-4), topography (Chapters 2 and 3) and wetland vegetation distribution patterns (Chapter 3). The present research constitutes a pioneer application of UAV technology in tropical tidal wetland hydrology and ecology. It may serve as a benchmark study to guide further studies and novel applications of UAVs in tropical saltmarshes - where applications of UAV technologies in tropical saltmarsh research have been particularly lacking (Chapter 1). The increasing availability of more accurate UAV sensors (LiDAR-UAV, Pinton et al., 2021; multi-spectral-UAV, Nardin et al., 2021) and high-resolution satellite data (e.g., Sentinel-2 multi-spectral imagery, González et al., 2023), further improve our understanding of saltmarsh functioning, and their applications in tropical tidal wetlands should be addressed in future studies (see section “6.7 Challenges and directions for future studies; Table 6.1). Overall, this study adds to the evidence of the benefits of novel technologies in tidal wetland ecology (Kalacska et al., 2017). Through standardised, multidisciplinary, and collaborative applications (Waltham et al., 2021), novel technologies should advance our abilities to monitor and understand tidal wetlands (Kimball et al., 2021), while contributing to their management and restoration (Waltham et al., 2021).

Overall, the findings of this thesis can be summarised in a simple framework (Figure 6.5) that emphasises the importance of: 1) defining the current contextual patterns and processes that may influence the values and functions of a tidal wetland site (Weinstein et al., 2014; Weinstein & Litvin, 2016): 2) evaluating potential scenarios of changes on the functioning and functions of a site, and hence potential long-term management or restoration outcomes (Sheaves et al., 2021): and 3) refining strategies as new knowledge become available through monitoring and experiments ("adaptive management", Zedler, 2017; Waltham et al., 2021), where novel technologies may play a central role (Kimball et al., 2021).

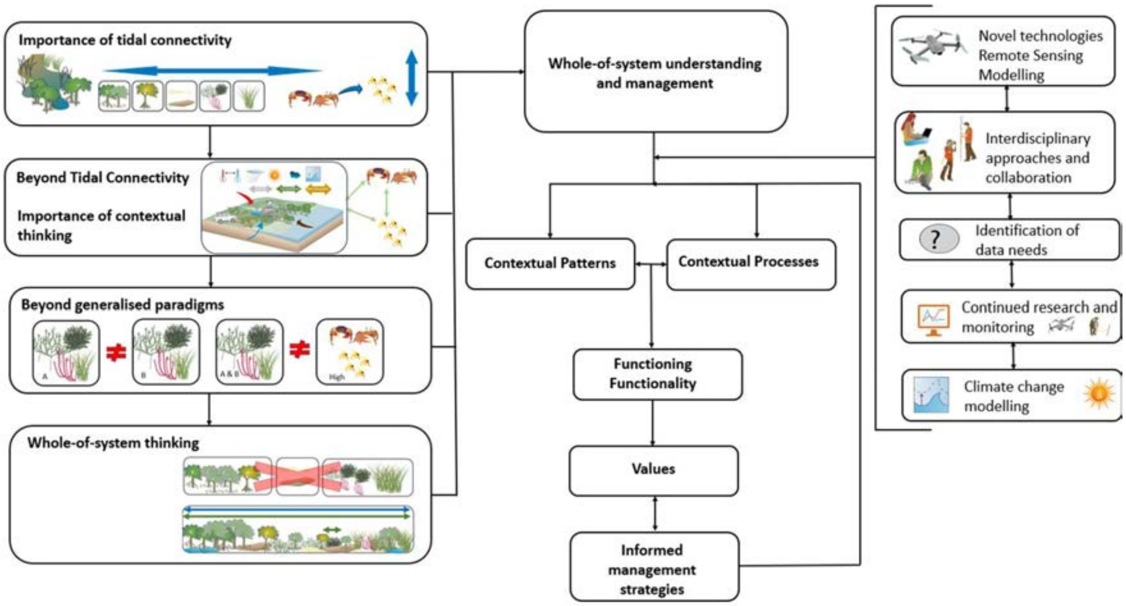


Figure 6.5 Conceptual framework summarising some of the central aspects that need to be considered to move towards a whole-of-system management and understanding of tropical saltmarshes. These aspects have been discussed throughout this thesis.

6.7 Challenges and directions for future studies

The eco-hydrological approach developed throughout this thesis would benefit from additional studies related to the modelling, ecological and modelling and ecological aspects of the study (Table 6.1). Specifically, this study encountered some modelling challenges related to the digital elevation model and hydrodynamic modelling accuracies that would benefit from more examination (see Table 6.1 for detailed challenges and examples of future studies). In addition, only topographic and tidal data were used to parameterise the two-dimensional hydromodel (Chapter 2) that was used to understand tidal inundation patterns (Chapters 2-4). Similarly, only elevation and hydroperiod were considered as potential drivers of tidal wetland distribution (Chapter 3). The approach did not consider potentially important additional factors, such as groundwater dynamics, past rainfall, the effects of atmospheric pressure, wind-induced waves, soil properties, and biological feedback (e.g., root-soil hydrology dynamics), that may contribute to the eco-hydrological patterns (Chapters 2 and 3). The development of multifactorial approaches that reflect these dynamics (e.g., Moffett et al., 2012; Xin et al., 2022) needs to be an area of prioritised research in our understanding of saltmarsh-mangrove distribution in the tropics (Chapter 1), but also higher latitudes (Rogers & Krauss, 2019; Pétillon et al., 2023).

This thesis has emphasised that there are uncertainties in our understanding of saltmarsh responses to SLR due to limited data on the effects of SLR on saltmarshes in this region - such as related to eco-geomorphologic dynamics and accommodation of space for landward (elevation up) migration (Chapters 3 and 5). Obtaining quantitative data on saltmarsh accretion rates and sediment dynamics, and modelling the responses of saltmarshes and mangroves to SLR using eco-morphodynamic modelling approaches (Kumbier et al., 2022) should be a priority for future research in tropical seascapes. This knowledge is particularly important given the increasing threats of SLR to saltmarsh vegetation (Chapters 1,2, and 5) and important ecological processes such as the export of prey pulse by intertidal crabs (Chapter 5). A better understanding of how saltmarshes will respond and adapt to SLR will enable effective, long-term management and restoration strategies to be developed with greater certainty of future outcomes.

Table 6.1 Limitations, challenges, and directions for future studies in tropical saltmarshes together with examples of studies where this has been raised. “Type” refers to whether the limitations/challenges/questions address mostly modelling, modelling and ecological or ecological dimensions. “Discussed” refers to the chapter in which the limitations/challenges/questions were addressed in more depth. “*” indicates that the research aspect/question was included in the early genesis of the thesis but was not carried on due to methodological challenges determined during pilot studies (i.e., fish habitat uses of saltmarshes and crab population distribution) or time constraints (i.e., crab dietary studies).

