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Decadal Trends in Surface Elevation and Tree Growth in Coastal Wetlands of Moreton Bay, Queensland, Australia

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Abstract

Coastal wetlands surrounding urban environments provide many important ecosystem services including protection from coastal erosion, soil carbon sequestration and habitat for marine and terrestrial fauna. Their persistence with sea-level rise depends upon their capacity to increase their soil surface elevation at a rate comparable to the rate of sea-level rise. Both sediment and organic matter from plant growth contribute to gains in soil surface elevation, but the importance of these components varies among sites and with variation in climate over long time scales, for which monitoring is seldom available. Here, we analysed variation in surface elevation, surface accretion and mangrove tree growth over 15 years in Moreton Bay, Queensland, Australia, a period that spans variation in the *El Niño/La Niña* (ENSO) cycle, which strongly influences rainfall and sea level in the region. Piecewise structural equation models were used to assess the effects of biotic (tree growth, plant cover and bioturbation by invertebrates) and environmental factors on annual surface elevation increments throughout this period. Our model for mangroves identified that surface accretion and tree growth were both positively influenced by rainfall, but surface elevation was not, and thus, higher levels of compaction of the soil profile in high rainfall/high sea level years were inferred. In contrast, our saltmarsh model found that rainfall positively influenced surface accretion and elevation gains. Declines in surface elevation in the mangroves were influenced by the species composition of the mangrove, with higher levels of elevation loss occurring in mangrove forests dominated by Avicennia marina compared to those with a higher proportion of *Rhizophora stylosa*. Decadal-scale variation in ENSO affected mangrove tree growth, but surface elevation trends were more strongly influenced by variation in environmental conditions than by tree growth, although effects of biotic factors (mangrove species composition and bioturbation) on surface elevation trends were observed. Further research into tipping points with extreme ENSO events (either La Niña with high rainfall and high sea level or El Niño with low rainfall and low sea levels) will help clarify the future of mangrove and saltmarsh distribution within Moreton Bay.

Keywords Urban · Subsidence · Sea-level rise · Rainfall · ENSO · RSET

Introduction

Mangroves provide many important ecosystem services within urban settings (Barbier et al. 2011; Hochard et al. 2019). For example, they dampen waves and reduce coastal erosion, contribute to soil carbon sequestration and provide habitat for fisheries species (Barbier et al. 2011; Ewel et al. 1998). Mangrove persistence is influenced by rates

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Vicki Bennion v.bennion@uq.edu.au of soil surface elevation gains (Cahoon et al. 2002) which are important for the maintenance of their position in the intertidal zone over the long term, enabling them to avoid being inundated by sea-level rise and thereby contributing to adaptation to sea-level rise. Sea-level rise may lead to levels of inundation that exceed the thresholds of mangrove growth resulting in their mortality if they are unable to accumulate sediments at the same or higher rates than local rates of sealevel rise to maintain their relative elevation in the intertidal zone (Cahoon et al. 2019).

Mangroves possess several mechanisms that can contribute to the maintenance of their relative elevation within the intertidal zone, even under sea-level rise conditions (Table 1). On the soil surface, mangroves have above-ground roots that protrude from the soil surface,

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Table 1 Hypotheses of the factors that influence mangrove and saltmarsh surface elevation change

Factor (increasing)	Expected influence on surface elevation	Reference
Tree growth	Positive, associated with root growth	(Cormier et al. 2015; Krauss 2021; McKee 2011; McKee et al. 2007)
Surface accretion	Positive, associated with increasing material on the soil surface	(Chmura and Hung 2004; Furukawa et al. 1997; Lovelock et al. 2015)
Root growth	Positive, associated with increased soil volume	(Krauss et al. 2014; McKee 2011)
Bioturbation	Negative, associated with loss of sediment to the water column and subsidence of burrows	(Atwood et al. 2015; Krauss et al. 2014; Xiong et al. 2019a, b)
Basal area of trees	Positive, associated with root growth	(Kumara et al. 2010)
Canopy cover (mangrove)	Unknown, could be positive associated with root growth, or negative associated with reducing evaporation of soil water	(Lovelock et al. 2021; Swales et al. 2015)
Plant cover (saltmarsh)	Positive, associated with below-ground biomass growth and surface accretion	(Baustian et al. 2012; Elschot et al. 2013)
Species composition (proportion of <i>Rhizophora</i> species)	Positive, associated with root growth	(Krauss et al. 2003; Lang'At et al. 2013)
Bulk density	Negative, associated with reduced root growth	(Krauss et al. 2014; Ola et al. 2018; Slocum et al. 2005)
Rainfall	Positive, associated with root growth	(Rogers and Saintilan 2008; Voulgaris and Meyers 2004)
Elevation relative to lowest astronomical tide	Negative, associated with lower sediment delivery in the high intertidal zone, but also associated with compaction of soils from overburden	(Adame et al. 2010; Blum et al. 2021; Lovelock et al. 2011; Rogers and Saintilan 2021)

transporting oxygen below-ground to support root growth. Above-ground roots interact with water flow and trap tidal sediments, increasing surface sediment accretion (Cahoon et al. 2019; Furukawa et al. 1997). Thus, the rate of surface elevation change is linked to the availability of sediments (Lovelock et al. 2015) that is determined by geomorphic setting (Cahoon and Lynch 1997) and the capacity of mangroves to trap sediments. Sediment trapping efficiency differs among species due to variation in root structure, stem densities and forest structure (Huxham et al. 2010a; Krauss et al. 2003; Kumara et al. 2010). For example, higher surface accretion rates were observed around the prop roots of *Rhizophora* species or bare soil (Krauss et al. 2003).

