

Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes

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Abstract

Shifts in ecosystem structure have been observed over recent decades as woody plants encroach upon grasslands and wetlands globally. The migration of mangrove forests into salt marsh ecosystems is one such shift which could have important implications for global 'blue carbon' stocks. To date, attempts to quantify changes in ecosystem function are essentially constrained to climate-mediated pulses (30 years or less) of encroachment occurring at the thermal limits of mangroves. In this study, we track the continuous, lateral encroachment of mangroves into two south-eastern Australian salt marshes over a period of 70 years and quantify corresponding changes in biomass and belowground C stores. Substantial increases in biomass and belowground C stores have resulted as mangroves replaced salt marsh at both marine and estuarine sites. After 30 years, aboveground biomass was significantly higher than salt marsh, with biomass continuing to increase with mangrove age. Biomass increased at the mesohaline river site by $130 \pm 18 \text{ Mg biomass km}^{-2} \text{ yr}^{-1}$ (mean \pm SE), a 2.5 times higher rate than the marine embayment site ($52 \pm 10 \text{ Mg biomass km}^{-2} \text{ yr}^{-1}$), suggesting local constraints on biomass production. At both sites, and across all vegetation categories, belowground C considerably outweighed aboveground biomass stocks, with belowground C stocks increasing at up to $230 \pm 62 \text{ Mg C km}^{-2} \text{ yr}^{-1}$ (\pm SE) as mangrove forests developed. Over the past 70 years, we estimate mangrove encroachment may have already enhanced intertidal biomass by up to 283 097 Mg and belowground C stocks by over 500 000 Mg in the state of New South Wales alone. Under changing climatic conditions and rising sea levels, global blue carbon storage may be enhanced as mangrove encroachment becomes more widespread, thereby counteracting global warming.

Keywords: biomass, blue carbon, carbon sequestration, climate change, ecosystem services, mangrove, mangrove encroachment, salt marsh, saltmarsh, sea level rise

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Introduction

Shifts in ecosystem structure have been observed over recent decades as woody plants (shrubs and trees) encroach upon grasslands and wetlands globally (Saintilan & Rogers, 2015). A recent synthesis of shrub encroachment into terrestrial grasslands has shown that while structural change may have mixed effects on ecosystem functional traits, significant increases in aboveground and soil carbon (C) pools are common (Eldridge *et al.*, 2011). Such a change in 'blue carbon' habitats – that is, C-rich, marine habitats – could have significant implications for regional and global C pools,

as mangroves (trees and shrubs) and salt marshes (communities of grasses, succulent herbs, rushes and low shrubs) are disproportionately important in sequestering C relative to their spatial extent (Duarte *et al.*, 2005; Mcleod *et al.*, 2011). This is due to (1) high productivity in both ecosystems (Nixon, 1980; Alongi, 2002) manifest in C bound within aboveground and belowground biomass; (2) effective trapping of particulate organic C originating from within the ecosystem (autochthonous) or external (allochthonous) riverine and oceanic sources (Mcleod *et al.*, 2011); and (3) anoxic, saline subsurface conditions which slow down the rate of decay of organic material (Magenheimer *et al.*, 1996; Duarte *et al.*, 2005; Mcleod *et al.*, 2011).

Mangroves and salt marshes are dynamic ecosystems found in a range of sedimentary settings along low-

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energy coastlines. They generally share a similar ecological niche in the intertidal zone and have different but overlapping latitudinal distributions. Globally, mangrove range is limited chiefly by physiological intolerance to subfreezing temperature, with most species confined to tropical or subtropical climes (Duke *et al.*, 1998). In contrast, salt marshes appear to be less constrained by temperature, being found from tropical through to arctic zones, although extent and species diversity is greater in higher latitudes (Adam, 1993, Friess *et al.*, 2012), where mangrove distributions decline. In temperate and subtropical zones, these two distributions often overlap, forming adjacent and/or ecotonal communities in the intertidal zone. In recent years, a poleward expansion of mangroves has been reported on each of the continents mangroves and salt marshes co-inhabit – Asia, Africa, North America, South America and Australasia (Saintilan *et al.*, 2014 and references therein). To date, much of the research effort has focussed on encroachment by the species *Avicennia germinans* throughout the northern Gulf of Mexico (Stevens *et al.*, 2006; Comeaux *et al.*, 2012; Bianchi *et al.*, 2013) and Atlantic coast (Cavanaugh *et al.*, 2014) of the United States. Concurrent with this, poleward range expansion, however, is a lateral ‘within-range’ mangrove expansion into treeless salt marsh communities. This phenomenon is best documented throughout Australasia, where encroachment into salt marsh is a near-ubiquitous trend in south-eastern Australia and New Zealand (Burns & Ogden, 1985; Saintilan & Williams, 1999).

At a global scale, mangrove encroachment of salt marsh may be driven by a suite of changing environmental factors favouring mangrove, including rising sea level, elevated atmospheric CO₂ and higher temperatures (McKee *et al.*, 2012; Saintilan *et al.*, 2014). Among regions, however, the relative importance of specific drivers may vary. In south-eastern USA, for example, it has been well documented that mangrove abundance and coverage is winter temperature-sensitive with *A. germinans* strongly regulated by air temperatures of –4.0 to –8.9°C or less (Stevens *et al.*, 2006; Osland *et al.*, 2013; Cavanaugh *et al.*, 2014). In the absence of extreme winter events, mangrove cover and abundance increases, with encroachment into salt marsh occurring, as has been observed across the region since extreme freezes in the 1980s (Stevens *et al.*, 2006). Landward encroachment of mangroves has also been attributed to sea level rise and alteration of freshwater flow in this region (Krauss *et al.*, 2011). Across Australasia, however, winter temperature extremes are not considered a primary control on mangrove encroachment. In this region, where encroachment has most commonly been reported as *A. marina* moving into *Sarcocornia*–*Sporobo-*

lus salt marshes, numerous local and regional drivers have been proposed. These include increased rainfall in subtropical locations (Eslami-Andargoli *et al.*, 2009), increases in sedimentation following catchment development in New Zealand (Lovelock *et al.*, 2007), altered tidal regimes, enhanced nutrient concentrations and regional subsidence (Saintilan & Williams, 1999). It has also been demonstrated that mangroves have a higher capacity than salt marshes to respond to sea level rise through vertical sediment accretion throughout the region (Rogers *et al.*, 2006).

Global estimates of mangrove biomass density and its associated C storage potential (237–563 tonnes CO₂ equivalent ha⁻¹) far outweigh those of salt marshes (12–60 tonnes CO₂ equivalent ha⁻¹) (Murray *et al.*, 2011), suggesting that mangrove encroachment may cause a substantial increase in biomass C pools. Such a case has been highlighted recently, with Doughty *et al.* (2015) reporting large increases in C storage as a result of encroachment into a Florida salt marsh, with this increase driven by aboveground biomass, but not belowground biomass or non-biomass (soil) C pools.

Belowground C pools – inclusive of live and dead root biomass, accumulated litter and allochthonous organic matter – are by far the largest C store in coastal, intertidal wetlands. Higher sediment C densities have been reported in mangroves than salt marshes, globally, although density may be highly variable both within and between settings for both ecosystems (Chmura *et al.*, 2003; Pendleton *et al.*, 2012). While comparative data of mature ecosystems suggest belowground C storage should increase with mangrove encroachment of salt marsh, no measurement of the magnitude or temporal dynamics of such a C change has been examined in ‘within-range’ encroachment settings. By contrast, a number of studies have assessed belowground C responses to encroachment of *Spartina alterniflora* dominated salt marshes by *A. germinans* in the northern Gulf of Mexico, although to date, results have been mixed and are largely inconclusive. For example, in Fourchon, Louisiana, Perry & Mendelssohn (2009) reported similar sediment accretion, belowground production, decomposition, and C assimilation between salt marshes and areas encroached by *A. germinans*, proposing that the small stature and areal extent of mangroves after only 15 years of encroachment may have muted any significant effects. Similarly, no effects on bulk density or organic matter content were seen using sediment core depth as a 60-year temporal proxy in ecotones in the same locality (Henry & Twilley, 2013). In Texas, Comeaux *et al.* (2012) assessed, among other factors, the impact of encroachment on C sequestration and sediment geochemistry in back-barrier, sand-dominated wetlands. They found significant

increases in live root density in mangrove sediments at some locations, but did not report any higher organic matter densities associated with this – in fact, sediment organic matter density in new mangrove sediments was lower than in adjacent salt marsh cores. Based on the substantially higher sediment C, and lignin accumulation rates, Bianchi *et al.* (2013) proposed that future mangrove encroachment of all Gulf of Mexico salt marsh could sequester 129 ± 45 Tg C belowground over 100 years.