Type	**Challenges or needs of more research**	**Examples of studies**	**Directions for future studies**	**Further details in thesis**
Modelling	Digital Elevation Model (DEM) inaccuracies	Pinton et al., 2020; Pinton et al., 2021 Islam et al. (2022b)	-Uses of Light Detection and Ranging (LiDAR)-Unattended-Aerial-Vehicle (UAV)	Chapter 2
Modelling	Potential 2D-hydromodelling inaccuracies due hydromodelling parameter choice	Alizad et al. (2016a); Symonds et al. (2016); Kumbier et al. (2022)	-Uses of additional parameters (e.g., wind, soil parameters) -Uses of the Shallow Water Equation -Uses of 3D hydrodynamic modelling software	Chapter 2
Modelling	Manual classification of land cover features due to poor classification outcomes with supervised and unsupervised classification	Nardin et al. (2021); González et al. (2023); Pinton et al. (2020); Cao et al. (2021)	-Uses of multi-spectral UAV - Development of classification algorithms specific to coastal ecosystems	Chapters 2 & 3
Modelling & Ecological	Limited factors in the modelling approach of tidal wetland distribution (e.g., groundwater dynamics not included) – only hydroperiod and elevation variables were included	Moffett et al. (2012); Xin et al. (2022)	-Surface and subsurface hydromodelling -Multifactorial modelling	Chapter 3
Modelling & Ecological	Availability of space for saltmarsh landward migration not assessed	Schuerch et al. (2018); Kumbier et al. (2022)	-Geospatial assessement of space availability for landward migration landward of saltmarsh position -Model saltmarsh dynamics under SLR with and without availabilty of space for landward migration	Chapters 3 & 5
Modelling & Ecological	2D modelling approach to SLR (sediment and biological dynamics not assessed and incorporated in modelling, vertical accretion dynamics not assessed)	Kirwan and Megonigal (2013); Fagherazzi et al. (2012); Best et al. (2018); Kumbier et al. (2022)	-Gather and integrate data on saltmarsh accretion and sediment dynamics - Gather and integrate data on eco-geomorphic feedbacks -Uses of dynamic 3D eco-geomorphic models	Chapter 3
Ecological	On-ground crab or crab burrows distribution not assessed	Mazumder and Saintilan (2003); Vermeiren and Sheaves (2014b); Herrera et al. (2020)	-On-ground assessments of crab distribution	Chapter 4 *
Ecological	Assimilation of prey pulses by fish not assessed	Hollingsworth and Connolly (2006); Mazumder et al. (2011)	-Fish dietary studies	Chapter 4 *
Ecological	Seasonal variability in crab zoeae in mangrove dominated estuaries not assessed	Robertson et al. (1988)	-Additional contextual research on the seasonal variability in crab zoeae export in tropical mangroves	Chapter 5
Ecological	Poor understanding of tropical saltmarshes values (e.g., blue carbon; fisheries)	Radabaugh et al. (2023); Waltham et al. (2023)	-Additional contextual research on the values and functions of tropical saltmarshes	Chapter 5
Ecological	Diet of upper intertidal crabs	Guest and Connolly (2005); Guest et al. (2006); Mazumder and Saintilan (2010)	-Trophic support of intertidal crabs depending on contexts (e.g., patch size, dominant vegetation cover)	*
Ecological	Fish direct uses of saltmarsh	Thomas and Connolly (2001)	-What are the patterns of fish habitat uses of tropical saltmarshes?	*

Additional directions for future studies relate to obtaining further ecological understanding of tropical saltmarsh functions and values (Table 6.1). For instance, obtaining an understanding of the role of saltmarshes to crabs (e.g., diet and habitat) (Guest & Connolly, 2005; Mazumder, 2009) as well as the extent to which fish visit inundated saltmarshes (Thomas & Connolly, 2001) would extend our understanding of the values of saltmarsh to aquatic fauna. In addition, dietary studies on the assimilation of crab prey pulse export (Hollingsworth & Connolly, 2006) would provide further evidence of the importance of crab zoea prey pulses to estuarine fish production. Further examples of directions for future studies are found in Table 6.1.

6.8 Final conclusion

Situated at the interface between tropical grasslands and aquatic biomes, tropical saltmarshes are fascinating ecosystems, that are able to thrive with considerable variability in their environment, while playing key roles in supporting ecological functions more broadly in the coastal estuarine mosaic. Yet, tropical saltmarshes are threatened by climate change and human activities. They are also considerably understudied. Therefore, developing a better understanding of the functioning and functions of saltmarshes in tropical seascapes is important to address the management and restoration of tropical seascapes more effectively. Overall, this study has: 1) contributed to filling important knowledge gaps identified in the systematic literature review conducted in Chapter 1; 2) emphasised the importance of contextual-based and whole-of-system approaches to study and manage tropical tidal wetlands; and 3) provided methodological tools and guidelines for future studies to develop a more holistic understanding and management of saltmarsh ecosystems. Together, this study is, to the best of my knowledge, the first to have developed: 1) an application of UAV-SfM to develop a two-dimensional hydromodel of tidal inundation dynamics in a tropical complex composed of saltmarshes, mangroves, and unvegetated flats; 2) a high-resolution assessment of tropical tidal wetland vegetated and unvegetated cover distribution in relation to elevation and tidal hydroperiod; and 3) a detailed eco-hydrological study of prey pulses export under the form of crab zoeae from upper tropical tidal wetland habitats – which also constitutes the first study to have conducted such eco-hydrological assessments in Australia and the tropics. Overall, this work has provided important insights into the ecological functions and values of tropical saltmarshes, which should encourage further research into these understudied but important and threatened ecosystems.

REFERENCES

Appendix A

Associated to Chapter 2 "*Assessing tidal hydrodynamics in a tropical seascape using structure-from-motion photogrammetry and 2D flow modelling*".

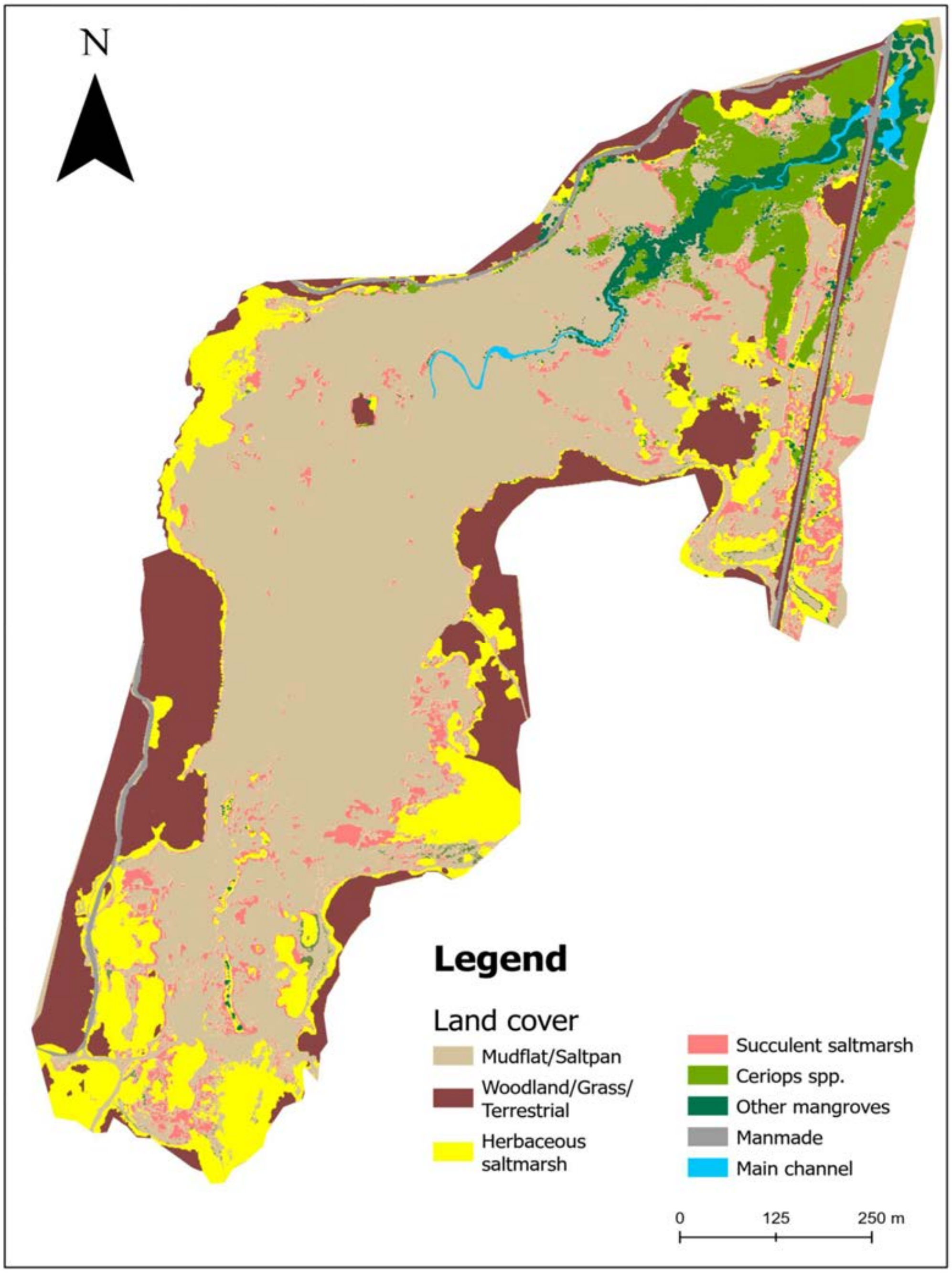


Figure A1 Land cover classified from the orthomosaic generated from Unoccupied Aerial Vehicle (UAV)- structure from motion photogrammetry (SfM).