Below the soil surface, root production also contributes to vertical accretion, increasing the volume of soils by adding organic matter (McKee 2011). Our understanding of this contribution is limited; however, studies that assessed the relationship between root growth and surface elevation increments found high contributions of root growth to elevation increments in locations with organic sediments (Krauss et al. 2017; Kumara et al. 2010; McKee et al. 2007; Sidik et al. 2016), but lower contributions in locations with mineral soils (Lovelock et al. 2015; Swales et al. 2019). Measuring long-term root growth in the intertidal zone is technically difficult (Arnaud et al. 2021). However, root growth is linked to above-ground growth in mangroves (Adame et al. 2017; Hayes et al. 2017b) that is often used as an indicator of root growth and which may allow assessment of contributions of mangrove growth to the maintenance of soil surface elevation (Supplementary 1).

In addition to sediment accretion on the soil surface and root growth in the upper levels of the soil profile, other processes contribute to the vertical movements of mangrove soil surface elevation. Shallow subsidence, a term that describes the loss of soil volume and elevation, is higher in soils containing high volumes of coarse pore space that were associated with crab burrows and root channels (Xiong et al. 2019b). Bioturbation by crabs and other invertebrates has been observed to increase mangrove biomass production and surface elevation increments in coastal wetlands (Penha-Lopes et al. 2009). However, crab bioturbation has been linked to loss of sediment if excavated sediment is exported from tidal flows (Lee 1998) that could lead to losses in surface elevation (Xiong et al. 2019b). Rates of subsidence were also influenced by groundwater levels, subsiding with groundwater extraction (Whelan et al. 2005) and also with evapotranspiration of porewater (Lovelock et al. 2021; Swales et al. 2015). Decomposition of roots and soil organic matter that vary spatially and over a range of time scales (Cahoon et al. 1995) also influences long-term trends in soil surface elevation increments (Cahoon 2006). For example, rapid losses of surface elevation were observed after tree mortality, attributed to the decomposition of root biomass (Cahoon 2006; Lang'At et al. 2014).

The proportion and presence of different mangrove species influence a wide range of processes influencing surface elevation and accretion discussed earlier. Mangrove species have morphological and physiological differences, and thus, variation in species composition can lead to differences in the responses of surface elevation to environmental factors. For example, differences in root morphology (Furukawa et al. 1997), tree growth and biomass allocation to roots (Djamaluddin 2019) and tree density (Krauss et al. 2010; Lang'At et al. 2013) have been observed to influence long-term rates of surface elevation change (Ellison et al. 2022).

In comparison to mangroves, saltmarsh in much of Australia occupy higher intertidal areas on the landward edge of the intertidal zone, and therefore, the processes affecting surface elevation and surface accretion may differ in importance compared to those occurring in mangroves (Table 1). The high density of saltmarsh plant material close to the sediment surface can enhance the trapping and binding of mineral sediments delivered in tidal water, along with supporting the accumulation of plant material that can increase surface elevation (Baustian et al. 2012; Elschot et al. 2013). Increased rainfall can result in increased accretion by enhancing sediment delivery (Rogers et al. 2013). Similar to mangroves, saltmarsh environments are however sensitive to changing groundwater levels, where lowering levels results in subsidence of the soil profile that results in a loss of surface elevation (Rogers and Saintilan 2008; Whelan et al. 2005). Saltmarsh soils are typically less porous compared to mangrove soils having higher sheer strength that may reduce erosion from the soil surface (Xiong et al. 2019b). Similar to mangroves, the processes influencing saltmarsh surface elevation gains vary with soil sediment type and plant community composition (Reef et al. 2017; Rogers et al. 2005a).

Most assessments of surface elevation change using rodsurface elevation tables with marker horizons (RSET-MH) are short term (4.8 ± 2.9) years for surface elevation; Breithaupt et al. 2018). Globally, there are few studies where variations in surface elevation and accretion have been monitored over decadal timescales (Artigas et al. 2021; Blum et al. 2021; Feher et al. 2020; Jankowski et al. 2017; Osland et al. 2020; Rogers et al. 2014). Rates of soil surface elevation tend to be higher over shorter records (Sasmito et al. 2016). Therefore, predictions of the resilience of mangroves to sea-level rise based on measurements taken over short time scales can misrepresent variations over longer time scales (Cahoon et al. 2011; Paquette et al. 2004; Parkinson et al. 2017; Webb et al. 2013). Long-term records also enable understanding of the influence of variation in environmental conditions, for example, variation in climatic cycles such as El Niño-Southern Oscillation (ENSO) on surface elevation dynamics.

ENSO cycles give rise to warm periods with drought (*El Niño*) and cool periods with flooding (*La Niña*) in parts of eastern Australia. Extreme *El Niño* can result in coastal wetland mortality (Abhik et al. 2021; Hickey et al. 2021). Previous reports of ENSO affecting surface

elevation dynamics from south-eastern Australia showed a decrease in surface elevation and accretion rates following drought associated with *El Niño* events (Rogers and Saintilan 2008; Rogers et al. 2013). Projections for ENSO with climate change indicate intensifying cycles (Cai et al. 2014; McPhaden et al. 2020), and thus, understanding the impacts of these long-term cycles on surface elevation dynamics is important to understanding the resilience of mangroves to sea-level rise.

The multiple factors that act on surface elevation and plant growth may interact giving rise to variable and complex outcomes. Many processes that influence surface elevation and tree growth are non-linear and can have positive effects at low-to-moderate levels but negative influences at higher levels. For example, rainfall positively influences tree growth at moderate levels (Santini et al. 2015) but can have negative effects, even resulting in mortality at higher levels when flooding occurs (Asbridge et al. 2018). Surface accretion can have a neutral to positive influence on tree growth (Young and Harvey 1996), but extreme sediment loads can lead to mortality (Ellison 1999) or low growth rates (Sidik et al. 2016). The complexity of interacting factors requires analytical techniques that can accommodate complexity and help determine the most important factors underlying surface elevation change and therefore the resilience of coastal wetlands to sea-level rise. In this study, we use structural equation modelling to incorporate factors that both directly and indirectly influence surface elevation change in mangroves and saltmarshes in Moreton Bay, Queensland, Australia.