A difficulty faced by these North American studies is the episodic nature of encroachment at the poleward limit of mangroves. Attempts to quantify changes in ecosystem function are essentially constrained to climate-mediated ‘pulses’ of encroachment; that is, mangrove expansion has historically been interrupted or set back every 30 years or less, rather than there being a continuous shift in ecosystem structure. In our study, we track continuous mangrove encroachment into two south-eastern Australian salt marshes over a 70-year period and undertake biomass and sediment core measurements at locations representing known encroachment timeframes. Using this approach, we aim to: (1) quantify changes in biomass and belowground C stores across the 70-year history of encroachment; (2) identify rates of change for aboveground and belowground stores between sites of contrasting salinity/geomorphic setting, and (3) investigate relationships between mangrove encroachment and surface elevation. The findings from our experimental setting will offer insights relevant into other regions, where changing climate is likely to shift encroachment from ‘pulses’ towards longer term ecosystem change.

Materials and methods

Sampling locations

The Georges River/Botany Bay estuary of south-eastern Australia (Fig. 1a) was chosen as a study estuary because its history of mangrove encroachment is well known from a long time series of aerial photograph coverage (Haworth, 2002). Georges River is a drowned-river valley estuary which flows into the oceanic embayment of Botany Bay. The estuary has a catchment of 930 km² comprising Triassic sandstone and shale. European settlement of the catchment from the early 1800s saw extensive clearing of the northern section of the catchment for farmland. More intensive disturbance to catchment soils occurred from the first half of the 20th century, as residential development began to dominate the northern catchment.

Two salt marsh-mangrove complexes within the system were chosen for analysis (Fig. 1b). An upstream site, referred to hereafter as ‘Georges River’, was chosen within the fluvial-influenced section of the river, located on a ‘half-moon’

embayment adjacent to the main river, ~ 14 km upstream of Botany Bay. A marine site was chosen at Towra Point – a sandy peninsula largely isolated from terrestrial influence on the southern shoreline of Botany Bay. Both sites are currently conservation reserves, with Towra Point also listed as a Ramsar Wetland of International Importance. Rainfall in the region is spread throughout the year, with annual rainfall of 1084 mm y⁻¹ in Botany Bay (Sydney Airport weather station) and 1024 mm yr⁻¹ near the Georges River site (Lucas Heights weather station). Mean \pm SD salinity of open water is 32 ± 3 ppt and 15 ± 8 ppt near the Towra Point and Georges River sites, respectively (Geoscience Australia, 2015).

Avicennia marina is the dominant mangrove in the region. It is a cosmopolitan species with a wide latitudinal distribution ranging from the tropics to the southernmost location of mangroves in Australia (38°S). The root system is structurally complex, comprising cable roots, pneumatophores, fine feeding roots and anchor roots which grow from the trunk. Cable roots grow belowground to a depth of about one metre (Purnobasuki & Suzuki, 2005). The only other mangrove species present in the Sydney region is the river mangrove *Aegiceras corniculatum*, a species more commonly found in lower salinity settings. This species is uncommon at Towra Point, but forms an understorey along with low-statured *A. marina* in parts of the riverine fringe at the Georges River site.

Salt marsh vegetation at both sites is typical of New South Wales coast salt marshes, where the majority of mid-intertidal marsh is considered a single community complex dominated by the low-growing chenopod *Sarcocornia quinqueflora* and grass *Sporobolus virginicus* (Zedler *et al.*, 1995) and upper marsh communities dominated by the taller rush *Juncus kraussii* (Adam *et al.*, 1988). Salt marsh sampling was restricted to the *Sarcocornia* and *Sporobolus* complex at both sites, as this is the community most commonly encroached by mangroves in the region.

Experimental design

A chronosequence experimental design – that is, one which uses space as a substitute for time – was developed to explore the biomass and sediment C changes associated with mangrove encroachment into salt marsh at each of the two study sites. For the Georges River site, orthorectified aerial photographs taken in the years 1943, 1955, 1970, 1982, 1998 and 2013 were georeferenced and overlaid in ARCGIS 10.1 (Esri, Redlands, CA, USA). Overlaying of successive images allowed the identification of field sampling locations where mangrove encroached into salt marsh over the following time periods relative to 2013: 0–15 years; 31–43 years; 58–70 years (Fig. 1c). Mangrove and salt marsh vegetation were easily distinguished based on texture and colour differences in the aerial photographs. For Towra Point, maps of vegetation change created using historical aerial photography (1943, 1956, 1970, 1983, 1999) by Wilton (2002) were used to identify field sampling locations corresponding to the following past time intervals: 0–14 years, 30–43 years and 57–70 years (Fig. 1d). Interpretation of the 1943 images allowed the identification of mature mangrove stands >70 years old at each site. Locations

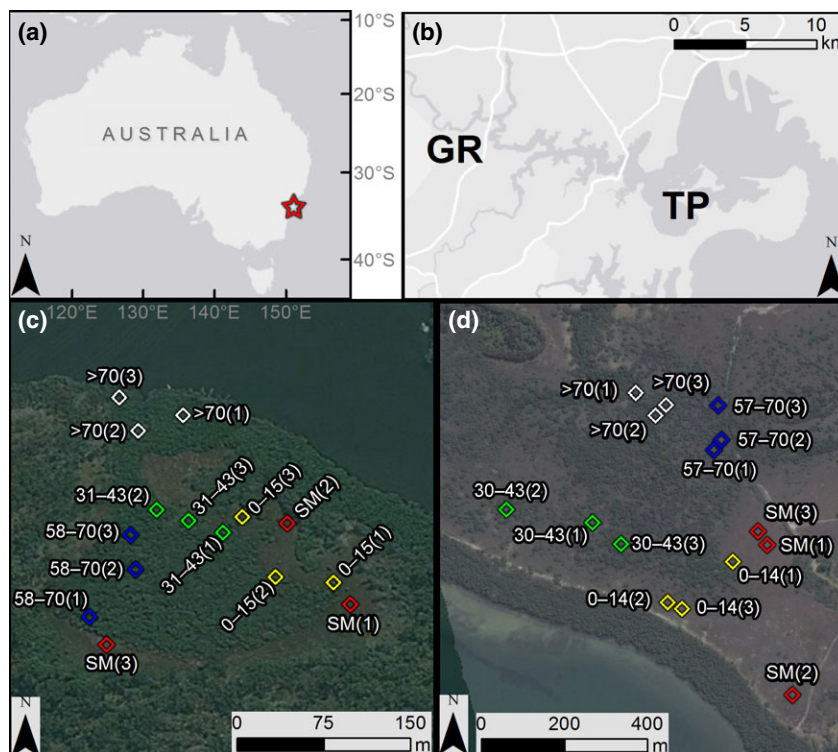


Fig. 1 Maps of the study region (starred) within Australia (a); the Georges River/Botany Bay estuary with Georges River National Park (GR) and Towra Point Nature Reserve (TP) study sites labelled (b); Georges River (c) and Towra Point (d) study sites with core locations labelled and marked by diamonds (white = ≥ 70 years mangroves; blue = 57/58–70 years mangroves; green = 30/31–43 years mangroves; yellow = 0–14/15 years mangroves; red = salt marsh (SM)).

currently vegetated exclusively by salt marsh were identified in the field, with historic photographs/maps used to confirm the absence of mangrove at these sampling locations throughout the 70-year study period. Together, five distinct chronosequence zones were identified at each site: a mature mangrove community >70 years old, three zones where mangrove has replaced salt marsh within the past 0–70 years, and a salt marsh zone which has not been encroached. Three replicate sampling locations were identified for each age zone at each site (Table S1).