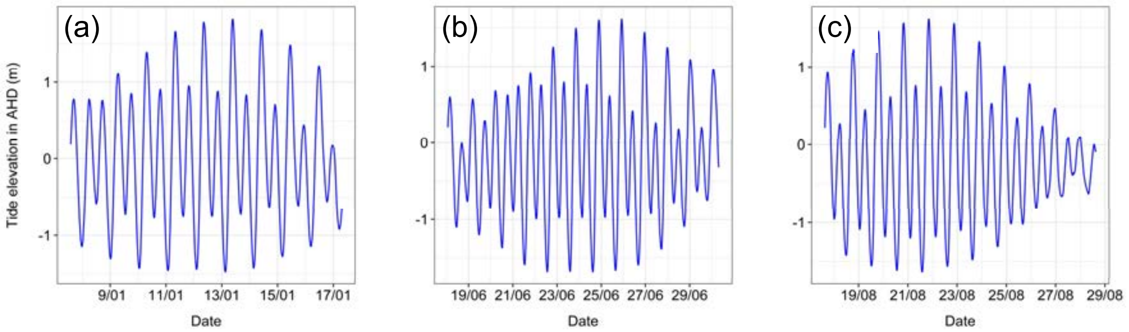


Figure A2 Stage hydrograph (tidal flow data in Australian Height Datum (AHD) taking into account the 0.35 m offset) used at the boundary condition of the (a) January, (b) June, and (c) August simulations.

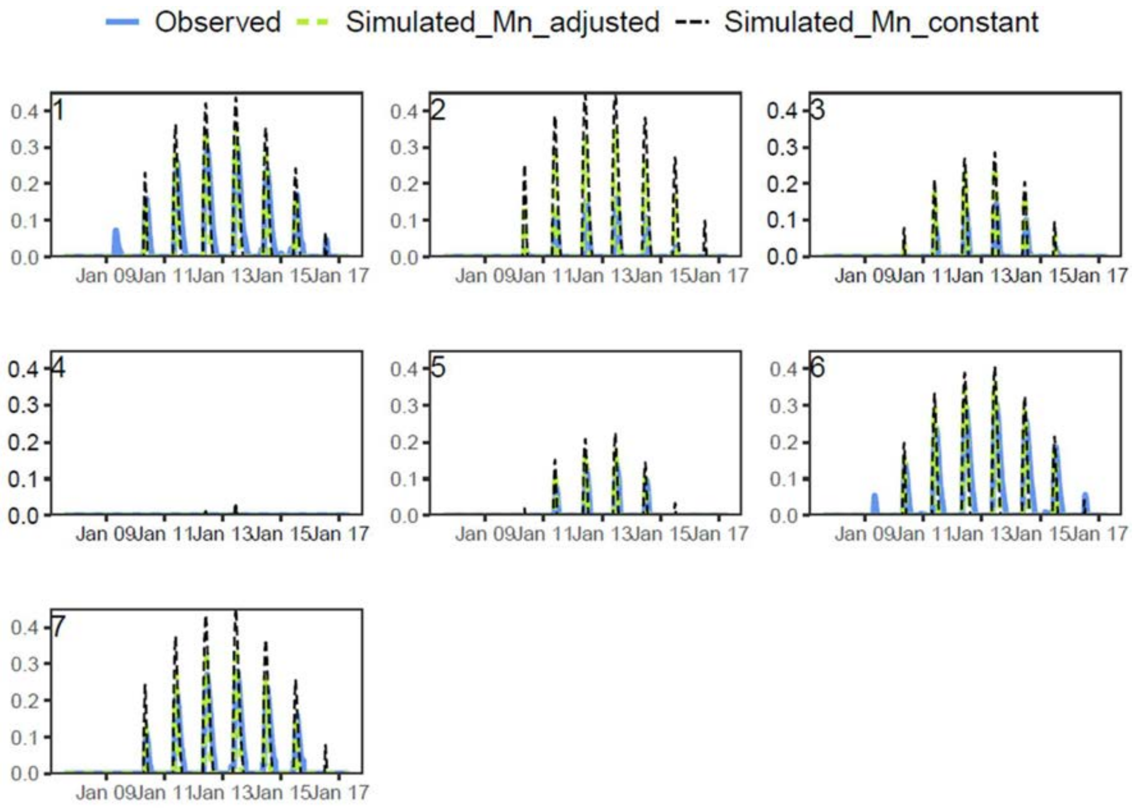


Figure A3 Examples of model performance based on water depth fluctuations computed with a constant Manning's value of 0.035 ("Simulated_Mn_constant") and with the values adjusted to the corresponding land cover ("Simulated_Mn_adjusted"). The detailed Manning's n values can be found in the Table 4 in the main manuscript. The number in the upper-left side of the box correspond to a depth logger deployed in the field ("observed") whose positions can be cross-checked with Fig 2b in the main manuscript.

Table A1 Correlation coefficients (R^2) and Root Mean Square Error (RMSE) between observed (depth loggers) and simulated (HEC-RAS simulations) depth at each logger position if the delay in arrival time and maximum depth (time difference) is adjusted to maximise model performance (R^2 and RMSE). Decrease performance means that delaying arrival time did not increase performance. The table shows that if the model could have simulated water arrival 20-60 minutes later, the overall model performance (R^2 and RMSE) would have been improved.

Logger	Simulation timing adjusted for delay		Time Difference (minutes)
	R^2	RMSE	
1	0.845	0.0294	60
2	0.946	0.0401	60
3	NA	NA	Decrease performance
4	NA	NA	
5	0.907	0.0170	60
6	0.833	0.0448	60
7	0.85599	0.0392	50
8	NA	NA	Decrease performance
9	NA	NA	
10	NA	NA	
11	0.834	0.003	30
12	0.826	0.006	20
13	0.786	0.009	20
14	0.882	0.050	50
15	0.813	0.0483	40
16	Null	0	
17	0.255	0.0456	60
18	0.789	0.032	40
19	0.818	0.050	60

Appendix B

Associated to Chapter 3: "*Linking tidal wetland vegetation mosaics to micro-topography and hydroperiod in a tropical estuary*".