This study aims to improve current knowledge and understanding of decadal-scale processes in coastal wetlands that contribute to the maintenance of surface elevation. Using long-term records of surface elevation, we assess the following hypotheses:

- 1. Variations in ENSO affect mangrove tree growth (direct), mangrove and saltmarsh soil surface elevation and surface accretion (indirect). Mangrove tree growth is higher in years of higher rainfall (direct). We anticipated increments in soil surface elevation would be higher in years of high rainfall due to both surface accretion (direct) and mangrove tree growth (indirect).
- 2. Local site environmental, sedimentary and biological characteristics surrounding the rod-surface elevation table benchmark contribute to local variations in surface elevation, surface accretion and tree growth.
- 3. Surface elevation gains in mangroves and saltmarshes of Moreton Bay are influenced by bioturbation and accumulation of sediments (direct) which is dependent on their relative elevation within the intertidal zone, and therefore tidal inundation (indirect).

Materials and Methods

Study Site

The study was conducted in Moreton Bay (Quandamooka), Queensland, Australia (27.4°S, 153.4°E), which is on the eastern edge of the rapidly growing urban settlements that comprise the city of Brisbane. Moreton Bay is a large subtropical semi-open bay protected by islands containing an estimated 18,500 ha of intertidal communities, comprising mixtures of mangroves and saltmarshes over a range of geomorphic settings (Accad et al. 2016; Dowling and Stephens 2001). The eastern bay is enclosed by two large sand islands, Moreton Island (Mulgumpin) and North Stradbroke Island (Minjerribah). The eastern bay has coarse sandy sediments from marine sources, whereas the western bay is a deltaic coastline with networks of tidal creeks that have fine sediments delivered from the five coastal catchments that are connected by rivers to the bay (Hayes et al. 2017a). The climate is subtropical with an average annual rainfall of 1148 mm. The highest monthly average rainfall is in January (159 mm) with typical drier months between July and September (monthly average of 45 mm; Bureau of Meteorology 2022a). Mean air temperatures are higher from October to April (25.5–29.1 °C) during the wetter period and lower during the drier May to September (21.0-24.2 °C). The winds are predominately south-eastern trade winds with the occurrence of north-easterlies in September and October (McPhee 2017). Tides are semi-diurnal, ranging from a minimum of 0.20 m to a maximum of 2.79 m (measured at the Brisbane Bar over the last 10 years, based on the highest and lowest astronomical tide; Bureau of Meteorology 2022a).

The annual mean sea level measured from 1980 to 2022 at Bishop Island (survey marker PSM 21764, GLOSS number 58) at the mouth of the Brisbane River indicates a 0.2 m rise, with yearly variations of up to 15 cm influenced by the *El Niño-La Niña* Southern Oscillation (Tide Gauge Data 2022). Mean sea-level rise predictions for 2100 at this location under the latest climate change scenarios using a baseline of 1950-2014 are 0.53 m (under shared socioeconomic pathways (SSP) 2-4.5) and 0.68 m (under SSP3-7.0; Garner et al. 2022). These two scenarios are the mediumrange emission scenarios provided through the IPCC 6th Assessment Report (Garner et al. 2022).

In South-east Queensland, patterns of rainfall and variation in sea level are strongly influenced by the *El Niño-La Niña* Southern Oscillation (Chowdhury and Beecham 2009; Suppiah 2004). The Southern Oscillation Index (SOI) describes the variance in atmospheric patterns and sea surface temperatures across the Pacific Ocean, where it measures the intensity and strength of the Walker Circulation (Bureau of Meteorology 2022b). Values of SOI higher than positive 8 indicate *La Niña* events, whereas values below negative 8 indicate *El Niño* events. In Southeast Queensland, *La Niña* events bring higher than average rainfall with the averages for December to March 20% higher than the long-term averages, and higher than average sea levels (Chowdhury and Beecham 2009). *El Niño* events bring lower than average rainfall with the regular occurrence of drought and lower sea levels. These events occur over a 2- to 7-year cycle (Bureau of Meteorology 2022b), but are predicted to intensify with climate change (Cai et al. 2014; McPhaden et al. 2020).

Study Design

Thirty-six rod-surface elevation table-marker horizon (RSET-MH) instruments were established over six sites in Moreton Bay between March and June 2007 (Cahoon et al. 2002). Three sites are in the western bay (Tinchi Tamba Reserve, Nundah Creek-Boondall Wetlands and Point Halloran Reserve) and three sites on North Stradbroke Island in the eastern bay (Amity North, Amity South, Adams Beach; Fig. 1). The six sites contain well-developed mangrove forests with landward saltmarsh communities. The western bay sites lie within three reserves that include networks of tidal creeks and are managed by local city councils. The eastern bay sites are within mangroves that fringe the sand island coastline and are within the Moreton Bay Marine Park.

Each site contains three replicate fringing mangrove RSET-MH benchmarks and three replicate landward saltmarsh RSET-MH benchmarks. In each vegetation type, benchmarks are approximately 30-50 m apart. Mangrove communities on the western side of the bay are dominated by Avicennia marina (Fig. 1d), although the most southern site at Point Halloran Reserve also had Rhizophora stylosa present. The North Stradbroke Island sites in the eastern bay area have much higher abundances of R. stylosa, where the two species co-occur over the intertidal zone (Fig. 1f). In the western bay, saltmarsh sites are hypersaline and communities are dominated by species of the genera Sarcocornia, Suaeda and Sporobolus (Fig. 1c). In the eastern bay, the brackish landward saltmarsh community is dominated by Juncus kraussii (Fig. 1e; Lovelock et al. 2019). Each site was monitored every 3 months for the first 2 years (2007–2009), bi-annually (wet and dry seasons) from 2010 to 2013 and annually thereafter (2014-2022).