Field measurements

At each location, elevation was measured using a modified version of the tidal inundation method described by English *et al.* (1994), whereby three vertical rods marked with water-soluble dye were inserted within 2 m of each core location immediately prior to a summer Spring tide (Georges River: 06/12/2013 predicted tide 1.95 m above lowest astronomical tide (LAT) datum; Towra Point 04/12/2013 predicted tide 1.99 m above LAT). Depth of inundation was measured immediately after the tide receded and subtracted from the predicted tide height. English *et al.* (1994) report an accuracy of within 5 cm elevation for tidal inundation methods. Care was taken during the measurement procedure and in the selection of calm days (to minimize wind and waves effects)

to minimize error among plots. Comparison of three replicate rods revealed a standard error of the mean ≤ 1 cm for each plot. Aboveground biomass measurements were undertaken from October 2013 through January 2014. At each location, mangrove aboveground biomass was determined using a 10×10 m plot centred at location coordinates. All mangrove trees >2 m height were measured for stem height (m) using extendable measuring sticks/tapes and diameter in cm at breast height (DBH; 1.3 m). In cases where *A. marina* had multiple stems branching from the same buttress, each of these stems was measured and treated as a separate tree (Clough *et al.*, 1997). In cases of leaning trees, DBH was measured at 1.3 m along the natural height of the trunk. Allometric equations specific to the species and region as modified by Saintilan (1997) were used to calculate aboveground biomass (W , in kg) of all trees >2 m height:

$$W = \frac{h[0.214(D_{\text{BH}} \times \pi) - 0.113]^2}{10} \quad (1)$$

where, h = stem height (m); D_{BH} = diameter at breast height (cm).

Mangroves <2 m in height (which encompasses saplings and dwarf trees, hereafter referred to collectively as ‘shrubs’) were measured for height, crown depth, maximum crown width and crown length (perpendicular to the maximum width). All shrubs were measured within a 100-m^2 quadrat,

except where >100 shrubs were present and the shrub layer appeared uniform. In such instances, all shrubs were counted, with measurements restricted to the first 25 shrubs encountered in a clockwise direction from bearing 0°. Similarly, in a single Georges River >70 years quadrat where there were more than 400 small *Aegiceras corniculatum* trees (approximate height range 2.5–3.7 m), all trees were counted and the first 25 trees measured. The species *A. marina* and *A. corniculatum* have similar morphology in the height range 0–2.0 m. In the absence of allometric equations for *A. corniculatum* shrubs, shrub biomass was calculated for both species using allometric equations for *A. marina* developed by Woodroffe (1985):

$$W^{-1/3} = 0.489 + 0.100 C \quad (2)$$

where W = total aboveground biomass (g) and C = average canopy width (cm) (calculated as the average of the greatest canopy width and the width of the canopy at right angles to the greatest width).

Salt marsh aboveground biomass was determined by cutting aboveground material from three 30 × 30 cm quadrats randomly located within 2 m of the plot centre. Material was transferred to the laboratory where it was rinsed to remove attached sediment, oven dried to constant mass (60 °C for 72 h) and then weighed. Previous research has suggested no seasonal trends occur in aboveground biomass of *S. quinqueflora* and *S. virginicus* (Clarke & Jacoby, 1994). Because the turnover times of aboveground biomass vary substantially between mangrove (years to decades or more) and salt marsh plants (annual to years), we chose to compare standing biomass stocks across the chronosequence, rather than rates of net primary production; that is, changes in aboveground biomass across the chronosequence are reported in terms of the total standing aboveground biomass (sum of mangrove tree + mangrove shrub + salt marsh biomass per unit of area).

Sediment cores

A sediment core of 1 m depth was collected from the centre of each 100-m² plot, using a piston coring device and a 5-cm-diameter PVC pipe with sharpened edges to cut through root material. Compaction of sediments was estimated by measuring the difference in elevation of the sediment surface within the core barrel and the outer sediment surface. A linear compaction correction factor was later applied along the length of each core based on this measure. Mean ± SD compaction was 14.9 ± 9.1% at Towra Point and 16.8 ± 6.4% at Georges River.

After extraction, cores were capped and transported to the laboratory, where they were kept at 4 °C until analysis. Magnetic susceptibility was measured downcore using a Bartington loop sensor (Model: MS2C) attached to a Multisensor Core Logger (MSCL; GeoTek, UK) to determine the downcore variability of magnetic mineral concentration. The ease with which sediments are magnetized is related to the concentration and composition of magnetisable material contained within the sample (Thompson *et al.*, 1975). In most recent sediment samples, magnetic susceptibility of sediments is a measure of the amount of the mineral magnetite (or its oxidized derivative, haematite) present by unit volume. In addition to

mineralogic sources (mainly soils), human introduced magnetic materials and biogenic sources (including bacterially generated ferrimagnetic material) can also produce magnetic anomalies. 'Wiggle matching' of magnetic peaks among cores is commonly used to correlate stratigraphy among multiple cores (Buylaert *et al.*, 2008) and to correlate stratigraphy in undated cores to a dated reference core in order to verify the timing of sedimentation from catchment erosion (Dearing *et al.*, 1981).

²¹⁰Pb dating

²¹⁰Pb dating of Georges River 58–70 years core #3 was used to confirm the age of the magnetic susceptibility peaks present in Georges River cores. Ten dried and ground sediment aliquots from sediment core depth intervals (0–1; 10–11; 15–16; 20–21; 25–26; 30–31; 40–41; 50–51; 70–71 and 90–91 cm) were analysed by alpha spectrometry at the Australian Nuclear Science Technology Organisation.

A constant rate of supply (CRS) model (Appleby & Oldfield, 1978) using unsupported ²¹⁰Pb activities between 0 and 71 cm was used to calculate the sediment age and mass accumulation rate for each interval (Fig. S1). This type of model was chosen because we expect mass accumulation rates to vary throughout the core chronology, in accordance with changes in vegetation (from low accumulation under salt marsh to high accumulation under mangrove) and due to historic catchment disturbance.

Belowground C analysis

All cores were longitudinally split into half to provide one subsample for current analyses and another subsample for future analyses. Half-cores for this study were subsectioned for bulk density and chemical analysis. Compaction-corrected depth intervals of 0–5, 5–10, 10–15, 15–20, 20–30, 30–50 and 50–100 cm were sectioned for analysis. Bulk sediment was oven dried to constant mass (60 °C for 72 h), and measured to determine bulk density. Sediment was homogenized and ground into a fine powder using a ball mill (MM 301 Ball Mill, Retsch, Germany). The 'Champagne test' (Schlacher & Connolly, 2014) was used to determine whether samples contained inorganic C. Only six aliquots from Towra Point and none from Georges River contained sufficient carbonate to cause bubbling upon acidification. Subsequently, those samples were subject to acid washing with 1M HCl and shaken for 24 h prior to centrifugation, rinsing with Milli-Q (Merck Millipore, Darmstadt, Germany) water and re-drying. Elemental C (total organic C) content (%) was measured for all samples using a CN analyser (LECO TruSpec, LECO Corporation, St. Joseph, MI, USA). Organic C density (g cm⁻³) was determined by multiplying %C by bulk density.

Statistical analyses

Generalized linear models (GzLMs) (Nelder & Baker, 1972) is a statistical approach applied extensively in ecological research because of their ability to deal with the multitude of

distributions that define ecological data (Guisan *et al.*, 2002; Venables & Dichmont, 2004). GzLMs are extensions of general linear models, but are more flexible to data with non-normal error distributions. This is because GzLMs enable analysis of data from a range of distribution types based on an assumed relationship (called a link function) between a linear predictor function of the explanatory variables and the mean of the response variable (Guisan *et al.*, 2002). Separate analyses were performed for each site to test for differences between salt marsh and each of the four ages of mangrove stand. Test variables were total aboveground biomass (mangrove tree + mangrove shrub + salt marsh) (kg m^{-2}), total belowground C store in the surface 1 m (kg C m^{-2}) and C density (g C cm^{-3}) in each of the seven sediment depth intervals.