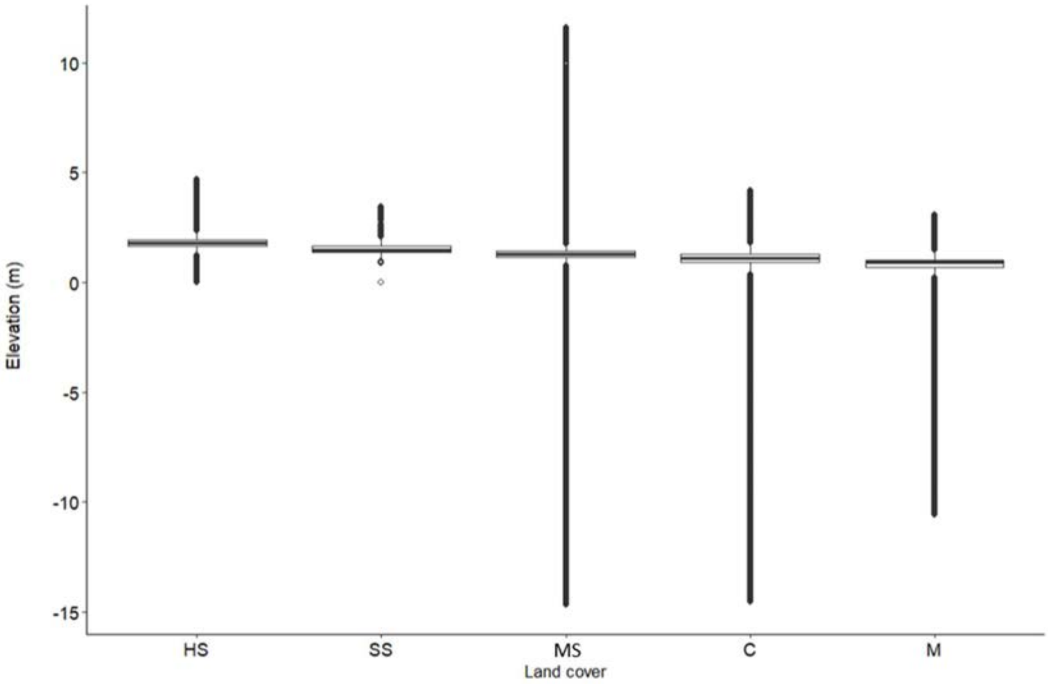


Figure B1 Boxplot of the distribution of elevation per land cover extracted from on 10-cm spaced land cover data points.

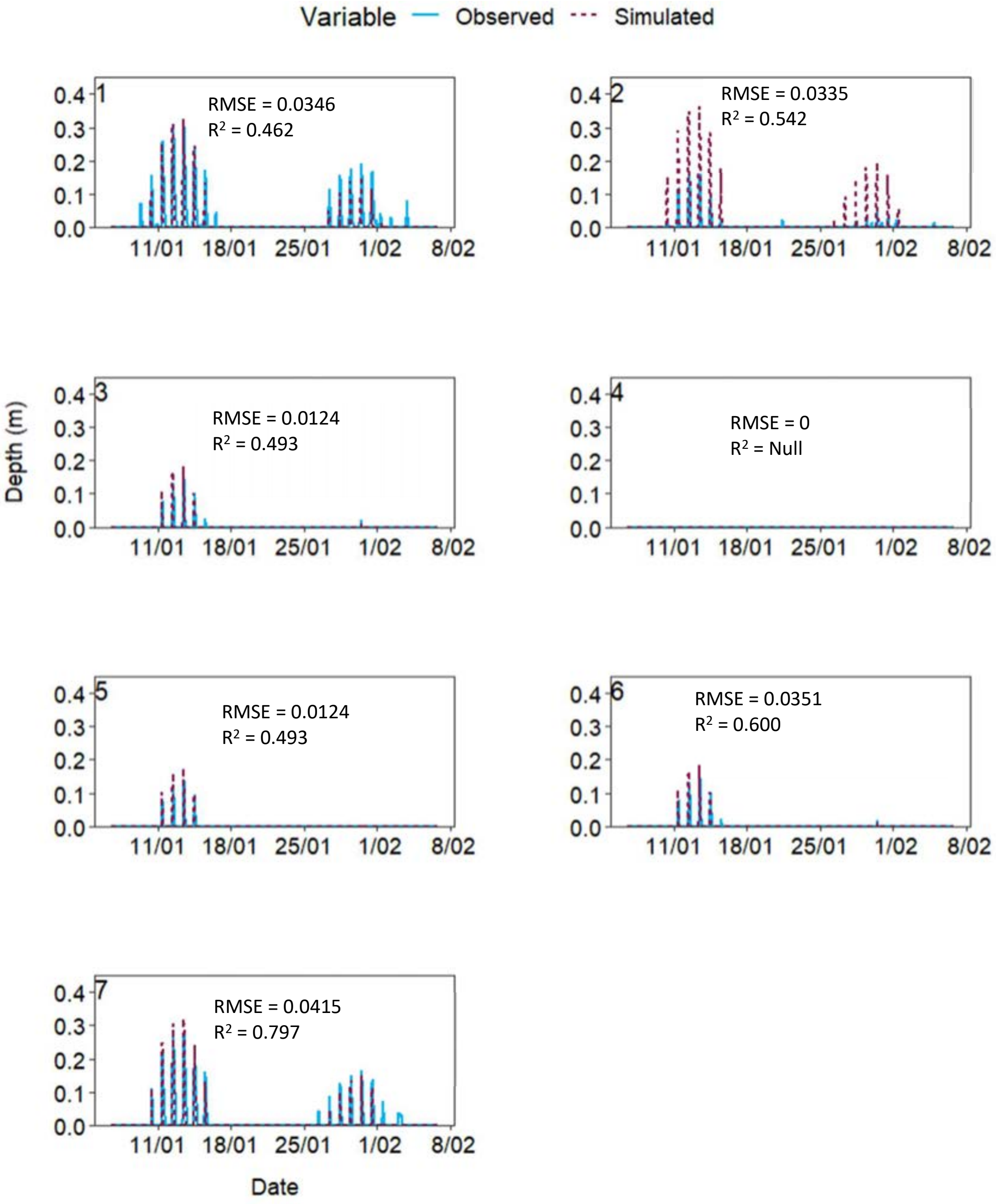


Figure B2 Cross-validation of the simulated and observed water levels at the position of the pressure loggers for the higher-than-average- tides simulation. The root mean square error (RMSE) and the coefficient of correlation (R2) between observed and simulated water levels are also shown.