Surface Elevation Change

RSET benchmarks were established by hammering a series of threaded stainless-steel rods (1.2 m lengths, 9/16" diameter) together until refusal (benchmark installation depths for mangroves 3.6–13.1 m, average 8 m; saltmarsh 4.8–16.8 m,



Fig. 1 Location of study sites within **a** Moreton Bay (Quandamooka) on **b** the south-east coast of Queensland, Australia. Examples of the dominant coastal wetland vegetation communities on the western (**c** and **d**) and eastern (**e** and **f**) sides of Moreton Bay: **a** saltmarsh communities of *Sarcocornia, Suaeda* and *Sporobolus* on the western bay;

average 10.8 m) to provide a vertically fixed benchmark that enables high precision repeat point measurements (Cahoon et al. 2002). A receiver was attached to the top rod and cemented into place to minimise horizontal movements. A portable platform is used for measurements to not disrupt the sediment surface. During measurements, a removable arm is attached and levelled, and nine fibreglass pins are carefully lowered to the sediment surface. The proportion of pin protruding above the horizontal arm is measured to the nearest millimetre with a metal ruler. This process is performed in four cardinal directions for a total of 36 measurements that are then averaged to provide a single mean surface elevation value for each measurement period for each RSET benchmark. Pins that are within animal burrows/excavations (the frequency of bioturbation), pneumatophores/roots or any other obstructions to the sediment surface were recorded. These points were later removed from the data set to establish trends over time.

Surface Accretion

Upon installation of the benchmarks, a feldspar marker horizon (MH) was applied on the surface. The marker horizon was approximately 2 cm thick and was dispersed over three 0.25 m^2 areas around the RSET plot. This was later reduced

e brackish saltmarsh communities of *Juncus kraussii* on the eastern bay on North Stradbroke Island (Minjerribah); **d** dominant mangrove community of *Avicennia marina* on the western bay; **f** common community structure of mangroves on the eastern bay on North Stradbroke Island

to one marker horizon at each benchmark to reduce maintenance as variances between the three horizons at each benchmark were negligible. Surface accretion is the depth of material deposited on top of the marker horizon and was assessed by extracting a small core using a modified 3-mm syringe (Krauss et al. 2003). Soil subsidence rates were recorded as the measurable difference of surface accretion minus surface elevation for each benchmark throughout all time periods.

Biomass Characteristics

In July 2007, dendrometer bands that assess changes in mangrove stem circumference over time were attached to five trees of *A. marina* and where present *R. stylosa*, surrounding each mangrove RSET-MH benchmark. Stainless-steel dendrometer bands were placed around the stem of the trees (approximately 1.3 m height) and tightened with a tension spring (Krauss et al. 2007). Changes in the circumference of trees were measured to the nearest 0.2 mm using digital Vernier callipers. Dendrometer band measurements were recorded at the same time as the RSET-MH measurements.

At each RSET-MH site, a range of site characteristics were measured, including the abundance of *A. marina* and *R. stylosa* stems within a 7-m radius of each mangrove RSET. Canopy cover was estimated using a spherical convex

densitometer (Lemmon 1956), and pneumatophore density was assessed by counting the number of pneumatophores within ten 0.04 m² quadrats. At saltmarsh sites, the percentage of saltmarsh vegetation cover was estimated by visual inspection of four 0.25 m² plots.

At each RSET-MH site, a surface soil sample (10 cm depth) was collected using a modified 50-mL syringe and soil dry bulk density and organic matter were assessed. Porewater salinity was assessed in water samples extracted from 30 cm depth using a suction device (McKee 1993). Salinity was measured using a handheld refractometer (Sper Scientific Ltd., Arizona, USA). The elevation of each benchmark relative to the lowest astronomical tide (LAT) was measured as the depth of water covering the sites at high tide using the dyed cotton strip method (English et al. 1997). Daily rainfall was obtained for the period of this study from the Queensland Governments SILO gridded climate data set (The State of Queensland 2022). The monthly SOI data for the duration of this study was collected from the Bureau of Meteorology (Bureau of Meteorology 2022b).

Data Analysis

Piecewise structural equation models (SEMs) were used to understand the complex nature of relationships that relate to the processes influencing surface elevation, surface accretion and tree growth in coastal wetlands. The models test a network of causal multivariate hypothesised relationships that are first developed and fitted into the model (Supplementary 2). Arrows are used to indicate the directional relationship of pathways created from hypotheses (Lefcheck 2016). Models were fitted separately to mangrove and saltmarsh data, with both models having two levels (site and time within site). The mangrove data included 18 sites, with each site having between 16 and 20 measurement times. The mangrove SEM included four response variables that varied by site and time (surface elevation, surface accretion, tree growth and bioturbation frequency), one predictor variable that also varied by site and time (rainfall) and five explanatory variables that varied only by site (canopy cover, pneumatophore density, bulk density, species composition and initial elevation relative to LAT; Supplementary 3). Tree growth diameter increments were divided by the number of days in each measurement period to create diameter growth rates (mm day⁻¹) and averaged for each site and time period. These average growth rates were logtransformed to normalise variance. Rainfall was also divided by the number of days in each measurement period to create a daily rainfall value for each site for each measurement period. SOI was calculated as the average SOI value reported for each measurement period. The relationship between rainfall and SOI was added to the model as a non-causal relationship to test the correlation between rainfall patterns in Moreton Bay and SOI (displayed in the SEM as a double-headed arrow). Results of the SEMs were displayed as path coefficients and associated p-values (alpha = 0.05). Fisher's C statistic was used to evaluate the overall model fit with a higher p-value indicating that the data fit the hypothesised model.

