Anthropogenic impacts on mangrove and saltmarsh communities in eastern Australia

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Contents

Summary

Currently, half of the global population is living in urban areas and it is expected to rapidly grow by 13% until 2050. In Australia, 85% of its population lives within 50 km of the coastline. Population growth will strongly impact intertidal coastal wetlands, such as mangroves and saltmarshes. In particular saltmarshes occur in a vulnerable position between mangroves on the seaward side and freshwater plants and human development on the landward side. Saltmarshes are facing threats from rising sea level, landward migration of mangroves, and in urban regions, from stormwater run-offs carrying litter, nutrients, oil, petrol and agrochemicals.

This thesis used various approaches to examine the anthropogenic effects on the mangrove and saltmarsh communities of south-east Australia. First on a local scale, where we investigated the impact of polluted urban stormwater on saltmarsh and mangrove species composition and distribution. We showed that stormwater facilitates the growth of exotic freshwater plants into saltmarsh vegetation downslope of stormwater outlets and the expansion of mangroves into saltmarsh vegetation from the seaward side. This results in a squeezing effect on the saltmarshes that occur between urban development and mangrove forest. This effect was found to be strongest in industrialised areas.

In a second study, we aimed to validate our findings of the field study in a controlled greenhouse experiment. We established 28 mesocosms containing a mixture of native saltmarsh community and invaded them with four different exotic plant seedlings. The nutrient and salinity levels were adjusted according to those found in natural and industrial areas. Our findings suggest that under natural conditions of saltmarsh habitat (high salinity-low nutrients), the establishment of exotic plant seedlings is restricted. Lower salinity through freshwater input increased the survival of invading exotic species significantly. Additional nutrients increased biomass production but not necessarily survival of exotics.

In another glasshouse experiment, we investigated the effect of elevated CO_2 and changes in salinity on seedling growth of two mangrove species grown individually and in a model saltmarsh community. Elevated CO_2 promoted mangrove and saltmarsh growth. It can be assumed that under rising CO_2, mostly caused by anthropogenic climate change, mangrove encroachment into saltmarshes will be facilitated. Especially if other disturbing factors, such as herbivory or rising sea level, will reduce the competition effect of saltmarshes.

Finally, at the regional scale, we used a remote sensing approach to assess if the changes in vegetation pattern, observed in our field study (Chapter 2), can be detected in aerial images of extremely modified catchments over a 42-year period. Our analysis showed that large areas of saltmarshes have been lost since 1970. By contrast, saltmarsh fringing Casuarina and Melaleuca communities greatly increased, indicating seaward encroachment into saltmarsh communities. However, based on the number of our imagery, the loss of saltmarsh could not be associated with mangrove expansion.

While intertidal coastal wetlands are generally not considered as threatened through species invasion, due to their adaptation to saline environments, we showed that urban saltmarshes are indeed threatened by a squeezing effect from the seaward side by mangroves and from the landward side by exotic plants and freshwater plants. This trend is particularly threatening with high disturbances in industrialised estuaries by freshwater and nutrient input. Management strategies, such as buffer zones and educational programs to foster the avoidance of overfertilization, are needed to avoid the freshening of intertidal wetlands in proximity to urban development. Further squeezing of saltmarsh communities in urban areas will lead to its destruction and thus to a loss of important habitat as well as ecosystem services they provide to us humans.

Zusammenfassung

Aktuell lebt die Hälfte der Weltbevölkerung in urbanisierten Regionen und es wird erwartet, dass diese bis 2050 um weitere 13 % steigen wird. In Australien leben 85% der Bevölkerung in Küstennähe und durch die global steigende Bevölkerungsdichte sind dadurch auch insbesondere die tidebeeinflussten Feuchtgebiete entlang von Küsten, wie Mangroven und Salzmarsche, stark bedroht. In Südostaustralien nehmen insbesondere Salzmarsche einen empfindlichen Platz entlang des Höhengradienten von Gewässerufern ein. Sie kommen zwischen Mangroven, auf der seewärtigen Seite, und Süßwasservegetation sowie urbaner Bebauung, auf der landwärtigen Seite, vor. Zusätzlich zur landwärtigen Migration von Mangroven und dem steigenden Meeresspiegel, werden Salzmarsche durch abgeleitetes Regenwasser, insbesondere bei Extremwetterereignissen, bedroht. Das verschmutzte Regenwasser, in dem sich Straßenabfälle, Öl, Benzin und Chemikalien anlagern, wird in vielen Fällen direkt in die Feuchtgebiete geleitet.

Die vorgelegte Dissertation kombiniert verschiedene Forschungsansätze, um auf unterschiedlichen geografischen Skalen den anthropogenen Einfluss auf Salzmarsch-Mangroven Gesellschaften entlang der Südostküste Australiens zu untersuchen. Zunächst untersuchten wir auf lokaler Ebene den Einfluss von kontaminiertem Süßwasser auf die Komposition und Verbreitung von Salzmarsch- und Mangrovengesellschaften. Wir konnten zeigen, dass das Einbringen von kontaminiertem Regenwasser, die Etablierung von exotischen Süßwasserpflanzen entlang der Salzmarsche begünstigt. Das abgeleitete Regenwasser und die dadurch erhöhten Nährstoffgehalte unterstützen zudem die Ausbreitung von Mangroven. Da die Invasion von Süßwasserpflanzen von der Landseite, und die Mangrovenexpansion von der Seeseite her geschieht, werden die Salzmarschen von beiden Seiten bedrängt. Dies konnte besonders in industrialisierten Gebieten gezeigt werden.