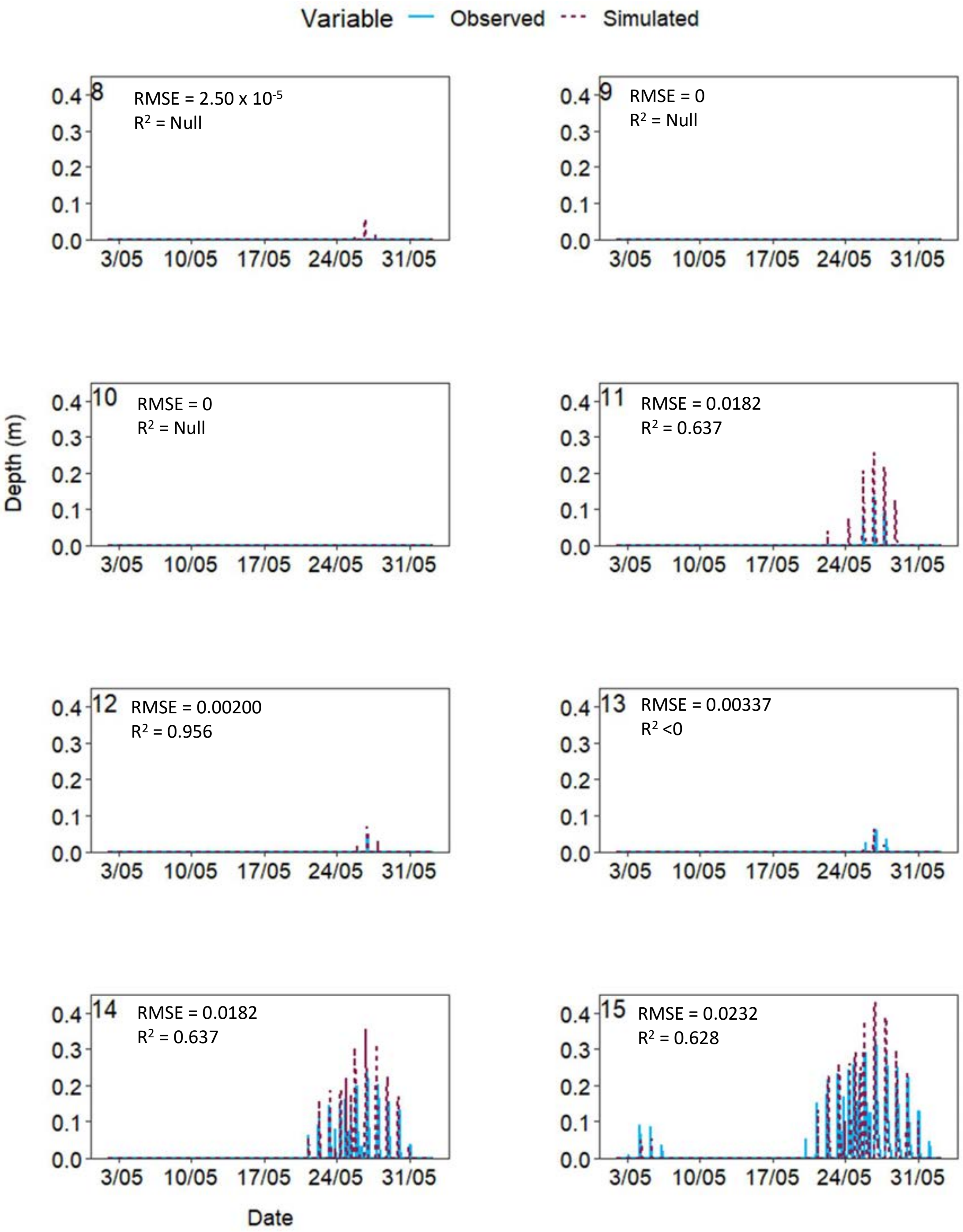


Figure B3 Cross-validation of the simulated and observed water levels at the position of the pressure loggers for the average tide simulation. The root mean square error (RMSE) and the coefficient of correlation (R^2) between observed and simulated water levels are also shown.

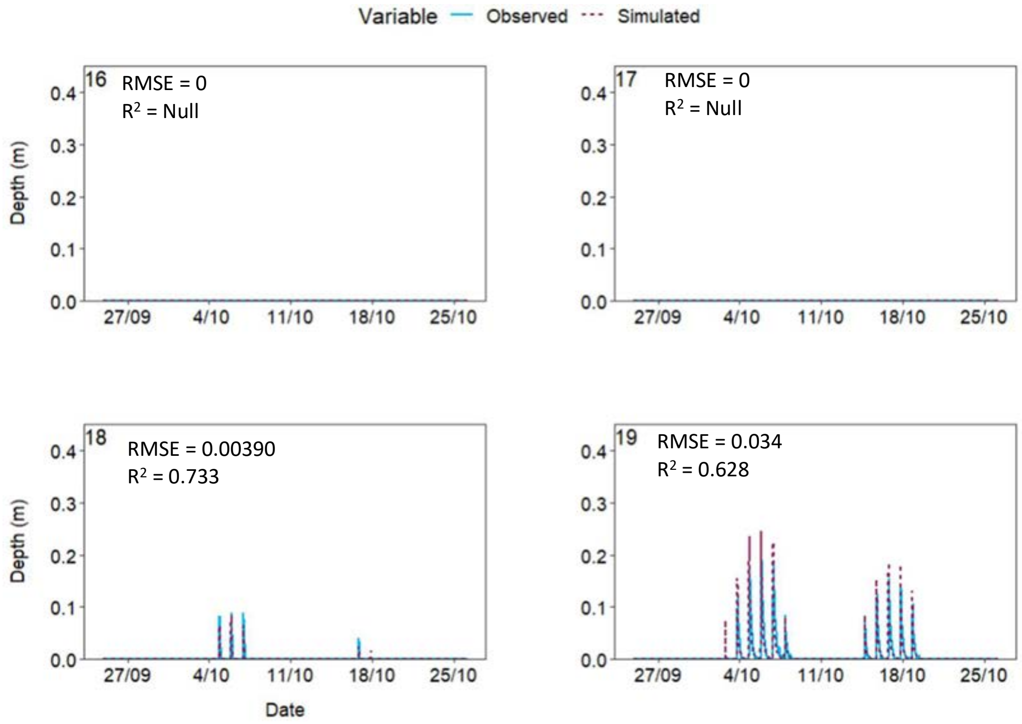


Figure B4 Cross-validation of the simulated and observed water levels at the position of the pressure loggers for the lower-than-average tide simulation. The root mean square error (RMSE) between observed and simulated water levels are also shown.

Table B1 Summary statistics computed from the Field Statistics To Table Data Management Tools in ArcgisPro (Esri 2022) on elevation points extracted from the 0.1 m-spaced land cover point datasets without and with outliers. HS” = Herbaceous saltmarsh; “SS” = Succulent saltmarsh; “MS” = Mudflats/saltpans; “C” = Ceriops spp.; “M” = R. stylosa/A. marina (abbreviated as “M” for mangroves others than Ceriops spp.).

	Min	Max	Mean	SD	Median	Count	Outliers	Mode	Range	Interquartile range	1st Quartile	3rd Quartile	Coef. of variation	Skewness	Kurtosis
Without outliers															
HS	1.214	2.355	1.781	0.210	1.783	10664219		1.61	1.141	0.279	1.640	1.919	0.118	0.080	2.716
SS	0.934	2.054	1.487	0.209	1.473	6397998		1.23	1.114	0.278	1.358	1.636	0.141	-0.040	2.563
C	0.482	1.801	1.088	0.240	1.077	4801605		1.27	1.319	0.343	0.911	1.253	0.221	0.317	2.840
M	0.251	1.44	0.851	0.226	0.891	1865553		0.6	1.191	0.286	0.678	0.964	0.265	0.081	3.175
MS	0.796	1.757	1.23	0.170	1.269	42455150		1	0.961	0.232	1.155	1.386	0.132	0.364	2.231
With outliers															
HS	-0.322	4.696	1.793	0.234	1.787	10869890	205671	1.61		0.285	1.927	1.919	0.131	0.589	6.383
SS	0	3.436	1.486	0.213	1.473	6409788	11790	1.243	3.436	0.278	1.358	1.636	0.143	-0.189	3.661
C	-14.551	4.200	1.004	0.958	1.079	5123976	322371	1.27	18.751	0.360	0.900	1.260	0.954	-9.108	107.599
M	-10.591	3.092	0.830	0.676	0.899	2118684	253131	0.6	13.683	0.309	0.670	0.979	0.814	-5.926	65.162
MS	-14.696	11.602	1.2805	0.298	1.272	44065019	1609869	1	26.298	0.242	1.153	1.396	0.232	-9.814	399.979

Table B2 Calculations of the total area inundated of succulent saltmarsh (SS) and herbaceous saltmarsh (HS) for 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”) and sea level rise scenarios.

	“High”			“Average”			“Low”		
	Current	*+0.3*	*+0.8*	*Current*	*+0.3*	*+0.8*	*Current*	*+0.3*	*+0.8*
Total SS inundated (ha) (% total SS area)	4.24 (66.04%)	6.10 (95.10%)	6.20 (96.65%)	1.51 (23.61%)	4.39 (68.45%)	6.19 (96.58%)	0.66 (10.26%)	2.01 (31.41%)	6.06 (94.46%)
Total HS inundated (ha) (% of total HS area)	1.37 (22.58 %)	5.64 (51.93 %)	10.12 (93.07%)	0.10 (0.96%)	1.47 (13.54%)	8.74 (80.37%)	0.01 (0.095%)	0.17 (1.58%)	5.17 (47.55%)

Table B3 Summary statistics of hydroperiod variables (mean maximum depth, mean duration of inundation, and percent of simulation time inundated) calculated per land cover for 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”).