To analyse the factors affecting saltmarsh surface elevation change, we used a simpler SEM following the same methodology and data output as the mangrove SEM (Supplementary 2). The casual multivariate relationships tested were between surface elevation, surface accretion, bioturbation frequency, rainfall, bulk density, plant cover and initial elevation relative to LAT (Supplementary 3). The saltmarsh data had 17 sites with 22 to 23 measurement times each. One of the saltmarsh sites at Adams Beach on the eastern side of the bay was removed from the analysis as an unexplainable hydrological change occurred surrounding the site, resulting in the loss of measurement points. The strength of the hypothesised casual relationships was assessed by the model and significant relationships (p = < 0.05) were reported.

Soil subsidence rates were analysed using a linear mixedeffect model with the same random and fixed variables used within the respective mangrove and saltmarsh SEM.

The influence of the environmental variable 'side of the bay' that represented the location of sites within Moreton Bay (being either on the ocean-influenced North Stradbroke Island or riverine-influenced western side of the bay) was analysed using a linear mixed-effects model. Surface elevation increments and surface accretion increments were included as random variables in the model with 'side of the bay' as the fixed effect.

Our decadal mangrove tree growth data set was analysed using a linear mixed-effect model. The measured growth in circumference for each measurement period was averaged to create the daily growth for each tree during each measurement period. These were then analysed using linear mixed-effect models with random effects of species, previous measurement stem diameter, rainfall during the measurement period, bulk density, number of trees in the plot and initial elevation relative to LAT. The RSET sites were considered fixed effects in the model.

All statistical analysis was undertaken in R version 4.2.1 (R Core Team 2022) using R (R Studio Incorporated 2022) with the SEM analysis performed using the piecewiseSEM package (Lefcheck 2016). Mixed-effect models were performed using the package lmer (Bates et al. 2015) with graphics created using ggplot2 (Wickham 2016).

Results

Surface Elevation Change in Mangroves

The outcome of the mangrove SEM (Fig. 2) indicated that surface elevation change was not strongly and directly influenced by many of the variables included in the model, except for bioturbation (p = 0.043, path coefficient = 0.11) and the abundance of *A. marina* (p = 0.026, path coefficient = -0.34), where the increased abundance of *A. marina* had a negative influence on surface elevation increments. There was a non-significant relationship between mangrove tree growth ($R^2 = 0.25$) and surface elevation increments (p = 0.319, path coefficient = -0.07, $R^2 = 0.13$). This relationship tended to be negative, indicating that an increase in mangrove stem growth tended to be associated with lower surface elevation change. Fisher's *C* statistic for the mangrove SEM indicated that the hypothesised model fitted the data well (Fisher's C = 8.93, df = 20, p = 0.98).

The average annual rate of mangrove surface elevation change occurring on North Stradbroke Island (4.96 mm year⁻¹) was significantly higher than that observed in the western bay (1.49 mm year⁻¹, p < 0.001; Fig. 3). However, the average annual rate of surface accretion observed throughout the bay was not significantly different among the eastern and western bay (7.26 mm year⁻¹ and 6.05 mm year⁻¹ respectively, p=0.138). Elevation relative to LAT was not significantly associated with surface elevation and surface accretion rates in Moreton Bay.

Rainfall

Mangrove tree circumference growth rates were positively influenced by the average daily rainfall within the measurement period (p < 0.001, path coefficient = 0.37). Our linear mixed-effect model for tree growth identified that tree stem growth increased until rainfall reached 6 mm day⁻¹, after which it did not increase further despite increased rainfall (Fig. 4). The tree growth model identified that *R. stylosa* has a higher growth rate compared to *A. marina* (p < 0.001) and that larger trees also grow faster than smaller trees (p < 0.001; Supplementary 4).

In the SEM, rates of surface accretion $(R^2 = 0.04)$ were also positively linked to average daily rainfall (p=0.002, path coefficient = 0.18), but surface elevation increments were not significantly directly influenced by rainfall (p=0.767, path coefficient = 0.02) or surface accretion (p=0.139 path coefficient = 0.08). The relationship between the SOI and rainfall for each measurement period was strongly significantly



Fig. 2 The results of the structural equation model (SEM) for mangroves of Moreton Bay, indicating the significant relationships identified among predictor and response variables. Black lines indicate a positive relationship and red lines indicate a negative relationship, where the thickness of the lines and the value associated with the line indicate the relationship of connection strength and the response of the dependant variable to a unit change in the predictor variable. Greyed out lines indicate no significant relationship was detected. The relationship between rainfall and the Southern Oscillation Index was added to the model as a non-causal relationship and therefore displayed in the SEM as a double-headed arrow. The abundance of *A. marina* represents the proportion of *Avicennia marina* stems present, compared to those of *Rhizophora stylosa* within 7 m of the benchmark. Elevation relative to LAT=elevation relative to the lowest astronomical tide

Fig. 3 Surface accretion and surface elevation change in mangroves throughout the 15.9 years in Moreton Bay, Queensland, Australia. The three lines in each panel represent each individual RSET-MH at each site. The average annual rate for each site $(\pm$ STD error) is included as text in each panel. The average annual rate of surface accretion is 7.26 mm year⁻¹ for the eastern bay (Adams Beach, Amity North, Amity South) and 6.05 mm year⁻¹ for the western bay (Halloran, Nundah, Tinchi). The average annual rate of surface elevation change is $4.96 \text{ mm year}^{-1}$ for the eastern bay and $1.49 \text{ mm year}^{-1}$ for the western bay



correlated (p < 0.001, path coefficient = 0.44). The linear mixed-effect model for mangrove subsidence also indicated a positive relationship with rainfall (p = 0.014).