Regression analyses were performed to assess rates of change in biomass and total belowground C across the chronosequence. Biomass and belowground C were regressed against the mid-point of each of the three transitional time periods. Contemporary salt marsh and >70 years mangroves were excluded because salt marsh to mangrove shift has not yet occurred (contemporary salt marsh), or a start point for the shift cannot be verified by aerial photographs (>70 years). Regressions performed for each site and with sites combined. Statistical analyses were performed using SPSS v19 (IBM Corp., Armonk, NY, USA).

Results

Biomass

Mean \pm SE aboveground biomass in the contemporary salt marsh zone was $0.89 \pm 0.09 \text{ kg m}^{-2}$ at Towra Point and $0.71 \pm 0.06 \text{ kg m}^{-2}$ (Fig. 2). Biomass of 0–14/15 years mangroves was not significantly higher than salt marsh (Table S2; Table S3), and again, was similar between the two sites. After 30 years, however, biomass was significantly higher than salt marsh, with total aboveground biomass increasing with mangrove age at both sites (Fig. 2a, b; Table S2; Table S3).

A shrub layer of *A. marina* was present at both sites, although contributions to overall biomass varied. At Georges River, biomass change was primarily driven by mangroves >2 m in height (Fig. 2a), with saplings populating the <2 m layer. At this site, young trees reached nearly 4 m in the 0–15 years zone and maximum tree height (7.8 m) was reached within 31–43 years. At Towra Point, saplings <2 m were the major component of recent transition areas (52 of 54 individuals measured in 0–14 years zone), and dwarf trees (<2 m) were encountered throughout the older mangrove zones. The contribution of this layer to total biomass declined with age, however, and was negligible in >70 years quadrats (Fig. 2b). Although encountered in one 58–70 years location (nearest the riverine fringe) at Georges River, the smaller river mangrove *Aegiceras corniculatum* did not represent a large contribution,

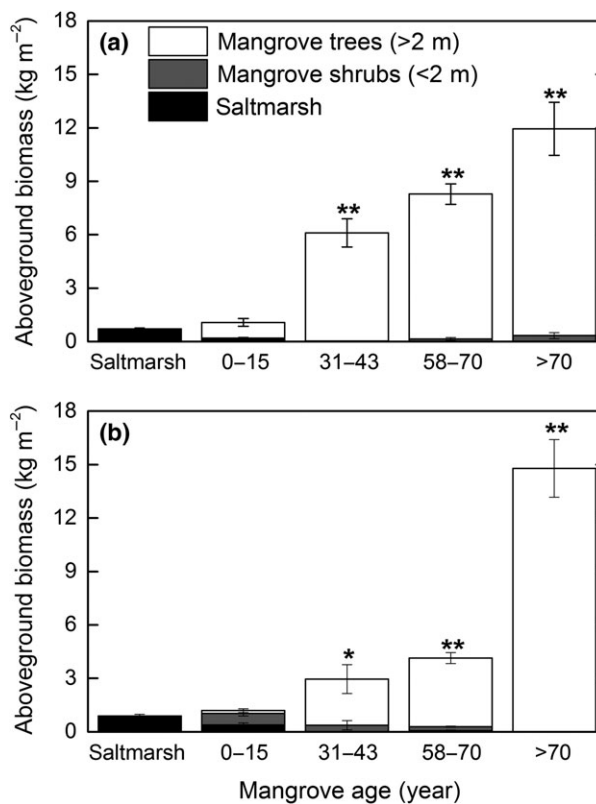


Fig. 2 Mean aboveground biomass by vegetation component across the chronosequence at Georges River (a) and Towra Point (b). Error bars represent 1 SE each side of the mean for each vegetation component. Significant difference from salt marsh value represented by asterisks for $P < 0.05$ (*) and $P < 0.01$ (**) where appropriate.

representing just 1.3% of the total biomass for this age zone.

Belowground C

Total belowground C storage (0–100 cm) was higher at Georges River than Towra Point across all chronosequence zones (Fig. 3). The largest site difference was in salt marsh, where belowground C was 2.4 times higher in Georges River salt marsh (mean \pm SE = 17.32 ± 1.71) relative to Towra Point salt marsh (7.18 ± 0.79), despite similar aboveground biomasses between sites (Figs 2, 3). Site differences in salt marsh belowground C were most pronounced below 15 cm of depth (i.e. below the live rooting zone of salt marsh), where C densities in Towra Point salt marsh were negligible (Fig. 4d–g). At Towra Point, total C storage increased with mangrove age and was significantly higher than salt marsh for 30–43 years and older zone classes relative to salt marsh, but was not significantly higher in 0–14 years mangroves ($P = 0.33$; Table S3).

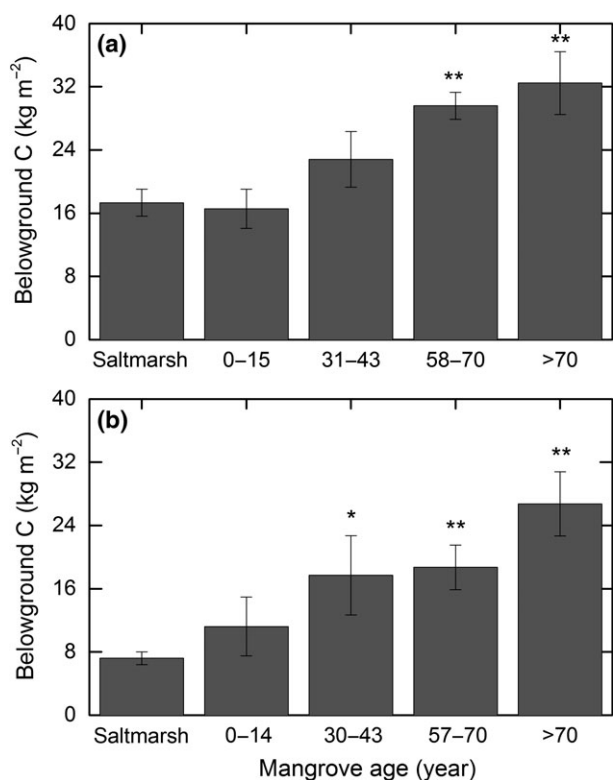


Fig. 3 Mean belowground carbon store (0–100 cm depth) within each vegetation community category at Georges River (a) and Towra Point (b). Error bars represent 1 SE each side of the mean. Significant difference from salt marsh value represented by asterisks for $P < 0.05$ (*) and $P < 0.01$ (**) where appropriate.

There was also a trend of increasing C density at subsurface depths with mangrove stand age (Fig. 4d–g), reflected in depth interval ANOVAs where C density was significantly higher in older mangroves than salt marsh at depths >15 cm, but not within the surface 15 cm (Table S3).

At Georges River, an increasing trend in total belowground C is apparent from 31 to 43 years onward; however, stocks were only significantly higher than salt marsh in 58–70 and >70 years zones ($P < 0.05$) (Fig. 3a). Significant increases above salt marsh C densities were observed in surface depths (0–5 cm) for all mangrove ages with the peak C densities achieved within the first 15 years of encroachment (0.04–0.05 g cm⁻³). By 58–70 years, C densities were significantly higher in 5–10 cm and 10–15 cm ($P < 0.05$), and to a lesser extent at 15–20 cm ($P = 0.06$) (Fig. 4a–d; Table S2). Like Towra Point, increases in belowground C density were apparent in the 15–50 cm depth range (Fig. 3d–f) with the increase becoming apparent across a broader depth range with increasing mangrove stand age (Table S2). Mangrove stands >70 years had significantly higher C