Land cover	**Mean max. depth (mm)**			**SE (mm)**			**SD (mm)**		
	“High”	“Average”	“Low”	“High”	“Average”	“Low”	“High”	“Average”	“Low”
Herbaceous saltmarsh	13.96	0.84	0.095	0.014	0.0035	0.0012	46.60	11.66	4.14
Succulent saltmarsh	130.82	38.69	11.55	0.058	0.035	0.016	148.00	87.89	40.80
Ceriops spp.	472.96	311.04	177.37	0.12	0.10	0.083	271.94	231.73	188.17
R. stylosa/A. marina	657.85	491.87	348.80	0.24	0.21	0.17	343.51	300.76	254.42
Mudflat/Saltpan	275.66	114.59	36.49	0.051	0.040	0.024	168.97	131.18	81.17

Land cover	**Mean duration (hrs) (days)**			**SE (hrs) (days)**			**SD (mm) (hrs) (days)**		
	“High”	“Average”	“Low”	“High”	“Average”	“Low”	“High”	“Average”	“Low”
Herbaceous saltmarsh	6.97 (0.30)	0.24 (0.01)	0.015 (4.16 x 10^{-4})	0.018 (7.5 x 10^{-4})	0.0017 (7.49 x 10^{-5})	4.90 x 10^{-4} (2.05 x 10^{-5})	9.68 (0.40)	5.63 (0.23)	1.61 (0.07)
Succulent saltmarsh	28.25 (1.18)	4.76 (0.20)	2.15 (0.01)	0.038 (1.67 x 10^{-3})	0.0075 (3.12 x 10^{-4})	0.0091 (3.79 x 10^{-4})	97.40 (4.06)	19.15 (0.80)	23.17 (0.97)
Ceriops spp.	146.40 (6.10)	65.14 (2.71)	39.99 (1.70)	0.089 (0.0038)	0.039 (0.0017)	0.076 (0.0032)	201.68 (8.40)	89.49 (3.70)	97.84 (4.08)
R. stylosa/A. marina	282.34 (11.76)	201.19 (8.38)	159.76 (6.66)	0.17 (0.0071)	0.14 (0.0058)	0.14 (0.0058)	238.74 (9.95)	186.50 (7.80)	201.67 (9.40)
Mudflat/Saltpan	61.16 (2.55)	19.99 (0.83)	13.54 (0.60)	0.037 (0.0015)	0.016 (6.66 x 10^{-4})	0.021 (8.75 x 10^{-4})	124.05 (5.17)	52.93 (2.20)	69.62 (2.90)

Land cover	**Mean percent of inundation simulation time (%)**			**SE (%)**			**SD (%)**		
	“High”	“Average”	“Low”	“High”	“Average”	“Low”	“High”	“Average”	“Low”
Herbaceous saltmarsh	0.92	0.03	1.96 x 10^{-3}	0.021	0.0062	0.0018	1.23	0.75	0.22
Succulent saltmarsh	3.76	0.63	0.29	0.14	0.027	0.033	12.97	2.55	3.08
Ceriops spp.	19.49	8.67	5.32	0.32	0.14	0.28	26.85	11.91	13.02
R. stylosa/A. marina	37.59	26.79	21.27	0.62	0.50	0.51	31.79	24.83	26.85
Mudflat/Saltpan	8.14	2.66	1.80	0.14	0.058	0.076	16.51	7.05	9.27

Appendix C

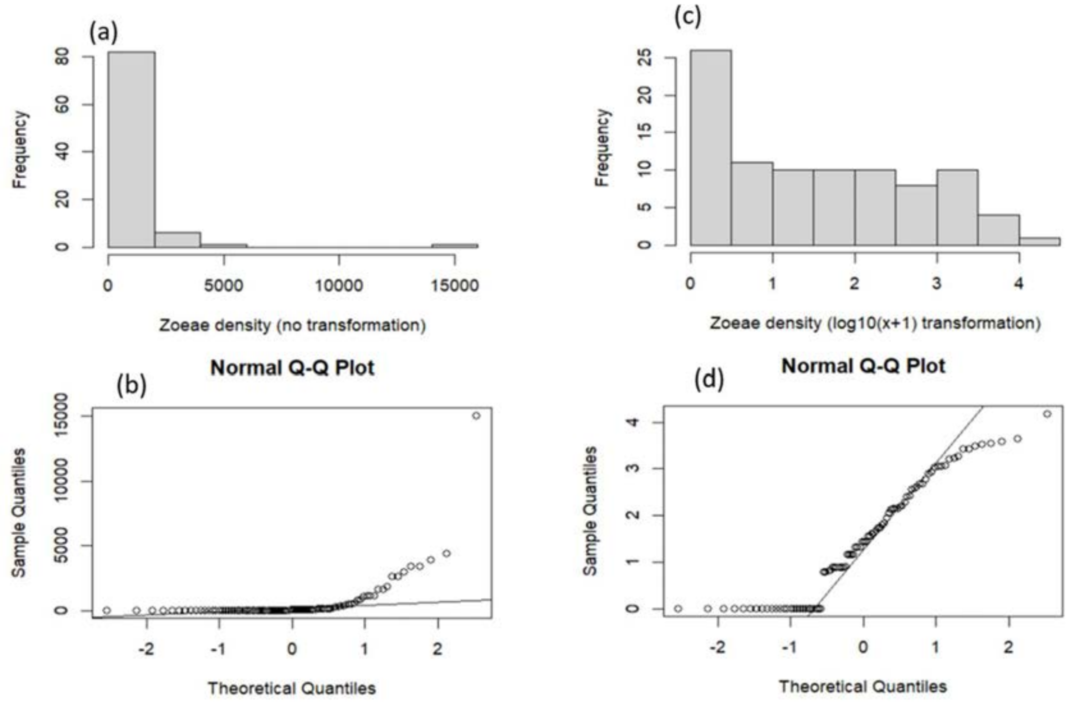


Figure C1 Normality distribution assessments on (a, b) untransformed and (b, c) log10(x+1) transformed crab zoea densities.

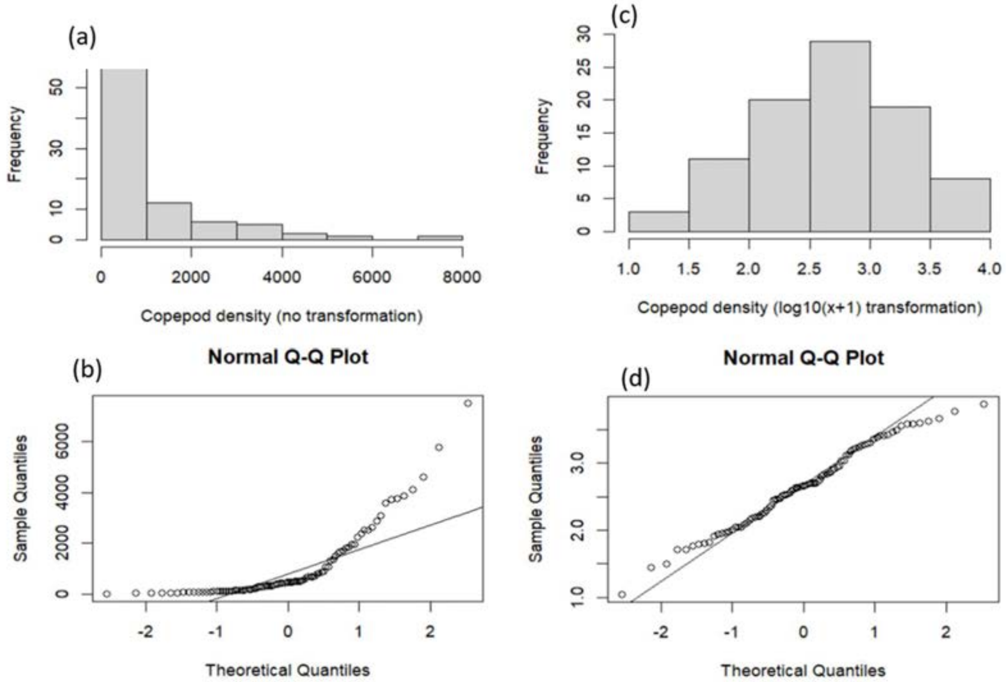


Figure C2 Normality distribution assessments on (a, b) untransformed and (b, c) log10(x+1) transformed copepod densities.