Bioturbation

The frequency of bioturbation ($R^2 = 0.09$) measured within the RSET plots was significantly positively related to canopy cover (p = 0.007, path coefficient = 0.40) and negatively affected by the intertidal position (initial elevation relative to LAT, p = 0.017, path coefficient = -0.33).

Surface Elevation Change in Saltmarsh

Surface elevation increments ($R^2 = 0.09$) in saltmarsh were directly influenced by rainfall (p = 0.000, path coefficient = 0.20), however not directly to surface accretion (p = 0.056, path coefficient = 0.10, $R^2 = 0.15$; Fig. 5). The



Rhizophora stylosa



Precipitation in period (mm / day⁻¹)

Fig. 4 The relationship between mangrove tree growth and average daily rainfall for each measurement period for *Avicennia marina* (left panel) and *Rhizophora stylosa* (right panel). Blue circles are tree diameters above 9 cm and red circles are mangrove tree diameters

below 9 cm. Lines of best fit indicate *R. stylosa* have an increased growth rate (p < 0.001) including their response to increased period rainfall (p < 0.001). The representative R^2 for the model = 0.39

SEM model indicated that surface accretion is significantly positively associated with plant cover (p = 0.023, path coefficient = 0.18) and rainfall (p = 0.000, path coefficient = 0.32). The occurrence of bioturbation within the RSET saltmarsh plots ($R^2 = 0.03$) was significantly negatively related to rainfall throughout the period (p = 0.002, path coefficient = -0.16), but was not related to any other variable within our hypothesised SEM. Elevation relative to LAT was not significantly associated with surface elevation change or surface accretion and neither was bulk density. Overall, the SEM fitted for the saltmarsh had a moderately good fit (Fisher's C = 6.01, df = 4, p = 0.20).

The average annual rate of saltmarsh surface elevation change occurring on North Stradbroke Island (1.57 mm year⁻¹) was not significantly different to that on the western side of the bay (0.56 mm year⁻¹, p = 0.132; Fig. 6). However, rates of surface accretion were significantly higher on the eastern side of the bay, compared to the western side of the bay (2.67 mm year⁻¹ and 1.29 mm year⁻¹ respectively, p = < 0.001). The saltmarsh soil subsidence model indicated no significant relationships with any variables measured.

Discussion

The Mangrove Structural Equation Model

Over our 15 years of monitoring and analyses using structural equation models to encompass complex relatedness among predictor and response variables, we found that surface elevation change in mangroves was significantly influenced by species composition and bioturbation and that environmental variables tended to have indirect effects. The increased presence of *R. stylosa* resulted in increased surface elevation (Fig. 2) that may be due to *R. stylosa* having higher growth rates in Moreton Bay compared to *A. marina*, as well as differences in root structural and chemical characteristics (Ola et al. 2020) and biomass allocation patterns (Alongi et al. 2000; Kairo et al. 2009).

Contrary to our hypothesis, surface accretion was not directly related to surface elevation (p = 0.139, path coefficient = 0.08). However, the SEM identified that increased rainfall was linked to higher rates of surface accretion, due to increased sediment supply to coastal mangroves (Lovelock



Fig. 5 The results of structural equation model (SEM) for saltmarshes of Moreton Bay, indicating the significant relationships identified among predictor and response variables. Black lines indicate a positive relationship and red lines indicate a negative relationship, where the thickness of the lines and the value associated with the line indicate the relationship of connection strength and the response of the

et al. 2015). Suspended sediment concentrations are higher in tidal waters following periods of rainfall with the resuspension of fine particles (Adame et al. 2010; Furukawa and Wolanski 1996; Sidik et al. 2016; Wolanski et al. 1992; Woodroffe et al. 2016). The importance of sediment supply for increasing surface accretion and maintaining surface elevation has previously been identified from many coastal fringing mangrove systems (Krauss et al. 2007; Rogers et al. 2005a; Sidik et al. 2016), but in this study, losses in elevation reduced the positive influence of surface accretion on surface elevation. In locations where surface accretion is not directly related to surface elevation, below-ground processes are proposed to be important in influencing compaction or expansion of the soil profile (Cahoon et al. 2021; Woodroffe et al. 2016). Therefore, processes that influence losses in soil elevation, often termed shallow subsidence or compaction, are highly influential in determining surface elevation dynamics of mangroves in Moreton Bay.

High levels of overburden pressure from additional water volumes in *La Niña* years can compress coarse soil pore spaces (Chambers et al. 2019). Shallow subsidence was previously linked to the volume of coarse pore spaces in mineral

dependant variable to a unit change in the predictor variable. Greyed out lines indicate no significant relationship was detected. The relationship between rainfall and the SOI was added to the model as a non-causal relationship and therefore displayed in the SEM as a double-headed arrow. Elevation relative to LAT=elevation relative to lowest astronomical tide

mangrove soils in Moreton Bay (Xiong et al. 2019b). Compaction from overburden has also been identified in mangroves in southern Australia (Rogers and Saintilan 2021) and marshlands in Essex, UK (Chirol et al. 2021). Coarse pore soil volumes may be higher in mangroves dominated by *A. marina* compared to *R. stylosa* due to their belowground root structure that may lead to higher subsidence in *A. marina* dominated mangroves, although this remains to be assessed.