Das zweite Projekt zielte darauf ab, die vorherige Feldstudie unter kontrollierten Bedingungen im Gewächshaus zu überprüfen. Dazu invadierten wir 28 Mesokosmen, bestehend aus nativen Salzmarscharten, mit vier verschiedenen exotischen Süßwasserpflanzen. Die Nährstoffgehalte und der Salzgehalt im Boden wurden den natürlichen Konzentrationen und denen in industriellen Gebieten angepasst. Unsere Ergebnisse zeigten, dass die Etablierung von exotischen Arten unter natürlichen Bedingungen (hoher Salzgehalt und niedriger Nährstoffgehalt) stark eingeschränkt ist. Geringer Salzgehalt im Boden durch Süßwassereintrag erhöhte die

Überlebensrate der exotischen Pflanzen signifikant. Erhöhte Nährstoffgehalte führten zwar zu stärkerer Biomasseproduktion, verbesserten allerdings nicht die Überlebensrate.

In einem weiteren Gewächshausexperiment untersuchten wir die Auswirkungen von erhöhtem CO_2 und variierendem Salzgehalt auf das Wachstum von zwei verschiedenen Mangrovenarten. Diese wuchsen zum einen isoliert und zum anderen in Konkurrenz mit einer Salzmarschgesellschaft, bestehend aus drei typischen Salzmarscharten Südostaustraliens. Hohe CO_2 Konzentrationen unterstützten sowohl den Mangroven als auch den Salzmarschwuchs. Klimawandelbedingte Erhöhung von CO_2 wird somit die Migration von Mangroven in Salzmarschhabitate erleichtern. Besonders wenn weitere Faktoren, wie Herbivorie und der Anstieg des Meeresspiegels, die Konkurrenzfähigkeit der Salzmarsche reduzieren.

In einer letzten Studie testeten wir auf regionaler Ebene die Ergebnisse aus der ersten Feldstudie, mit Hilfe von Fernerkundungstechniken. Anhand von Lauftaufnahmen über einen Zeitraum von 42 Jahren untersuchten wir, ob die Veränderungen innerhalb der Feuchtgebietvegetation in stark modifizierten Gewässern beobachtet werden können. Unsere Analyse zeigte, dass weite Bereiche von Salzmarschen seit den 1970er Jahren verloren gegangen sind. Im Gegensatz dazu, hat die Fläche von *Casuarina* spp. und *Melaleuca* spp. Pflanzengemeinschaften stark zugenommen, was uns vermuten lässt, dass diese von der Landseite aus in die Salzmarsche migrierten. Jedoch konnten wir anhand der Anzahl der Bilder, den Verlust von Salzmarsche durch Mangroven Migration nicht belegen.

Tidebeeinflusste Feuchtgebiete gelten in der Regel nicht als durch Süßwasserpflanzen invasionsanfällige Ökosysteme. Wir konnten jedoch zeigen, dass die Einengung der Salzmarsche, in unmittelbarer Nähe zu urbanen Gebieten, von Mangroven auf der Seeseite und von exotischen Pflanzen auf der Landseite durch Abwassereinleitung verschlimmert wird. Dieser Trend ist besonders stark entlang industrialisierten Ästuaren durch den erhöhten Süßwasser- und Nährstoffeintrag. Auch einheimische Süßwasserpflanzen, die natürlich am Rand der Salzmarschzone vorkommen, scheinen über die letzten 42 Jahre stark vom Frischwassereintrag profitiert zu haben. Dieser Trend ist besonders stark entlang industrialisierten Ästuaren durch den erhöhten Süßwasser- und Nährstoffeintrag. Managementstrategien, wie bepflanzte Pufferzonen und Bildungsprogramme, die zum Beispiel auf eine Verminderung des Nährstoffeintrages hinzielen, werden dringend benötigt. Wenn die Verdrängung der Salzmarsche nicht vermindert wird gehen nicht nur Lebensräume für viele Tierarten verloren, sondern auch wichtige ökosystematische Dienstleistungen, die uns Menschen betreffen.

Chapter 1

Introduction to anthropogenic impacts on mangrove and salt-marsh communities in Eastern Australia

Ina Geedicke

Introduction

The wetland system of mangroves and saltmarshes

Wetlands currently comprise 5 – 8 % of the earth's surface however it is estimated that more than half of the global distribution of wetlands has been lost, most of it during the twenty-first century (Mitsch and Gosselink, 2015). By definition under the Ramsar Convention (2016), wetlands are partially or completely inundated areas with static or flowing fresh, brackish or saline water, where the depth at low tide must be below 6 m. Saltmarshes and mangroves belong to coastal intertidal wetlands and their occurrence is determined by salt concentrations and tidal inundations, distinguishing these ecosystems from freshwater wetlands (Adam, 2009). Because of their ability to create habitat and support entire ecological communities, saltmarsh and mangrove species are considered as foundation species (Osland et al., 2015). They form important habitats and feeding grounds for bats, invertebrates and birds (Kelleway et al., 2017), as well as nursery grounds for many fish species (Alongi, 2002; Lee et al., 2014). A high abundance of juvenile fish and shrimps are found in mangroves, due to the high abundance of food, while at the same time aerial roots provide a shelter against predators (Beck et al., 2001). The infrequently inundated upper saltmarsh is not a constant habitat for juvenile fish, however here the highest concentrations of invertebrate larvae may be found within estuaries (Kelleway et al., 2017) and it has been shown that grazing of saltmarshes reduces the food availability of invertebrates to fishes (Friese et al., 2018). Mazumder et al. (2009) showed that burrowing crabs synchronize their spawning with the spring tide that reaches the saltmarsh, which in turn leads to an efficient feeding opportunity for fishes.

Coastal intertidal wetlands also provide important ecosystem services to humans. It is estimated that they provide services worth US$ 24.8 trillion annually, making them one of the most valuable ecosystems globally (Costanza et al., 2014). These services include the filtration and trapping of pollutants and nutrients, for example from oil spill and stormwater run-off, carbon sequestration and storage, elevation maintenance and cultural uses (Kelleway et al., 2017). While serving as an ecotone between the terrestrial and oceanic environments, saltmarshes and mangroves are the frontline for stabilization of coastal and intertidal zones by trapping sediment and providing protection against rising sea level and storm damage (Doody, 2008; Krauss et al., 2014; Mcleod and Salm, 2006; Möller et al., 2014). However, the level of coastal protection and vertical sediment accretion is variable, depending on the size of wetland area, the height and density of vegetation, as well as the sedimentation rates of the catchment (Craft et al., 2009; Kelleway et al., 2017; Lee et al., 2014).