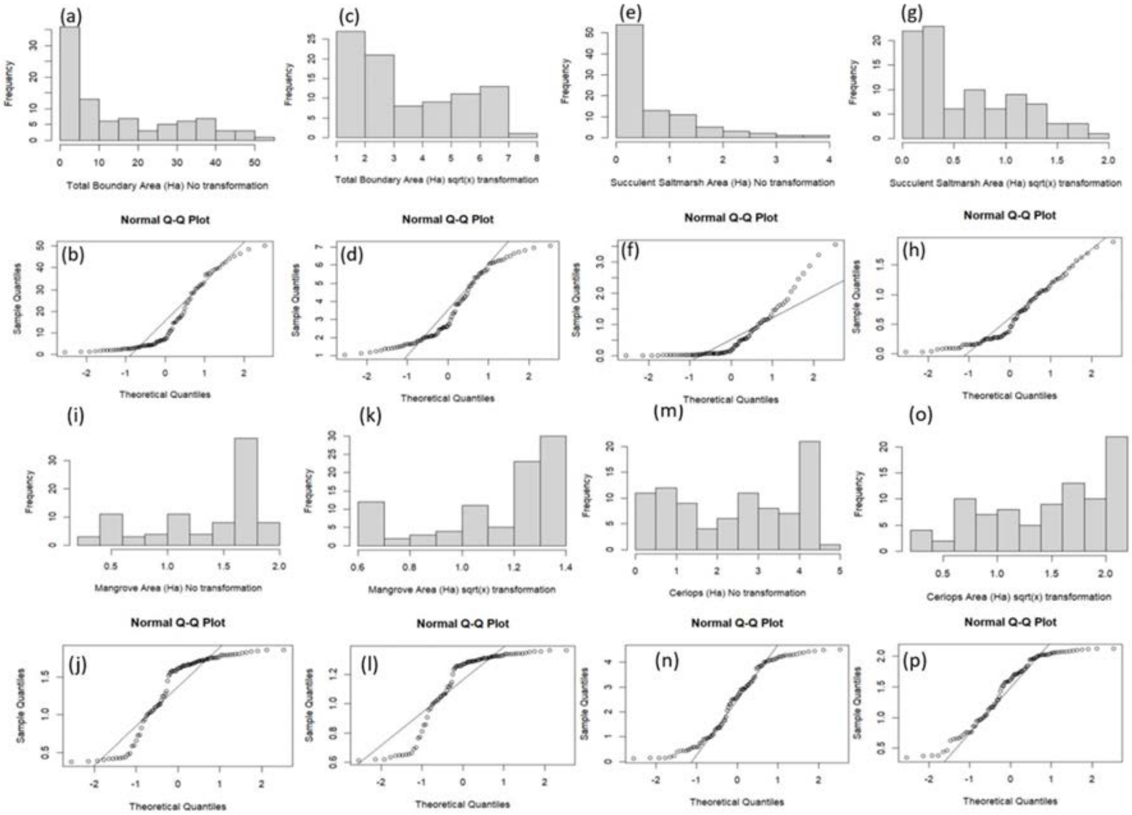


Figure C3 Normality distribution assessments on (a, b) untransformed and (b, c) sqrt(x) transformed Total Boundary area in hectares (Ha) and (e-h) for succulent saltmarsh area; (i-l) A. marina/R. stylosa area; and (m-p) Ceriops spp. area. Area in hectare (Ha) refers to area that was inundated.

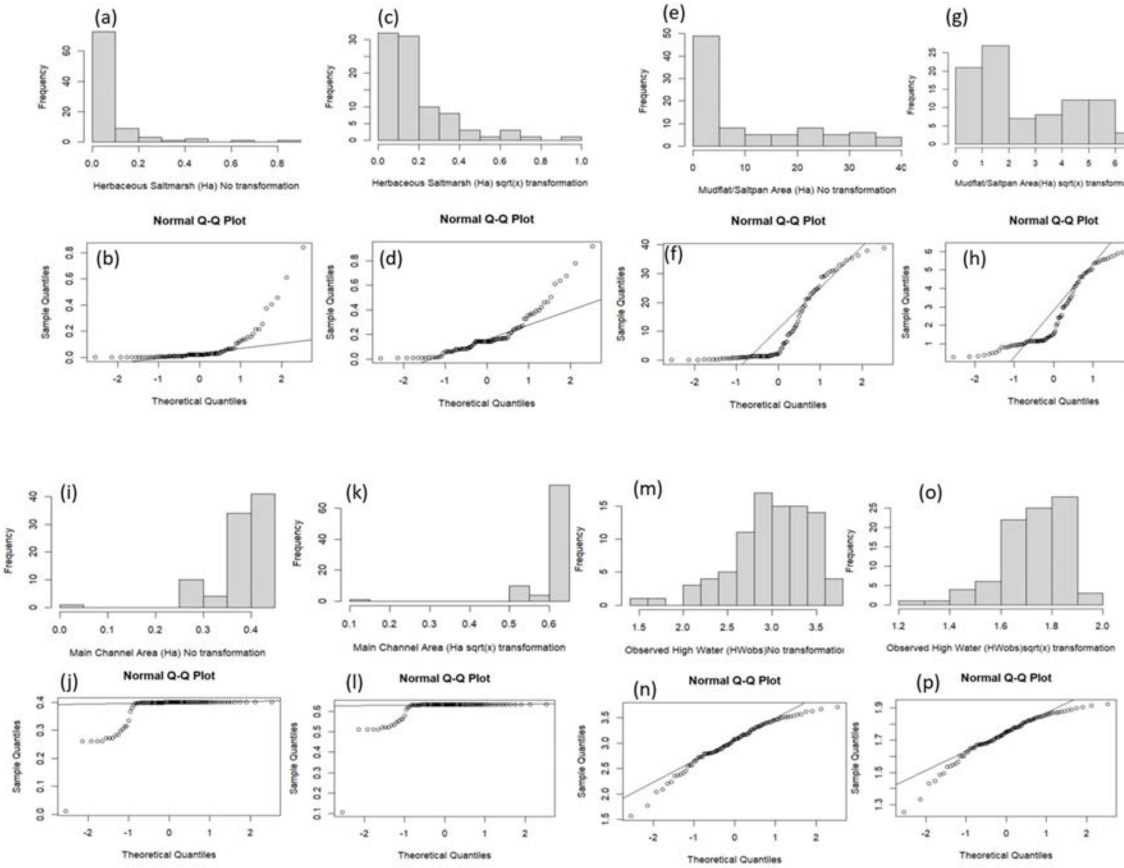


Figure C4 Normality distribution assessments on (a, b) untransformed and (b, c) sqrt(x) transformed herbaceous saltmarsh area in hectares (Ha) and (e-h) for mudflat/saltpan area saltmarsh area; (i-l) main channel area; and (m-p) observed high-water (HWobs). Area in hectare (Ha) refers to area that was inundated.