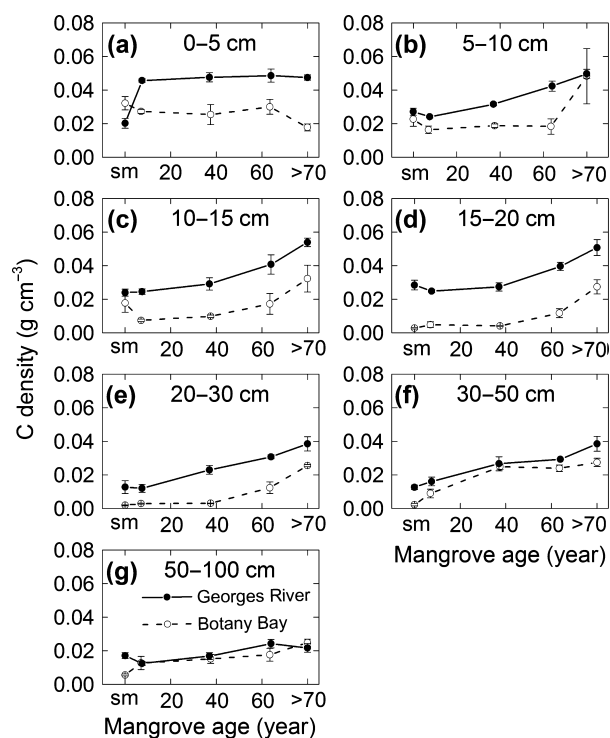


Fig. 4 Belowground carbon (C) density (g C cm⁻³) for Georges River (closed circle) and Towra Point (open circle) for each sampled depth section across the >70 years chronosequence – (a) 0–5 cm; (b) 5–10 cm; (c) 10–15 cm; (d) 15–20 cm; (e) 20–30 cm; (f) 30–50 cm; (g) 50–100 cm. X-axis data are presented as the midpoint of each chronosequence period. SM = salt marsh.

concentrations than salt marsh across the top 50 cm, but not within 50–100 cm (Table S2).

Rates of change

A strong relationship exists between mangrove age and aboveground biomass at each site, although the rate of biomass increase is 2.5 times higher at Georges River than Towra Point (Table 1). The average rate of biomass increase when the two sites are combined was 91 Mg km⁻² yr⁻¹ ($R^2 = 0.58$; $P < 0.001$).

Belowground C store at Georges River increased by ~230 Mg km⁻² yr⁻¹, representing an increase 1.7 times faster than aboveground biomass during the same period at this site. While belowground C was observed to increase throughout the chronosequence at Towra Point (Fig. 3b), the relationship with mangrove age over the period 0–70 years was not as strong as for Georges River.

An elevation gradient was apparent across the chronosequence at Towra Point, with more recent mangrove encroachment growing higher in the tidal frame than older mangrove zones, and salt marsh located at

Table 1 Summary of regression analyses for aboveground biomass and total belowground C store (0–100 cm). Adjusted R^2 values >0.5 as well as significant ($P < 0.05$) regression model P -values represented in bold, with rates of change presented for these cases only

Variable	Site	Slope coefficient \pm SE	R^2	Adjusted R^2	P -value	Mg km ⁻² yr ⁻¹ \pm SE
Elevation (cm)	Georges River	-0.015 \pm 174.11	0.075	0.038	0.167	
	Towra Point	-0.132 \pm 168.61	0.894	0.890	<0.001	
Aboveground biomass (Mg km ⁻²)	Georges River	0.130 \pm 0.018	0.885	0.868	0.000	130 \pm 18
	Towra Point	0.052 \pm 0.010	0.781	0.750	0.002	52 \pm 10
	Sites combined	0.091 \pm 0.019	0.603	0.579	0.000	91 \pm 19
Belowground C store 0–100 cm (Mg C km ⁻²)	Georges River	0.230 \pm 0.062	0.662	0.614	0.008	230 \pm 62
	Towra Point	0.134 \pm 0.094	0.226	0.116	0.196	
	Sites combined	0.184 \pm 0.066	0.326	0.284	0.013	

the highest elevation (Table S1). Regression analysis showed a strong linear relationship (adj. $R^2 = 0.89$) between elevation and mangrove age, suggesting an upslope mangrove encroachment rate of 0.132 cm yr⁻¹ at this site. No such relationship was present at Georges River for contemporary surface elevation, where salt marshes and all mangroves zones younger than 70 years occur at a similar elevation, between 1.72 and 1.77 m above LAT. Peak magnetic susceptibility depth – a proxy for historical surface elevations – did vary among cores, with a broad trend of deeper peak depth in older mangrove zones and more shallow peaks in recent mangroves and salt marsh zones at Georges River (Fig. S2). No magnetic peaks were apparent in Towra Point cores.

The Georges River magnetic susceptibility peak was dated to 1958 (± 7 years) based on ²¹⁰Pb dating of 58–70 years core #3, with an onset of increasing magnetic susceptibility from 1924 (± 11 years) (Fig. 5), which accords well with timing of intensive development in the catchment. Mass accumulation rates obtained from the CRS model show a rapid increase in mass accumulation from this time, with a peak of 0.185 g cm⁻² yr⁻¹ around the time of mangrove expansion to this area (~70 years ago) (Fig. 5). These depths correspond with low belowground C concentrations, with C content increasing rapidly above 20 cm (39 \pm 6 years), concurrent with decreases in both overall mass accumulation rates and magnetic susceptibility (Fig. 5).

Discussion

Intertidal wetlands are dynamic ecosystems that can respond quickly to natural or anthropogenic perturbations. This study tracked the shift from salt marsh to mangrove forest in two nearby, but geomorphically distinct, coastal wetlands over a period of 70 years. At both sites, a continuous landward migration of *Avicennia marina* into previously treeless salt marsh was apparent. As well as altering ecosystem structure, this

vegetation shift brought about a significant change in ecosystem function as demonstrated by significant increases in aboveground biomass and belowground C stocks at both sites.

Biomass growth increases C storage

Aboveground biomass increase was seen at both study sites, as mangroves encroached areas previously vegetated by salt marsh species. This may not be surprising, considering the low biomass of salt marshes relative to mangroves, and in particular, the low aboveground biomass of the *Sarcocornia quinqueflora* and *Sporobolus virginicus* salt marsh community encroached in south-eastern Australia. Rates of aboveground biomass increase across the 70-year chronosequence (130 Mg km⁻² yr⁻¹ at Georges River and 52 Mg km⁻² yr⁻¹ at Towra Point) were modest when compared to biomass production rates of mature forests of *A. marina* (310 Mg km⁻² yr⁻¹) and *Aegiceras corniculatum* (210 Mg km⁻² yr⁻¹) reported in the same region (Clarke, 1994). Alongi *et al.* (2003) report C values of 43.7%, 45.2% and 44.9% for *A. marina* leaves, stems and branches, respectively. If the average C content among these tissues (44.6%) is multiplied by the rates of aboveground biomass increase reported in our study then increases in aboveground C storage under mangrove encroachment are estimated to be 58 \pm 8 Mg C km⁻² yr⁻¹ for Georges River and 23 \pm 4 Mg C km⁻² yr⁻¹ for Towra Point.

Although our study cannot identify with certainty which factors are responsible for the 2.5 fold difference in biomass response between sites, we propose that salinity, nutrient limitation and sedimentation are likely to be key determinants of biomass response. First, growth studies have shown increased growth of *A. marina* seedlings under lower salinities (20–80% seawater concentrations) (Clarke & Hannon, 1970) and, more specifically, declines in photosynthetic capacities of both *A. marina* and *A. corniculatum* with increasing