A recent study reported a total saltmarsh area of 54950 km^2 across 43 countries and territories (Mcowen et al., 2017). Mangroves cover 83,495-137,760 km^2 of coastal areas across 118 countries and territories (Giri et al., 2011b; Hamilton and Casey, 2016) and are only found in tropical to subtropical regions (Figure 2). The distribution of mangroves is mainly limited by temperature. As they are intolerant of frost, they are completely replaced by saltmarshes at latitudes above 32°N and 40°S (Stuart et al., 2007) when the water surface temperature drops below 20°C in winter (Alongi, 2009). While species richness of mangroves decreases with distance from the tropics, saltmarsh species richness increases towards the poles (Duke et al., 1998; Saintilan et al., 2009). The coexistence of saltmarshes and mangroves can be found in subtropical to temperate Australia, Florida and along the northern coastline of New Zealand (Chapman, 1977; Morrisey et al., 2007). Normally, the boundaries between saltmarshes and mangroves are sharp, but at temperate sites they can become patchy, with mangroves interspersed amongst saltmarsh communities (Adam, 2009). Environmental and geomorphological parameters controlling the distribution of mangroves and saltmarshes have long been discussed (e.g. Adam, 1990; Woodroffe, 1990). Saltmarshes are governed by the sea-level and sediment-supply regime, as well as low wave energy (Bakker, 2014). It has been proposed that mangroves establish best at temperatures of the coldest month being higher than 20C, rooting of propagules in loose soil or sediment and at shores with low energy waves (Rogers and Krauss, 2018). In general, these assumptions hold true, but there are exceptions showing mangroves adapted to short freezing periods (Stevens et al., 2006; Stuart et al., 2007), and at different geomorphic settings (Saintilan et al., 2014; Semeniuk, 2013, 1983).

The accretion of sediment particles and low wave energy are a premise for mangrove trees to establish roots (Alongi, 2002). This is mostly the case in intertidal estuaries, where they usually occupy the area between mean sea level and mean spring tide (Alongi, 2009). Mangroves are shrubs and trees that grow in periodically waterlogged soil and in water of fluctuating salinity, that can vary between salinity of freshwater and three-times of seawater salt concentration (Feller et al., 2010). Fluctuations in salinity occur through evaporation leading to high soil salinity and through freshwater flushing leading to a decrease in soil salinity (Feller et al., 2010). These harsh conditions require special adaptations to overcome the lack of oxygen in the waterlogged soil and the restraint of water uptake due to salt induced negative osmotic pressure. To cope with high salt concentrations, mangrove species have developed different strategies of salt exclusion by the roots, salt sequestration by specialized tissue or secretion of excess salt through, for example, salt glands on leaves (Hogarth, 2007). To oxygenize their root systems, mangroves have developed aerenchyma and various forms of aerial roots (Scholander et al., 1962), such as the stilt roots in *Rhizophora* that can make up to 24% of the above-ground biomass of a growing tree (Figure 1A) (Hogarth, 2007). Mangroves of the family Avicenniaceae grow vertical structures known as pneumatophores, that emerge from the soil and can grow up to 30 cm tall. A single *Avicennia* tree of 2-3 m in height may grow up to 10,000 pneumatophores, emerging from the soil every 10-15 cm in a wide range around the tree (Figure 1B) (Hogarth, 2007). Mangroves often form dense forests with either no ground cover or sparse distribution of understorey herbs, frequently consisting of monospecific stands. Taking advantage of the tidal inundation, most mangroves have evolved a specialized reproductive strategy in which they grow viviparous propagules on the parental tree that are photosynthetically active and buoyant and are dispersed by tidal or ocean currents (Rabinowitz, 1978; Stieglitz and Ridd, 2001), often over long distances (Nettel and Dodd, 2007). Tolerances to flooding and salinity and the ability to persist in variable habitats have evolved multiple times through convergence, not from common descent, resulting in about 70 mangrove species from 20 families (Alongi, 2009).