Complexity in factors influencing mangrove surface elevation increments has been widely observed (Table 1; Cahoon et al. 2019; Krauss et al. 2014) and many researchers have concluded that surface accretion is often a poor predictor of surface elevation gains and that shallow subsidence, which can be due to a wide range of factors, adds to the complexity of projecting future surface elevation gains with sea-level rise in many sites (Cahoon and Lynch 1997; Lovelock et al. 2015; Rogers et al. 2005a). Despite this complexity, our analyses revealed that biotic factors had important influences on shallow subsidence and thus surface elevation increments and that environmental factors tended to have indirect effects on surface elevation change.

Fig. 6 Surface accretion and surface elevation change in saltmarshes throughout the 15.9 years in Moreton Bay, Queensland, Australia. The three lines in each panel represent each individual RSET-MH at each site. The average annual rate for each site $(\pm$ STD error) is included as text in each panel. The average annual rate of surface accretion is 2.67 mm year⁻¹ for the eastern bay (Adams Beach, Amity North, Amity South) and $1.29 \text{ mm year}^{-1}$ for the western bay (Halloran, Nundah, Tinchi). The average annual rate of surface elevation change is $1.57 \text{ mm year}^{-1}$ for the eastern bay and $0.56 \text{ mm year}^{-1}$ for the western bay



Effects of Mangrove Tree Growth and Species Composition on Surface Elevation

The growth rates of *R. stylosa* mangroves were higher than those of *A. marina* in locations where the two species cooccurred (p < 0.001; Fig. 4). Growth rates were also dependent upon size classes, with larger trees (>9 cm diameter at breast height) growing faster than smaller trees (p = < 0.001). Mangrove trees larger than 15 cm diameter were also observed to have higher growth rates than smaller trees in Indonesia, although this was species specific (Djamaluddin 2019). Higher growth rates observed in larger mangroves could be due to their extensive underground root systems utilising more nutrients and capturing more water through their canopies (Tomlinson 1986).

In addition to *R. stylosa* having higher growth rates than *A. marina* in Moreton Bay, these species differ in physical and biological traits such as root structure, wood density and temperature tolerances that could be underlying trends in tree growth rates that influence surface elevation

changes (Duke et al. 1998; Tomlinson 1986). For example, roots of A. marina showed higher rates of decomposition than roots of R. mangle in a mangrove forest in Kenya (Huxham et al. 2010b), although rates of decomposition can also vary among sites, even in mature reference sites (McKee and Faulkner 2000). Avicennia marina have cable roots which typically have more fine roots than coarse roots and may contribute less to subsurface soil volumes than roots of Rhizophora species (Arnaud et al. 2021). For example, 42% of surface elevation gains in Caribbean mangroves were from fine roots of Rhizophora (McKee et al. 2007). Additionally, Avicennia have higher root porosity (Youssef and Saenger 1996), lower lignin and high nutrient concentration in fine roots compared to Rhizophora (Ola et al. 2020) that enhances decomposition of Avicennia root tissues compared to those of Rhizophora (Middleton and McKee 2001; Ola et al. 2020).

There was a strong positive relationship of above-ground stem growth to increased rainfall (p < 0.001, path coefficient = 0.37) that has also been observed in other studies (Hayes et al. 2019; Mackey 1993; Rogers et al. 2005a; Santini et al. 2015; Xiong et al. 2019a). Despite mangroves growing in the salty waters of the intertidal zone, the availability of freshwater is important in supporting high growth rates, particularly in *R. stylosa* (Ball and Farquhar 1984; Ellison 2000; Robert et al. 2009). Our study indicates that the productivity of mangroves of Moreton Bay will be highly sensitive to variation in rainfall associated with ENSO cycles, which are predicted to intensify with climate change (McKay et al. 2023).

High rates of above-ground growth may result in preferential allocation to above-ground biomass that occurs at the expense of allocation to below-ground biomass (Krauss et al. 2014; McKee 1996; Saenger 2002) that may contribute to lower than anticipated rates of surface elevation gain in high rainfall years. For instance, seedlings grown for 3 years in greenhouse conditions resulted in a two-fold increase of root biomass allocation for R. stylosa compared to A. marina (Jacotot et al. 2019). Above-ground and belowground growth of A. marina were observed to scale similarly in previous studies in Moreton Bay (Hayes et al. 2017b), and thus, variation in biomass allocation in R. stylosa as well as other processes, particularly those linked to root characteristics (discussed earlier), may be responsible for the weak negative relationship between tree growth and surface elevation increments.

Most past accounts of mangrove species composition in Moreton Bay suggest that *A. marina* was dominant (Accad et al. 2016). However, more recent assessments suggest increasing abundance of *R. stylosa* (Hill et al. 2021) that may suggest global warming is contributing to their increasing abundance and growth, and as the temperatures increase further, the dominance of *R. stylosa* could be further enhanced (Sherman et al. 2000; Wilson 2009). Although this may change the character of the mangroves of Moreton Bay, it could lead to enhancing surface elevation increments and therefore resilience to sea-level rise.

Effect of Intertidal Position and Bioturbation on Surface Elevation Change

The position within the intertidal zone was not directly linked to surface elevation change but was identified as influencing the frequency of bioturbation (p=0.017, path coefficient = -0.33) that directly affected surface elevation. One of our hypotheses was that intertidal position would influence surface elevation increments because (1) low intertidal positions would have higher surface accretion, and (2) low intertidal positions would have higher levels of allocation to root growth because the soils are more saline and frequently inundated (Ball 1988; Clough 1984). The limited evidence for direct relationships between intertidal position and surface elevation and surface accretion suggests that subsurface processes like bioturbation are important in determining surface elevation change. Differences among sites in hydrological forces such as wind and wave energy, groundwater fluxes, sediment and nutrient availability could result in levels of variation that limit the detection of strong trends (Hayes et al. 2019).