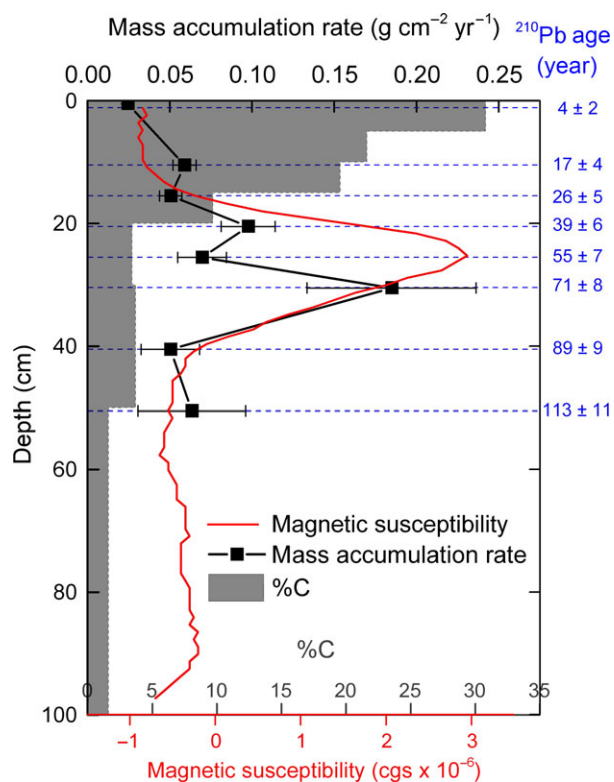


Fig. 5 Downcore profiles of sediment mass accumulation rate, magnetic susceptibility and carbon (C) content of the core chosen for detailed analysis - GR 58-70 years core 3. Peaks in sediment mass accumulation rate and magnetic susceptibility occur at 30 cm (71 ± 8 years) and 25 cm (55 ± 7 years), respectively, within a zone of low carbon content, above which high carbon content corresponds with fine root-dominated peat development. Unsupported ^{210}Pb activities between 0 and 71 cm were used to calculate the sediment age (years before 2013) and mass accumulation rate at each interval. Neither sediment ages nor mass accumulation rates were calculated below 50 cm due to low activities of unsupported ^{210}Pb .

salinity (Ball & Farquhar, 1984), both of which are consistent with the more vigorous biomass response in the mesohaline site. Second, mangrove biomass and forest architecture are known to vary substantially according to nutrient status, ranging from growth of vigorous tall trees in nutrient-rich riverine settings down to dwarf trees in nutrient-poor areas near the coastal fringe (Feller *et al.*, 2007) – a trend generally consistent with biomass differences in our study. Finally, differences in sedimentation among sites may alter the sensitivity of mangrove growth to nutrient enrichment and alter nutrient and carbon cycling (Lovelock *et al.*, 2007). This is of relevance because our data suggest enhanced sedimentation may have been a precursor to mangrove encroachment at the Georges River site (discussed further below). Together, these findings suggest that the

magnitude and rate of biomass change will vary among the range of settings in which mangrove encroachment of salt marsh is taking place, globally.

More broadly, biomass increases in our study were muted when compared to those measured for mangrove encroachment into salt marsh by Doughty *et al.* (2015) on the Atlantic coast of Florida. There, biomass increases were responsible for an overall C increase at the rate of $270 \text{ Mg C km}^{-2} \text{ yr}^{-1}$. The reason for the sharp disparity in biomass accumulation between studies is likely related to the encroachment settings within each location. In the south-eastern USA, encroachment of salt marsh is most often explained in terms of extreme winter climate events (Cavanaugh *et al.*, 2014) where severe freeze events cause an acute disturbance to mangrove survival and growth. In the absence of this disturbance, mangroves may outcompete local salt marsh species with few constraints on aboveground biomass growth. In south-eastern Australia, although the causes of mangrove encroachment are less understood, many of the leading theories – including sea level rise, increased atmospheric CO_2 and long-term changes in precipitation – may be considered more protracted changes; that is, we would expect: (i) a slow easing of the constraints which previously excluded mangroves from expanding into the areas that they now occupy, and (ii) such constraints may continue to operate, albeit to a lesser extent, across the encroachment front.

In this study, we have tracked increases in standing aboveground biomass as mangroves replace salt marshes and begin to develop into mature forests. A significant difference between the two vegetation types, however, is the turnover time of aboveground biomass between salt marshes (annual to years) and mangroves (years to decades or more). Studies which track the fate of aboveground biomass (and the C contained therein) over these timescales, and in relation to disturbances to biomass retention (e.g. storm damage to mangrove forests) will improve our understanding of the longer term C dynamics associated with salt marsh to mangrove transitions.

Importance of belowground C

Belowground stocks (inclusive of belowground biomass) are the most significant C pool in coastal wetlands and, due to their potential for long-term storage, are the primary reason for interest in coastal C initiatives (Sutton-Grier *et al.*, 2014). At both sites, and across all vegetation categories in this study, belowground C (quantified in the surface 100 cm) considerably outweighed aboveground biomass stocks. Mean salt marsh belowground C stocks were within the low (Towra Point mean \pm SE = $7.2 \pm 0.8 \text{ kg C m}^{-2}$) and mid-

ranges (Georges River mean \pm SE = 17.3 ± 1.7 kg C m⁻²) of values reported both within south-eastern Australia (range = 6.1–34.3 kg C m⁻²; mean = 19.1 kg C m⁻²; Saintilan *et al.*, 2013) and globally (mean = 16.2 kg C m⁻²; Duarte *et al.*, 2013). Mature (>70 years) mangrove stands at both sites were above average (Towra Point mean \pm SE = 26.7 ± 4.1 kg C m⁻²; Georges River mean \pm SE = 32.5 ± 4.0 kg C m⁻²) relative to global values (mean = 25.5 kg C m⁻²; Sükamäki *et al.*, 2012; Donato *et al.*, 2011) and *A. marina*-dominated forests in south-eastern Australia (range = 2.5–34.3 kg C m⁻²; mean = 23.1 kg C m⁻²; Saintilan *et al.*, 2013).

The increase in biomass measured aboveground as mangroves encroach salt marsh was also observed belowground in cores analysed for bulk C content. At Georges River, significant increases in belowground C coincided with fine root development of mangroves, with fine root biomass dominating sediment volume in surface layers of encroached areas. Here, both the density of C and depth of sediment in which fine root development was observed increased along the chronosequence. A similar phenomenon has been reported elsewhere, with Osland *et al.* (2012) observing upper sediment layer (0–10 cm) peat development (and associated sediment C accumulation) simultaneous with mangrove forest growth in restored wetlands. Such peat development not only increases belowground C stores, but also has implications for surface elevation dynamics and wetland response to sea level rise (McKee *et al.*, 2007), and we propose that surface peat development has played an important role in altering surface dynamics as mangroves have encroached the Georges River site (discussed further below).

Surface peat development was less pronounced at Towra Point, where C storage in the surface 15 cm did not vary along the chronosequence. Below this, however, C content generally increased with mangrove age, where occasional *A. marina* cable roots and anchor roots were more commonly encountered. At Georges River, similar trends in subsurface (>15 cm) root presence and C density were also apparent across the chronosequence – although, C density differences did not extend to the 50–100 cm depth. This ability of mangrove roots to penetrate to greater depths in the sediment profile may have significant implications for blue C stocks under mangrove encroachment. First, root penetration to 50 cm or more may increase deep C storage, as is suggested by both sites in this study. In terrestrial studies, deep storage has been identified as a key trait in long-term preservation of sediment C, possibly due to suboptimal conditions for microbes or increased protection through organic matter-mineral interactions (Schmidt *et al.*, 2011), although its importance in blue C

ecosystems is not well understood. Second, mangrove root penetration may alter redox potential down core by introducing oxygen to previously anoxic depths (Comeaux *et al.*, 2012). Third, root penetration may also stimulate microbial priming whereby the supply of fresh plant-derived C promotes the microbial mineralization of old, stored C. Such factors may be responsible for the lack of C increase in the 50–100 cm sections at Georges River (Fig. 4g), despite observations of considerable mangrove root biomass, and should certainly be considered in the broader global context of mangrove encroachment.

Timing of belowground C increases

At the higher C site, Georges River, belowground stocks were essentially unchanged in the first 15 years of encroachment despite the rapid change in aboveground vegetation structure (where almost half of all *A. marina* individuals had grown to a height >2 m). Similarly, increases over a similar period at Towra Point were insufficient to identify statistically significant change. These results mirror efforts from multiple authors in the C-rich deltaic wetlands of Louisiana, who have reported little change in belowground production and C assimilation after 15–20 years of *Avicennia germinans* expansion into *Spartina alterniflora* salt marsh (Perry & Mendelsohn, 2009; Henry & Twilley, 2013). Further, in their quantification of biomass change under recent (7 years) mangrove encroachment in Florida, Doughty *et al.* (2015) measured belowground biomass densities just 20% that of aboveground biomass, with belowground biomass C stocks subsequently playing just a small part in the overall C increase reported in that study. Interestingly, these authors proposed that if mangroves were to continue to grow and increase their structural complexity, then changes in sediment properties, including C content, may become apparent. The results of two contrasting wetland settings in our study show that in the absence of extreme winter events, and given sufficient time, significant increases in belowground C stocks do become apparent under mangrove encroachment (see also Lunstrum & Chen, 2014). Our results also have implications for mangrove restoration projects, as they suggest that demonstrating a carbon benefit may take time, and that it would be difficult to extrapolate from measures over just a few years.