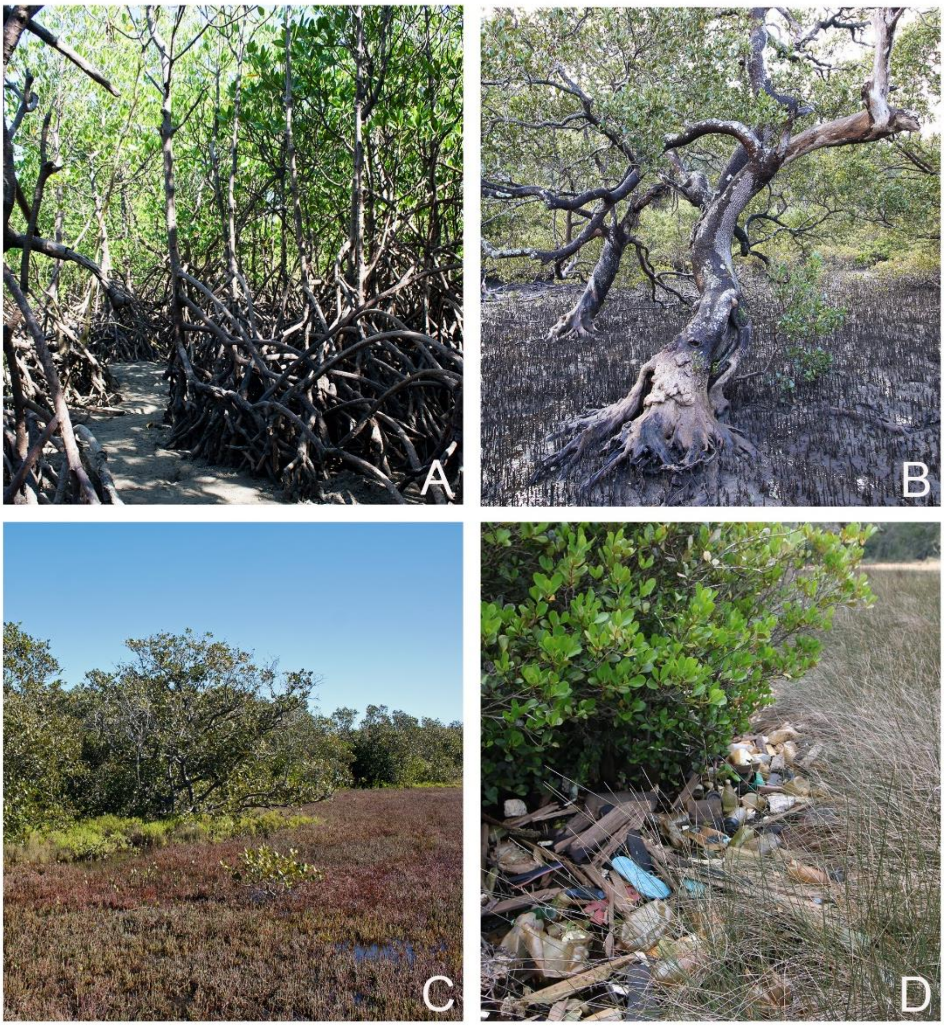

Figure 1| Australian coastal intertidal wetland vegetation. A shows the typical stilt roots of *Rhizophora stylosa* in Darwin, WA, and B the pneumatophores of a mature *Avicennia marina* tree in Jervis Bay, NSW. C depicts the mostly strict zonation of mangrove and saltmarsh communities (Careel Bay, NSW) and D illustrates a coastal intertidal wetland flooded with pollution and debris (Georges River, NSW).

Another vegetation type that inhabits areas subject to periodic flooding by the tide are coastal saltmarshes; they are restricted to the upper intertidal environment, in general between the elevation of the mean high tide and mean spring tide (Adam, 2009). They are found on soft substrate shores of estuaries and embayments, and on some open low wave energy coasts (Adam, 2009). In contrast to mangroves, saltmarsh communities are comprised of a mixture of herb, grass and low shrub species which are highly specialised to enable survival under saline and partially waterlogged conditions (Adam, 1990). At low-lying intertidal areas (lower marsh) saltmarsh plants experience soil salinity similar to the flooding water but also longer periods of waterlogging due to tidal inundation at least once a day (Bakker, 2014). Saltmarsh plants at higher elevation (upper marsh) need to be adapted to greater soil salt concentrations, due to evaporation of water and less frequent flooding, occurring only during spring tides (Clarke and Hannon, 1967). At higher elevations, the interaction of flooding and climate influences the soil salinity, which can lead to high salinity and salt crust forming during dry periods or diminish soil salinity to freshwater conditions under heavy rainfall (Adam, 1990). Generally, with higher elevation the species richness in saltmarshes increases, where often only a single species occupies the lower marsh (Adam, 1990; Suchrow et al., 2015). Globally there are approximately 500 described saltmarsh species (Silliman, 2014). The adaptation strategies of saltmarsh species to extreme environmental conditions are similar to those described for mangroves: excretion, sequestration and exclusion of salt (Rogers et al., 2017). Saltmarsh seeds are able to survive submergence in salt water; however, germination rates are often low (Adam, 1990; Wolters and Bakker, 2002). The long-term maintenance of saltmarsh communities suggests therefore that vegetative propagation is of importance (Adam, 1990).

Saltmarshes and mangroves of Australia

In Australia, mangrove and saltmarsh communities coexist mainly along the east coast of New South Wales (NSW), Victoria and Queensland (Figure 2). The diversity of mangrove species declines with distance from the equator (Rogers et al., 2017). For example, NSW has up to five co-occurring mangrove species at its northern border, while there are more than 41 species found in Australian tropical regions and only one species, *Avicennia marina*, is found at the southernmost occurrence of mangroves in Victoria (Rogers et al., 2017; Saintilan and Williams, 1999). For saltmarsh communities the reverse is true; saltmarsh species richness increases with distance from the equator (Adam, 2009). Northern Australian saltmarshes are dominated by grasses, such as *Sporobolus virginicus*, but Tasmania, Victoria, South Australia and NSW contain 90% of the saltmarsh flora of Australia, even though they only cover 2.5% of the available saltmarsh and saltpan area (Saintilan, 2009). Even though only a small number of species are generally found at one site, the total species pool of saltmarsh species in Australia is reported as 103 species of vascular plants (Saintilan and Rogers, 2013). Saltmarshes can be heterogenous due to variability in environmental factors at local scales with 6 – 8 species growing together within a few square meters, rather than in a continuous band or a single community (Zedler et al., 1995). Where mangroves and saltmarshes co-occur in Australia (Figure 3), saltmarshes are usually found landwards of mangroves occupying the lower and upper marsh, as well as brackish areas, which consist of pools of permanent water of moderate salinity (up to one third of sea water strength) (Rogers et al., 2017; Sainty, 2012). Because the adaptations to saline conditions and waterlogging comes often at the expense of growth rate, saltmarshes seldom penetrate the upslope freshwater systems (Adam, 1990). Landwards of saltmarshes, near the supratidal zone and often occupying the brackish zone as well, *Casuarina glauca* (Swamp She-oak) and *Melaleuca.* species occur (Rogers et al., 2017).