In the mangroves, the frequency of bioturbation positively influenced surface elevation (p=0.043, path coefficient=0.11) with an increase in bioturbation occurring in closed canopy locations. Burrow densities are often used as indicators of healthy or productive mangroves (Flint et al. 2021; Penha-Lopes et al. 2009). Mangrove crabs are known to bury organic material (Hogarth 2015; Smith 1987; Xiong et al. 2019b) and increase soil aeration (Cannicci et al. 2008; Smith et al. 1991) that in turn support greater root and plant growth (Huang and NeSmith 1999; Smith et al. 2009). Crabs (and other burrowing invertebrates) can also cause an increase in shallow subsidence through excavation of sediments that increase the presence of coarse soil pores (Xiong et al. 2019b). However, rather than subsidence, over the whole 15 years of our monitoring, bioturbation had a positive influence on surface elevation and thus on mangrove resilience.

The Saltmarsh Structural Equation Model

While surface elevation gains in saltmarshes in many parts of the world are strongly influenced by root growth (Morris et al. 2002), our long-term assessment found that saltmarsh surface elevation gains were influenced by processes influencing surface accretion. Rainfall, which results in fine sediments delivered to the bay, was identified as an important factor influencing surface accretion (p=0.000, path coefficient=0.32) and therefore surface elevation gains (p=0.000, path coefficient=0.20). The importance of rainfall for delivery of sediments in tidal flows to the saltmarshes has previously been identified from southern Australia (Rogers et al. 2013) and South Carolina, USA (Murphy and Voulgaris 2006). Compared to the mangrove environments, the influence of rainfall on increased surface accretion in saltmarshes was more prominent, possibly due to their location higher within the intertidal and the reduced complexity of the environmental factors that influence surface elevation gains.

In our study, surface accretion in saltmarshes was positively influenced by plant cover (p = 0.023, path coefficient = 0.18). This indicates that vegetation has a role in trapping suspended sediments from tidal water, which has been identified from a variety of other species of saltmarsh including grasses and shrubs from the Netherlands (Elschot et al. 2013) and *Spartina alterniflora* from North Inlet, South Carolina (Morris 2007), Louisiana (Baustian et al. 2012) and south-eastern China (Chen et al. 2018). In southern Australian saltmarsh, surface accretion levels differed between species, with *J. kraussii* (a rush) trapping higher levels of sediment compared to the succulent *S. quinquefolia* or the grass *S. virginius* (Kelleway et al. 2017b), a finding consistent with our results for Moreton Bay, Queensland.

In saltmarshes of southern Australia, shallow subsidence due to autocompaction was identified as an important process limiting surface elevation gains (Rogers et al. 2005b, 2006). Our study also inferred that shallow subsidence limits elevation gains, but it has a smaller effect on surface elevation change in the saltmarsh compared to the mangroves. Shallow subsidence in the saltmarsh showed no significant direct relationships with any variables measured within this study.

Unlike the mangroves (discussed earlier), bioturbation had no significant influence on surface accretion or surface elevation change. Saltmarshes in Morton Bay had lower levels of bioturbation compared to the mangroves. Saltmarshes occur in the higher intertidal landward of mangroves where hypersaline (western bay) or brackish (eastern bay) conditions may lead to a lower abundance of crabs and invertebrates than in the mangroves (Bloomfield and Gillanders 2005), thereby reducing their impacts on surface elevation.

The low overall fit of our saltmarsh SEM for Moreton Bay suggests there were additional factors that we have not included that could improve the model. For example, groundwater fluxes may influence subsurface processes, or hydrological patterns could be included in the model. Additionally, mangrove encroachment is occurring at both the Tinchi Tamba and Nundah Creek sites, which may be influencing surface elevation and accretion as well as other ecological processes (Kelleway et al. 2017a; Rogers et al. 2005b).

Limitations of this Study

Structural equation modelling is commonly used for the analysis of complex systems, providing a global fit model that otherwise would require numerous separate multiple regression tests (Grace and Bollen 2005; Tomarken and Waller 2004). While SEMs are useful in the analysis of coastal wetland surface elevation relationships, the models have a range of limitations. This includes the omission of unknown or unmeasured variables from the theoretical model. For example, further data on sediment properties, particle size, groundwater levels and hydrology could improve the models. Additionally, missing values for variables not measured throughout all time periods limit the power of the models. The SEMs are also unable to disentangle cyclic relationships (Lefcheck 2016), including the relationship between subsurface processes; for example, the relationships between bioturbation, sedimentation and forest productivity processes (Aschenbroich et al. 2016; Smith et al. 1991).

This study incorporated only one ENSO cycle, with *El Niño* early in the time series and *La Niña* dominating later in the time series. Thus, our insights on the effects of ENSO on Moreton Bay mangroves and saltmarshes are limited. Expanding our study over multiple decades to incorporate multiple ENSO cycles would improve our understanding of the effects of ENSO cycles on mangrove tree growth and surface elevation dynamics of coastal wetlands in Moreton Bay.

Conclusion

This study shows that mangroves in Moreton Bay currently have surface elevation rates comparable to or greater than current rates of mean sea-level rise that indicates they may be resilient to sea-level rise. In contrast, saltmarshes had low rates of elevation gain and are therefore vulnerable to sea-level rise and mangrove encroachment (Mazor et al. 2021). Surface accretion in mangroves and saltmarshes of Moreton Bay was dependent upon rainfall that in a future of intensifying ENSO cycles and the potential for longer drought periods as well as intense flooding could have negative impacts for their resilience to sea-level rise, although there are high levels of uncertainty in rainfall projections for the region. Surface elevation gains in saltmarshes and mangroves were dependent upon biological factors linked to species composition, plant cover and frequency of bioturbation. Our long-term study indicates that both physical and biological components of coastal wetlands are important for their resilience to sea-level rise.

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Data Availability Data on the measured ecosystem variables used within this study are included within this paper and its Supplementary Information files.

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