Mangrove encroachment, sea level rise and surface elevation gain

The long-held model of estuarine vegetation zonation in south-eastern Australia places mangroves lower in

the tidal frame than the *Sarcocornia-Sporobolus* salt marsh association (Clarke & Hannon, 1967), which would suggest mangrove encroachment of salt marsh in this region involves an upslope migration. Regression analysis showed a negative, linear relationship (adj. $R^2 = 0.89$; $P < 0.001$) between elevation and mangrove age at Towra Point, with younger mangroves zones growing at higher elevations than older mangrove forest. This suggests agreement with this model under a rising sea level scenario; that is, if relative surface elevations across the Towra Point chronosequence are assumed to be static, mangroves would appear to be moving vertically upslope at a rate of 0.132 cm yr^{-1} . This is only slightly faster than sea level rise recorded at nearby Fort Denison (0.108 cm yr^{-1}) over the 1943–2013 study period and within Botany Bay itself (0.115 cm yr^{-1}) for the period of data availability (Fig. S3). We argue mangrove encroachment at this site has occurred simultaneously with sea level rise, with little evidence of surface elevation change (e.g. low peat development) resulting from the ecosystem change.

A different scenario, however, is observed across the Georges River chronosequence, where contemporary surface elevations are similar across the salt marsh, 0- to 15-years-, 31- to 43-years- and 58- to 70-years-old mangroves, with only the >70 years mangroves (located along the riverine fringe) at a lower elevation. Here, we argue that although sedimentation associated with historical catchment changes may have played a role in triggering mangrove expansion, mangrove development has promoted surface elevation growth and increases in belowground C storage. Firstly, a large increase in mass accumulation and magnetic susceptibility beginning at 89 ± 9 years pre-dates the change in vegetation by at least 10 years (Fig. 5), and accords well with the timing of intensive development in the catchment. Second, the presence of strong magnetic peaks in cores from the current salt marsh zone and more recent encroachment areas highlights that this sedimentation did not cause an immediate vegetation change across the entire site. Third, the low C content associated with periods of high mineral deposition suggests sedimentation did not directly enhance C stocks to any great extent, or at least was poorly preserved over time (Fig. 5). Instead, the greater depth of magnetic peaks under older mangroves relative to recent mangrove and salt marsh zones (Table S1) points to an historical elevation gradient at the time of peak magnetic susceptibility (dated to the year 1958 ± 7 years and coinciding with early mangrove expansion at the site). Since that time, it appears that enhanced vertical elevation gains have taken place in the older mangroves (58- to 70-years zone), relative to more recent mangrove and salt marsh zones, producing a contemporary surface

which shows little to no elevation gradient across most of the site (Table S1). This enhanced elevation change in older mangroves is concomitant with both mangrove peat development and increasing belowground C storage, during a period in which sea level rise is known to occur in the region. It is also consistent with our growing understanding of the ability of mangroves to keep pace with changes in relative sea level rise through root contributions to soil volume and upward expansion of the soil surface (McKee *et al.*, 2007; Krauss *et al.*, 2014).

Mangrove encroachment may also alter surface elevation and C storage through access to new non-root materials (i.e. litterfall and downed wood from the developing mangrove canopy) and the enhanced capacity of mangrove pneumatophores to trap particulate organic carbon (POC) and mineral sediment from catchment sources. Such an enhanced sediment accretion capacity of mangroves over salt marshes has been described in south-eastern Australia (Rogers *et al.*, 2006), and this phenomenon is likely to be part of the explanation for surface elevation change and C storage increase seen in this study. Whether enhanced trapping capacity allows for greater accumulation of refractory, allochthonous inputs such as terrestrial POC under mangrove encroachment is still largely unknown, however, and deserves further attention.

Estimates of C storage increases

The present study adds to a small body of literature regarding the temporal dynamics of C stocks in sites experiencing mangrove encroachment of salt marsh (Perry & Mendelssohn, 2009; Comeaux *et al.*, 2012; Osland *et al.*, 2012; Bianchi *et al.*, 2013; Henry & Twilley, 2013; Doughty *et al.*, 2015). To our knowledge, this is the first study to quantify C changes in the south-eastern Australian setting, where mangrove encroachment is a continuous, long-term and widespread phenomenon. While further research across larger spatial scales is necessary (especially across latitudinal gradients), projections based on current data suggest mangrove encroachment has initiated substantial gains in blue C storage in the region. Over the past ~70 years, mangrove encroachment has resulted in the conversion of ~30% or more of salt marsh to mangrove forest across south-eastern Australia (Straw & Saintilan, 2006). While the exact timing and rates of change of mangrove encroachment cannot be determined at a regional scale with current data, extrapolation of findings from the present study suggests a significant increase in blue C stocks has already occurred. Based on a 30% conversion of the current extent of salt marsh in New South Wales (72.6 km^2 ; Creese *et al.*, 2009), biomass increases of $1618\text{--}4044 \text{ Mg yr}^{-1}$ ($113\text{--}239$

283 097 Mg over 70 years) and belowground C increases of up to 7155 Mg C yr⁻¹ (500 864 Mg C over 70 years; extrapolated from Georges River rate only) may have already occurred over the past 70 years in New South Wales alone. If mangroves continue to further encroach salt marshes in the region, as is predicted to happen, annual additions to above and belowground C stores of the magnitude reported here may continue.

Under changing climatic conditions and rising sea levels, mangrove encroachment and forest development of the magnitude reported in this study is likely to become more widespread. The outcomes of the present study may have particular application for regions such as the Gulf of Mexico and Atlantic coast of the USA, where attempts to investigate C changes with encroachment of *A. germinans* have been limited to windows of <30 years (i.e. since freezes in 1983 and 1989 last 'reset' mangrove encroachment across much of that region). Recent research in that region suggests future expansion of *A. germinans* may be accelerated by increases in mangrove forest resistance and resilience to extreme winter events as forests mature in size (Osland *et al.*, 2015). In other words, a more continuous long-term encroachment, such as that seen in south-eastern Australia, is likely to occur if mangroves mature sufficiently before the next 'reset' event. Then, C increases of the magnitude seen in the present study – but largely eluding those of shorter term studies in the USA – might be seen in coming decades.

At present, global estimates of salt marsh extent vary markedly, from 22 000 to 400 000 km² (McLeod *et al.*, 2011; Duarte *et al.*, 2013), and it is not currently known what proportion of global salt marsh extent is likely to be affected by mangrove expansion. Clearly, refinement of global salt marsh and mangrove encroachment extents are required. The C storage estimates provided in our study should encourage broader investigation of mangrove encroachment and long-term C dynamics associated with this important ecosystem change.