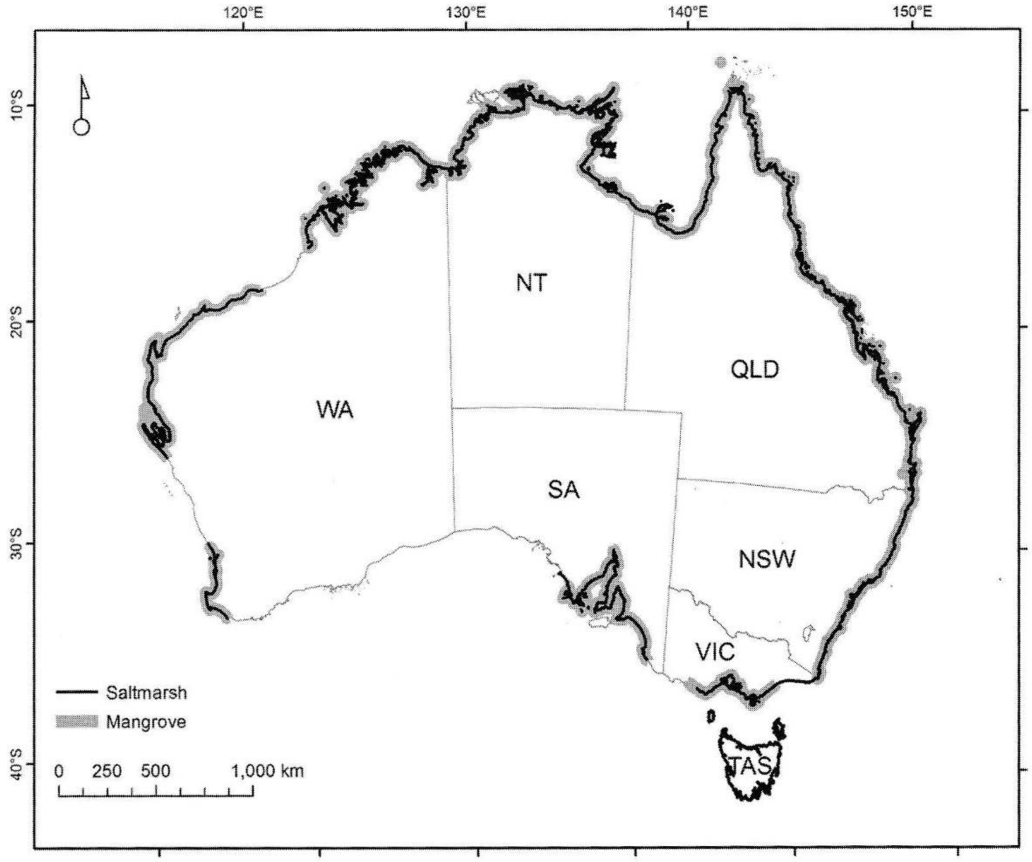

Figure 2| Saltmarsh and mangrove distribution along the coastline of Australia. Black lines indicate saltmarsh areas and grey shadings mangrove communities (Rogers et al., 2017)

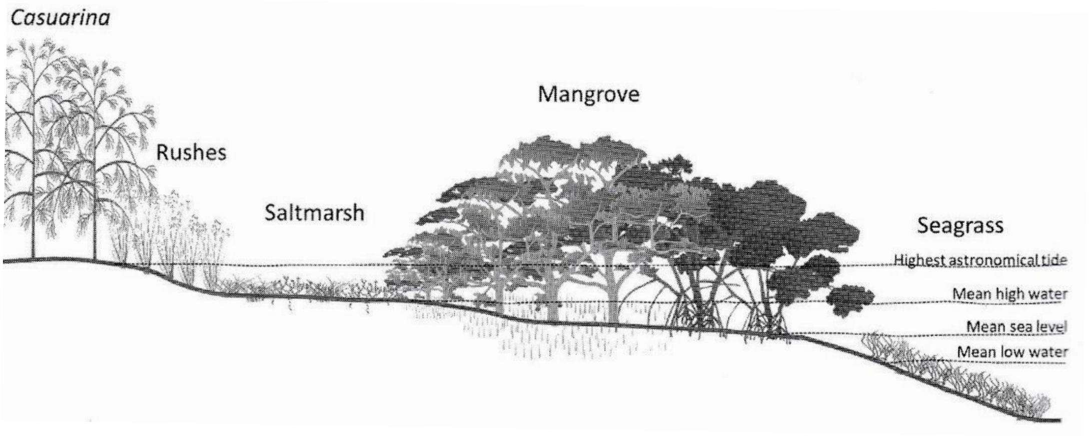

Figure 3| Zonation of subtropical and temperate Australian wetland vegetation across a tidal gradient (Rogers et al., 2017).

Threats to mangrove-saltmarsh system

Worldwide it has been observed that the extent of saltmarsh and mangrove communities is declining to an alarming extent. Saltmarshes have been used by humans for centuries (Adam, 2002) and because the total area of global saltmarsh distribution was only recently estimated (Mcowen et al., 2017), numbers on general saltmarsh loss are missing. However, over the last 200 years a 60% loss of total saltmarsh area was found in south-eastern Australia (Grayson et al., 1999). In regards to mangrove loss, 35% of mangrove area was lost in the past two decades through deforestation and habitat conversion (Valiela and Cole, 2002). This proportional loss exceeds the loss in global tropical rainforest and coral reefs (Valiela et al., 2001). However, mangrove expansion into saltmarshes where they co-occur has also been observed globally (Alongi, 2015, 2002; Saintilan and Rogers, 2013), leaving saltmarsh communities the only option being landwards retreat. Several studies have evaluated mangrove expansion and associated saltmarsh loss, for example in North America (Cavanaugh et al., 2014; Giri et al., 2011a; Osland et al., 2016, 2013; Stevens et al., 2006), Mexico (López-Medellín et al., 2011), Taiwan (Hsu and Lee, 2018) and New Zealand (Morrisey et al., 2010). Mangrove expansion does not necessarily lead to saltmarsh loss, for example in the gulf coast of Texas mangrove expansion of 74% and saltmarsh loss of 24% within 30 years was recorded by Armitage et al. (2015) but only 6% of saltmarsh loss could actually be associated with mangrove expansion. In south-east Australia, saltmarsh loss of 30% due to mangrove expansion was confirmed by Saintilain and William (1999) and Wilton (2001) from survey data, but there is also evidence that saltmarsh loss is less towards the southern limit of mangrove range in Victoria (5-15%) (Rogers et al., 2005).