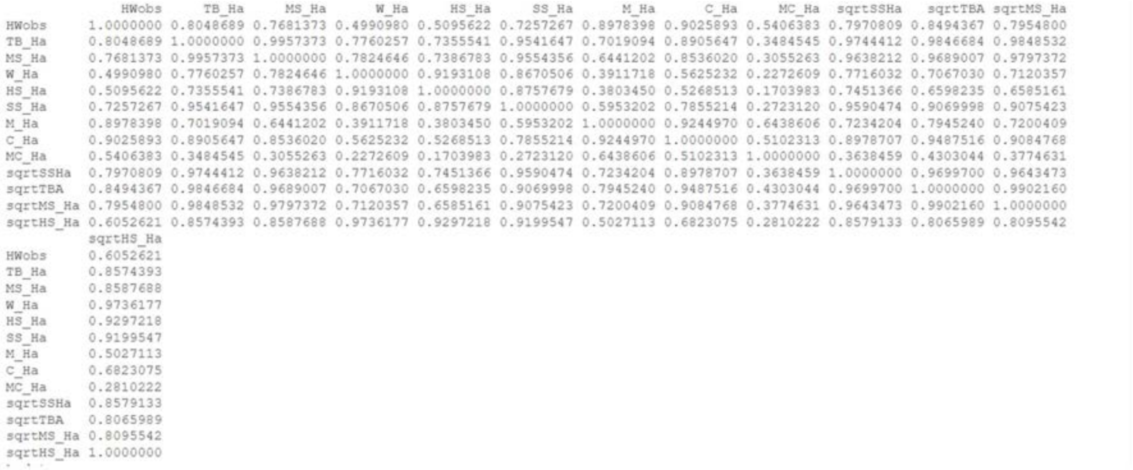
Table C1 Shapiro-Wilk normality test results on the crab zoea and copepod density data. $p < 0.05$ indicates non-normal distribution.

Data	**Transformation**	**W**	p
Crab zoeae	None	0.35	< 0.0001
Crab zoeae	$\mathrm{Log}_{10}(x+1)$	0.91	< 0.0001
Copepods	None	0.71	< 0.0001
Copepods	$\mathrm{Log}_{10}(x+1)$	0.99	0.394

Table C2 Shapiro-Wilk normality test results on the environmental variables. P-value <0.05 indicates non-normal distribution. Transformation in italics were retained for the analyses. Area in hectare (Ha) refers to area that was inundated.

Data	**Transformation**	**W**	p
Total Boundary area (Ha)	None	0.83	< 0.0001
Total Boundary area (Ha)	*Sqrt(x)*	0.89	< 0.0001
Succulent saltmarsh area	None	0.76	< 0.0001
Succulent saltmarsh area	*Sqrt(x)*	0.90	< 0.0001
A. marina/R. stylosa area	None	0.83	< 0.0001
A. marina/R. stylosa area	*Sqrt(x)*	0.80	< 0.0001
Ceriops spp. area	None	0.90	< 0.0001
Ceriops spp. area	*Sqrt(x)*	0.90	< 0.0001
Herbaceous saltmarsh area	None	0.51	< 0.0001
Herbaceous saltmarsh area	*Sqrt(x)*	0.81	< 0.0001
Mudflat/Saltpan area	None		< 0.0001
Mudflat/Saltpan area	*Sqrt(x)*	0.86	< 0.0001
Main Channel area	None	0.48	< 0.0001
Main Channel area	*Sqrt(x)*	0.37	< 0.0001
High Water Observed	None	0.95	0.00203
High Water Observed	*Sqrt(x)*	0.92	< 0.0001

Table C3 Pearson correlation coefficient between environmental variables (Variables codes: HWObs = Observed high water (m); TB_Ha = Total inundated boundary area (ha); MS_Ha = Mudflat/saltpan inundated area (untransformed); W_Ha = Woodland/terrestrial inundated area; HS_Ha = Herbaceous saltmarsh inundated area (untransformed); SS_Ha = Succulent saltmarsh inundated area (untransformed); M = A. marina/R. stylosa inundated area; C_Ha = Ceriops spp. inundated area; MC_Ha = Main Channel inundated area; sqrtSSHa = Succulent saltmarsh inundated area (square-root transformation); sqrtTBA = Total inundated boundary area (square-root transformation); sqrtMS_Ha = Mudflat/saltpan inundated area (square-root transformation); sqrtHS_Ha = Herbaceous saltmarsh inundated area (square-root transformation). Note Woodland/Terrestrial were not included in the analyses. Total boundary area was also excluded due to its high correlation (R2 > 0.95) with Mudflat/saltpan and Succulent Saltmarsh.



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              HWobs     TB_Ha     MS_Ha      W_Ha     HS_Ha     SS_Ha      M_Ha      C_Ha     MC_Ha  sqrtSSHa   sqrtTBA sqrtMS_Ha
HWobs     1.0000000 0.8048689 0.7681373 0.4990980 0.5095622 0.7257267 0.8978398 0.9025893 0.5406383 0.7970809 0.8494367 0.7954800
TB_Ha     0.8048689 1.0000000 0.9957373 0.7760257 0.7355541 0.9541647 0.7019094 0.8905647 0.3484545 0.9744412 0.9846684 0.9848532
MS_Ha     0.7681373 0.9957373 1.0000000 0.7824646 0.7386783 0.9554356 0.6441202 0.8536020 0.3055263 0.9638212 0.9689007 0.9797372
W_Ha      0.4990980 0.7760257 0.7824646 1.0000000 0.9193108 0.8670506 0.3911718 0.5625232 0.2272609 0.7716032 0.7067030 0.7120357
HS_Ha     0.5095622 0.7355541 0.7386783 0.9193108 1.0000000 0.8757679 0.3803450 0.5268513 0.1703983 0.7451366 0.6598235 0.6585161
SS_Ha     0.7257267 0.9541647 0.9554356 0.8670506 0.8757679 1.0000000 0.5953202 0.7855214 0.2723120 0.9590474 0.9069998 0.9075423
M_Ha      0.8978398 0.7019094 0.6441202 0.3911718 0.3803450 0.5953202 1.0000000 0.9244970 0.6438606 0.7234204 0.7945240 0.7200409
C_Ha      0.9025893 0.8905647 0.8536020 0.5625232 0.5268513 0.7855214 0.9244970 1.0000000 0.5102313 0.8978707 0.9487516 0.9084768
MC_Ha     0.5406383 0.3484545 0.3055263 0.2272609 0.1703983 0.2723120 0.6438606 0.5102313 1.0000000 0.3638459 0.4303044 0.3774631
sqrtSSHa  0.7970809 0.9744412 0.9638212 0.7716032 0.7451366 0.9590474 0.7234204 0.8978707 0.3638459 1.0000000 0.9699700 0.9643473
sqrtTBA   0.8494367 0.9846684 0.9689007 0.7067030 0.6598235 0.9069998 0.7945240 0.9487516 0.4303044 0.9699700 1.0000000 0.9902160
sqrtMS_Ha 0.7954800 0.9848532 0.9797372 0.7120357 0.6585161 0.9075423 0.7200409 0.9084768 0.3774631 0.9643473 0.9902160 1.0000000
sqrtHS_Ha 0.6052621 0.8574393 0.8587688 0.9736177 0.9297218 0.9199547 0.5027113 0.6823075 0.2810222 0.8579133 0.8065989 0.8095542
          sqrtHS_Ha
HWobs     0.6052621
TB_Ha     0.8574393
MS_Ha     0.8587688
W_Ha      0.9736177
HS_Ha     0.9297218
SS_Ha     0.9199547
M_Ha      0.5027113
C_Ha      0.6823075
MC_Ha     0.2810222
sqrtSSHa  0.8579133
sqrtTBA   0.8065989
sqrtMS_Ha 0.8095542
sqrtHS_Ha 1.0000000
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