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References

- Adam P (1993) *Saltmarsh Ecology*. Cambridge University Press, Cambridge.
- Adam P, Wilson N, Huntley B (1988) The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Australia)*, **7**, 35–85.
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation*, **29**, 331–349.
- Alongi DM, Clough BF, Dixon P, Tirendi F (2003) Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees*, **17**, 51–60.
- Appleby P, Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210 Pb to the sediment. *Catena*, **5**, 1–8.
- Ball MC, Farquhar GD (1984) Photosynthetic and stomatal responses of the grey mangrove, *Avicennia marina*, to transient salinity conditions. *Plant Physiology*, **74**, 7–11.
- Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW (2013) Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science*, **119**, 7–16.
- Burns B, Ogden J (1985) The demography of the temperate mangrove [*Avicennia marina* (Forsk.) Vierh.] at its southern limit in New Zealand. *Australian Journal of Ecology*, **10**, 125–133.
- Buylaert JP, Murray AS, Vandenberghe D, Vriend M, De Corte F, Van Den Haute P (2008) Optical dating of Chinese loess using sand-sized quartz: establishing a time frame for Late Pleistocene climate changes in the western part of the Chinese Loess Plateau. *Quaternary Geochronology*, **3**, 99–113.
- Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC (2014) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 723–727.
- Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, **17**, 22:1–22:12.
- Clarke PJ (1994) Base-line studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Australian Journal of Botany*, **42**, 37–48.
- Clarke LD, Hannon NJ (1967) The mangrove swamp and salt marsh communities of the Sydney district: I. Vegetation, soils and climate. *The Journal of Ecology*, **55**, 753–771.
- Clarke LD, Hannon NJ (1970) The mangrove swamp and salt marsh communities of the Sydney district: III. Plant growth in relation to salinity and waterlogging. *The Journal of Ecology*, **58**, 351–369.
- Clarke PJ, Jacoby CA (1994) Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia. *Marine and Freshwater Research*, **45**, 1521–1528.
- Clough BF, Dixon P, Dalhaus O (1997) Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Australian Journal of Botany*, **45**, 1023–1031.
- Comeaux RS, Allison MA, Bianchi TS (2012) Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, **96**, 81–95.
- Creese R, Glasby T, West G, Gallen C (2009) Mapping the habitats of NSW estuaries. In: *NSW Fisheries Final Report Series 113*. pp. 1–95. Industry & Investment NSW, Port Stephens, NSW, Australia.
- Dearing JA, Elnor JK, Happey-Wood CM (1981) Recent sediment flux and erosional processes in a Welsh upland lake-catchment based on magnetic susceptibility measurements. *Quaternary Research*, **16**, 356–372.
- Donato DC, Kauffman JB, Murdiyarto D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4**, 293–297.
- Doughty CL, Langley JA, Walker WS, Feller IC, Schaub R, Chapman SK (2015) Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries and Coasts*, doi:10.1007/s12237-015-9993-8.
- Duarte CM, Middelburg J, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, **2**, 1–8.
- Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, **3**, 961–968.
- Duke N, Ball M, Ellison J (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology & Biogeography Letters*, **7**, 27–47.
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722.
- English SS, Wilkinson CC, Baker VV (1994) *Survey Manual for Tropical Marine Resources*. Australian Institute of Marine Science (AIMS), Townsville.

- Eslami-Andargoli L, Dale P, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, **85**, 292–298.
- Feller IC, Lovelock CE, McKee KL (2007) Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems*, **10**, 347–359.
- Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews*, **87**, 346–366.
- Geoscience Australia (2015) Australian Online Coastal Information – Ozcoasts. www.ozcoasts.gov.au.
- Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.
- Haworth R (2002) Changes in mangrove/saltmarsh distribution in the Georges River estuary, southern Sydney, 1930–1970. *Wetlands (Australia)*, **20**, 80–103.
- Henry KM, Twilley RR (2013) Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. *Journal of Coastal Research*, **29**, 1273–1283.
- Krauss KW, From AS, Doyle TW, Doyle TJ, Barry MJ (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. *Journal of Coastal Conservation*, **15**, 629–638.
- Krauss KW, McKee KL, Lovelock CE, Cahoon DR, Saintilan N, Reef R, Chen L (2014) How mangrove forests adjust to rising sea level. *New Phytologist*, **202**, 19–34.
- Lovelock CE, Feller IC, Ellis J, Schwarz AM, Hancock N, Nichols P, Sorrell B (2007) Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, **153**, 633–641.
- Lunstrum A, Chen L (2014) Soil carbon stocks and accumulation in young mangrove forests. *Soil Biology and Biochemistry*, **75**, 223–232.
- Magenheimer J, Moore T, Chmura G, Daoust R (1996) Methane and carbon dioxide flux from a macrotidal salt marsh, Bay of Fundy, New Brunswick. *Estuaries and Coasts*, **19**, 139–145.
- McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16**, 545–556.
- McKee K, Rogers K, Saintilan N (2012) Response of saltmarsh and mangrove wetlands to changes in atmospheric CO₂, climate, and sea level. In *Global Change and the Function and Distribution of Wetlands* (ed. Middleton BA), pp. 63–96. Springer, Dordrecht, the Netherlands.
- Mcleod E, Chmura GL, Bouillon S *et al.* (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, **9**, 552–560.
- Murray BC, Pendleton L, Jenkins WA, Sifleet S (2011) Green payments for blue carbon: Economic incentives for protecting threatened coastal habitats. Nicholas Institute for Environmental Policy Solutions, Report NI, 11.
- Nelder JA, Baker R (1972) Generalized linear models. *Encyclopedia of Statistical Sciences*, **135**, 370–384.
- Nixon SW (1980) *Between Coastal Marshes and Coastal Waters: A Review of Twenty Years of Speculation and Research on the Role of Salt Marshes in Estuarine Productivity and Water Chemistry*. Springer US, New York, NY.
- Osland MJ, Spivak AC, Nestlerode JA *et al.* (2012) Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems*, **15**, 848–866.
- Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, **19**, 1482–1494.
- Osland MJ, Day RH, From AS, Mcleod ML, Mcleod JL, Kelleway JJ (2015) Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. *Ecosphere*, **6**, 1–15.
- Pendleton L, Donato DC, Murray BC *et al.* (2012) Estimating global “Blue Carbon” emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One*, **7**, e43542.
- Perry CL, Mendelsohn IA (2009) Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands*, **29**, 396–406.
- Purnobasuki H, Suzuki M (2005) Functional anatomy of air conducting network on the pneumatophores of a mangrove plant, *Avicennia marina* (Forsk.) Vierh.
- Rogers K, Wilton KM, Saintilan N (2006) Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science*, **66**, 559–569.
- Saintilan N (1997) Above-and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research*, **48**, 147–152.
- Saintilan N, Rogers K (2015) Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist*, **205**, 1062–1070.
- Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography*, **8**, 117–124.
- Saintilan N, Rogers K, Mazumder D, Woodroffe C (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science*, **128**, 84–92.
- Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, **20**, 147–157.
- Schlacher TA, Connolly RM (2014) Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. *Methods in Ecology and Evolution*, **5**, 541–550.
- Siikamäki J, Sanchirico JN, Jardine SL (2012) Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences*, **109**, 14369–14374.
- Schmidt MW, Torn MS, Abiven S *et al.* (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, **478**, 49–56.
- Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, **14**, 435–444.
- Straw P, Saintilan N (2006) Loss of shorebird habitat as a result of mangrove incursion due to sea-level rise and urbanization. In: *Waterbirds Around the World* (eds Boere GC, Galbraith CA, Stroud DA), pp. 717–720. The Stationery Office, Edinburgh.
- Sutton-Grier AE, Moore AK, Wiley PC, Edwards PET (2014) Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: operationalizing carbon sequestration and storage. *Marine Policy*, **43**, 246–253.
- Thompson R, Battarbee R, O’sullivan P, Oldfield F (1975) Magnetic susceptibility of lake sediments. *Limnology and Oceanography*, **20**, 687–698.
- Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries research*, **70**, 319–337.
- Wilton KM (2002) *Coastal Wetland Habitat Dynamics in Selected New South Wales Estuaries*. Australian Catholic University Sydney, Australia.
- Woodroffe CD (1985) Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science*, **20**, 265–280.
- Zedler J, Nelson P, Adam P (1995) Plant community organization in New South Wales saltmarshes: species mosaics and potential causes. *Wetlands (Australia)*, **14**, 1–18.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of estimated elevation of field sampling locations and depth and intensity of magnetic susceptibility within sediment core.

Table S2. Summary of Generalised Linear Model results for Georges River aboveground biomass, total belowground C store (0–100 cm) and depth intervals.

Table S3. Summary of Generalised Linear Model results for Towra Point aboveground biomass, total belowground C store (0–100 cm) and depth intervals.

Fig. S1. Georges River core #3 unsupported 210Pb activity profile and calculated CRS model sediment ages.

Fig. S2. Magnetic susceptibility profiles for each sediment core collected at Georges River.

Fig. S3. Mean monthly sea level at nearby Fort Denison for the entire study period (1943–2013) and within Botany Bay (data available from 1981).