Climate Change

As a transitional ecosystem between the terrestrial and marine environments, saltmarshes and mangroves are particularly vulnerable to climate change and its consequences (Feller et al., 2017), including sea-level rise (Lovelock et al., 2015), increasing sea surface temperature (Osland et al., 2017) and weather extremes such as drought (Duke et al., 2017) and flooding (Eslami-Andargoli et al., 2009). The Intergovernmental Panel on Climate Change (IPCC, 2014) predicted a global sea surface temperature increase of 1 – 3 ºC, and a mean atmospheric CO_2 increase to 450 ppm by 2100 (from 391 ppm in 2011). Sea surface temperature increase is thought to enable the poleward expansion of mangroves, resulting in replacement of saltmarsh where mangrove expansion was formerly inhibited by winter freezing events (Osland et al., 2013). Increasing sea-levels will lead to submergence of mangroves and saltmarshes and if vertical sediment accretion is sufficient to keep up with the rate of sea level rise, to landward migration of mangroves and saltmarshes (Krauss et al., 2014). It is not clear yet if mangroves can keep pace with rising sea level globally (Lovelock et al., 2011) and Lovelock et al. (2015) further reported that at 69% of their sites in the Indo-Pacific, mangroves were not accreting enough sediment to equal or exceed sea level rise. The landward migration of mangroves will result in the invasion of existing coastal wetlands such as saltmarshes or to the loss of mangroves if sediment accretion is not sufficient (Krauss et al., 2014; Woodroffe and Davies, 2009). Often, migration landwards is restricted by coastal development, leaving saltmarsh communities with little room to move (Alongi, 2015; Hughes, 2004).

Climate extremes are another consequence of climate change. Heavy rainfall events can lead to a decrease in soil salinity as well as flooding that can discharge large amounts of sediment, enabling mangroves to migrate landwards into less salty areas (Eslami-Andargoli et al., 2009) or migrate seawards onto new areas of sediment deposition (Asbridge et al., 2016). However, the rapid expansion might also lead to an increased vulnerability to a following drought (Lovelock et al., 2009), as shown in the current mangrove dieback at the Gulf of Carpentaria (Duke et al., 2017). Finally, the predicted rise in atmospheric CO_2 is likely to promote the growth and water use efficiency of C_3 plant species (McKee et al., 2012), resulting in increased competitive ability relative to co-occurring C_4 species. This effect is likely to be important in ecotonal communities where C_3 and C_4 species co-occur, for example mangroves (C_3) and saltmarshes (C_3, C_4 and CAM) (Adam, 1990). Laboratory experiments have shown that growth of mangrove species is increased under higher CO_2 conditions, but field and mesocosm experiments have shown mixed results, suggesting that only certain C_3 species will be advantaged by elevated CO_2 (Alongi, 2015; Ball et al., 1997). There is clearly a need for further studies to determine the effects of elevated CO_2 and changes in salinity on mangrove species and invasion of saltmarsh communities (Rogers and Krauss, 2018; Saintilan and Rogers, 2015; Williamson et al., 2011).

Urbanization

Anthropogenic impacts, such as agriculture, pollution, the conversion to aquaculture and urbanization have been shown to be the greatest threats to mangrove and saltmarsh systems (UNEP, 2014). In urban areas the ecological processes determining saltmarsh-mangrove boundaries are further influenced by tidal restrictions, fragmentation, pollution and invasive species (Figure 1D) (Laegdsgaard, 2006). Within urban areas, many saltmarsh and mangrove communities have been altered through the construction of levees, culverts and floodgates (Saintilan et al., 2009; Zedler and Kercher, 2004). The effects range from habitat destruction to modification of the geomorphological and ecological processes, especially when estuaries are tidally blocked or closed. Saltmarshes are affected particularly by land reclamation of urban areas and fragmentation, where the landward progression of saltmarshes, in response to sea level rise, is restricted by the placement of roads or densely built-up areas. The proximity of mangroves and saltmarshes to urban areas also increases their use for recreation, leading often to damage of saltmarshes by off-road vehicles (Slaughter et al., 1990) and foot traffic (Andersen, 1995). In urban areas, pollutants such as highly concentrations of nutrients and heavy metals enter wetlands via a range of pathways. Possible sources are industrial discharge into waterways, overflow and leakage from sewerage pipes, dumping of garden waste and stormwater run-off (Al Bakri et al., 2008; Birch, 2007). Previous studies on freshwater systems have shown that stormwater discharge in urban areas increases the availability of heavy metals and nutrients in soil (Grella et al., 2018; Leishman and Thomson, 2005; Wuana and Okieimen, 2011). The increase in nutrient levels, such as phosphorus and nitrogen, facilitates exotic plant growth (Goldberg et al., 2017; Liu and van Kleunen, 2017) and establishment, especially in naturally nutrient poor soils (Leishman et al., 2004; Uddin and Robinson, 2018). Mangroves respond to nutrients with increased growth which may affect the boundary between saltmarsh and mangrove communities (Reef et al., 2016).

As mangroves can only tolerate moderate salinities, the input of freshwater from stormwater run-off might lead to an encroachment of mangroves into the saltmarshes (Adam, 1990) as well as to the facilitation of exotic plant establishment from the landward site (Leishman et al., 2004). While organic pollutants, such as nutrients, deposited via stormwater into saltmarsh and mangrove communities, may be degraded or converted to harmless compounds through microbial activity in the rhizosphere (Batty and Dolan, 2013), heavy metals are not degraded and thus persist in soil for long periods of time (Kirpichtchikova et al., 2006). Most plant species are sensitive to the harmful effects of heavy metals, as they can inhibit growth, affect plant water status and inhibit photosynthesis, resulting in plant death (Lutts and Lefèvre, 2015). It is thought that because of their adaptation to high salinities, saltmarsh and mangrove species can also tolerate high concentrations of heavy metals and some species are considered as potential heavy metal bioaccumulators (Lutts and Lefèvre, 2015; Nath et al., 2014; Parvaresh et al., 2011). Moreover, due to the reputation of wetlands as pollutant filters, stormwater is often discharged into existing wetlands and in fact urban wetlands are often constructed for this purpose (Carleton et al., 2000; Keller et al., 2017). Apart from the effect of pulsing freshwater events on nutrient and heavy metal availability in wetland soils, it has also been shown that increased freshwater input accelerates soil organic carbon loss (Chambers et al., 2013). The consequences of loss of organic carbon is a reduction in saltmarsh resilience to sea level rise due to diminished vertical marsh accretion (Chambers et al., 2013).

The understanding of the importance of, and threats to, Australian saltmarsh vegetation has been reflected in the 2004 listing of coastal saltmarshes as a threatened ecological community under the NSW Threatened Species Conservation Act 1995 (Rogers et al., 2016). It was followed by the 2010 inclusion of tropical and subtropical saltmarsh on the Finalized Priority Assessment List under the Environmental Protection and Biodiversity Conservation (EPBC) Act (Saintilan and Rogers, 2013). However, there are no specific Commonwealth policies or Acts dealing with mangroves; they are rather included in more general legislation regarding environment, fisheries, coasts and wetlands (Rogers et al., 2016). Given the recognised importance of and threats to mangrove and saltmarsh communities, there is a clear need for better understanding of changes in these communities in response to climate change and urbanisation, and the implications of these changes for ecosystem processes such as carbon and nutrient storage and faunal habitat.

Thesis scope and structure

The overall aim of this thesis was to assess anthropogenic impacts on the co-occurring mangrove-saltmarsh systems of south-eastern Australia, on scales from local to regional, using a combination of field studies, glasshouse experiments and remote sensing analysis.

Saltmarsh and mangrove communities growing in proximity to urban areas experience high levels of anthropogenic disturbance. In Chapter 2, I present the results of a field study of the impact of stormwater run-off on mangrove and saltmarsh communities in highly industrialised compared to residential areas. The research questions addressed here were: (1) what is the effect of urban stormwater run-off on vegetation composition of saltmarsh-mangrove communities and (2) does this differ between residential and highly industrialised catchments? This chapter has been published in *Science of the Total Environment* (Geedicke et al. 2018). The findings of the field study were then tested under controlled conditions in a glasshouse experiment using a manipulative experiment with salinity and nutrient concentration as the factors (Chapter 3). We tested if the invasion of saltmarsh communities by exotic species was facilitated by nutrient addition and salinity reduction, comparable to the soil conditions associated with urban stormwater run-off described in Chapter 2. This chapter has been submitted for publication to the *Journal of Applied Ecology*. Chapter 4 also used a glasshouse manipulative experiment to test the effect of salinity and CO_2 concentration on invasion success of mangrove species into a mesocosm saltmarsh community. This chapter has been submitted for publication to *Oecologia*. Finally, disturbance at the catchment-scale needs to be considered when evaluating changes in mangrove-saltmarsh boundaries. Chapter 5 describes a remote sensing study that assessed if extremely modified estuaries of south-east Australia experienced greater changes in mangrove cover compared to mostly unmodified estuaries over a time period of 40 years. Aerial images from 1970 and 2012 were examined to evaluate if changes in the main vegetation classes (mangroves, saltmarshes and *Casuarina*) occurred. Finally, Chapter 6 provides a general discussion that integrates the thesis findings and places them into a broader context as well as providing ideas for future research directions.

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Chapter 2

Urban stormwater run-off promotes compression of saltmarshes by freshwater plants and mangrove forests

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Abstract

Subtropical and temperate coastal saltmarsh of Australia is listed as an endangered ecological community under the Commonwealth Environment Protection and Biodiversity Conservation Act (EPBC Act). Saltmarshes are under threat from sea level rise, landward migration of mangroves, and in urban regions from habitat loss, input of litter, nutrients, and other contaminants. In urbanised catchments, saltmarsh areas receive nutrient-enriched and pollutant-contaminated run-off, such as heavy metals, through the stormwater system. This study aimed to investigate the impact of urban stormwater on saltmarsh and mangrove species composition and distribution. To test the effect of stormwater run-off in urbanised catchments on saltmarsh communities, we analysed the soil for pollutant elements, salinity and nutrient concentration and recorded vegetation composition at eight sites in the Sydney region, Australia. We found that elevated total nitrogen (> 0.4 wt%) and reduced salinity of the soil downslope of stormwater outlets facilitates establishment of exotic plants and might promote migration of mangroves into saltmarshes, resulting in a squeezing effect on the distribution of saltmarsh vegetation. Saltmarsh cover was significantly lower below stormwater outlets and exotic plant cover increased significantly with sediment calcium concentrations above 8840 mg/kg, which are associated with stormwater run-off. However, this effect was found to be strongest in highly industrialised areas compared to residential areas. Understanding the impact of pollutants on coastal wetlands will improve management strategies for the conservation of this important endangered ecological community.

Keywords:

Exotic plants; heavy metals; intertidal wetlands; mangrove encroachment; nutrients; pollution

Introduction

Mangrove and saltmarsh communities occur along estuarine coasts and are composed of plants highly adapted to waterlogging and saline conditions. While serving as an ecotone between the terrestrial and oceanic environments, saltmarshes and mangroves also form important habitats and feeding grounds for invertebrates and birds, as well as nursery grounds for several fish species (Alongi, 2002; Mcleod and Salm, 2006). Saltmarshes are mostly confined to temperate climatic zones (Adam, 1990), whereas the distribution of mangroves is mainly limited by temperature. As mangroves are intolerant to frost (Hogarth, 2007; Stuart et al., 2007), they are completely replaced by saltmarshes at latitudes above 32°N and 40°S (Stuart et al., 2007). In the transition zone between tropical and temperate climates, saltmarshes and mangroves can share the same habitat. Their co-occurrence is highly dependent on the stability of the tidal system they inhabit. Saltmarshes are usually found landwards of mangrove forests as they can tolerate higher salt concentrations than mangroves (Osland et al., 2013; Saintilan et al., 2009b). Coexistence of saltmarshes and mangroves can be found in Florida, the Gulf of Mexico, between the north and south islands of New Zealand and along the eastern coast of Australia (Chapman, 1977). Anthropogenic influences in the form of reclamation and pollution, together with the consequences of climate change, are considered the biggest threat to mangroves and saltmarshes (Saintilan et al., 2009a; Zedler and Kercher, 2004). In Australia, ‘Subtropical and temperate coastal saltmarsh of Australia’ has been listed as an endangered ecological community under the Commonwealth Environmental Protection and Biodiversity Conservation (EPBC) Act. These arrangements were taken after a 60% loss of total saltmarsh area was found in south-eastern Australia (Grayson et al., 1999).

Saltmarshes in particular are primarily threatened by physical disturbances, such as reclamation, dredging and sea level rise (Valiela, 2006). These physical factors are impacting the tidal system and can influence the saltmarsh-mangrove boundary as well as environmental conditions such as nutrient availability and salinity (Laegdsgaard, 2006; Rogers et al., 2013). Much of the tenfold increase in urban population within the 20th century has occurred in coastal regions (Elmqvist et al., 2013) and has resulted in a decline of intertidal wetlands globally. Nevertheless, intertidal wetlands such as mangrove and saltmarsh communities, provide important services to urban areas and their population such as stabilization of the coastline, protection from storm surges and the filtration of pollutants (Guo et al., 2017; Woodward and Wui, 2001). In urban areas, pollutants such as highly concentrated nutrients and heavy metals enter adjacent wetlands via different pathways. Possible sources are industrial and agricultural discharge into waterways, overflow and leakage from sewerage pipes, dumping of garden waste and stormwater run-off (Al Bakri et al., 2008; Birch, 2007). Previous studies on freshwater systems have shown that stormwater discharge in urban areas increases the availability of nutrients and heavy metals in soil (Grella et al., 2018; Leishman and Thomson, 2005; Wuana and Okieimen, 2011).

The increase of nutrient levels, such as phosphorus and nitrogen, facilitates exotic plant growth (Goldberg et al., 2017; Liu and van Kleunen, 2017) and establishment, especially in naturally nutrient poor soils (Leishman et al., 2004; Uddin and Robinson, 2018). Mangroves respond to nutrients with increased growth which seems to affect the boundary between saltmarsh and mangrove communities (Reef et al., 2016). The landward migration of mangroves, and consequently loss of saltmarsh, has been observed worldwide (Saintilan and Rogers, 2015). The replacement of saltmarsh by mangroves changes not only the plant community in these ecosystems but also the faunal diversity, microclimate, soil organic content and sediment accretion (Guo et al., 2017; Smee et al., 2017). As mangroves can only tolerate moderate salinities, the input of freshwater from stormwater run-off might lead to an encroachment of mangroves into the saltmarshes (Adam, 1990) as well as to the facilitation of exotic plant establishment from the landward site (Leishman et al., 2004). While organic pollutants, such as nutrients, deposited via stormwater into saltmarsh and mangrove communities, may be degraded or converted to harmless compounds through microbial activity in the rhizosphere (Batty and Dolan, 2013), heavy metals are not degraded and thus persist in soil for long periods of time (Kirpichtchikova et al., 2006). Most plant species are sensitive to the harmful effects of heavy metals, as they can inhibit growth, affect the plant water status and inhibit photosynthesis, resulting in plant death (Lutts and Lefèvre, 2015). It is thought that because of their adaptation to high salinities, saltmarsh and mangrove species can also tolerate high concentrations of heavy metals and some species are considered as potential heavy metal bioaccumulators (Lutts and Lefèvre, 2015; Nath et al., 2014b; Parvaresh et al., 2011). Moreover, due to the reputation of wetlands as pollutant filters, stormwater is often discharged into existing wetlands and in fact wetlands are constructed for this purpose (Carleton et al., 2000; Keller et al., 2017). Apart from the effect of pulsing freshwater events on nutrient and heavy metal availability in wetland soils, it has also been shown that increased freshwater input accelerates soil organic carbon loss. Consequences of the loss of organic carbon is a degradation of saltmarsh resilience to sea level rise due to a diminished ability of vertical marsh accretion (Chambers et al., 2013).

As urban development increases, impervious surfaces will increase and with it the amount of urban catchment run-off discharged into wetlands at the edge of urban development (Grella et al., 2018). It is unclear to what extent the input of nutrient and pollutant-laden freshwater from stormwater discharge affects saltmarsh vegetation and its sensitive boundary to the adjacent mangrove forests. It is unknown whether a higher density of impervious surfaces and historical industrial use in highly urbanised areas increases the effect of stormwater run-off on urban wetland ecosystems.

In this study, we assessed the sediment salinity, pollutant elements, such as heavy metals, and nutrient content below stormwater run-off outlets in highly industrialised and residential areas of Sydney and analysed whether elevated concentrations influenced the abundance of three different plant types, i.e. saltmarsh species, mangroves and exotic plants. The questions we addressed were: (1) Is the nutrient (i.e. nitrogen, phosphorus and potassium) and pollutant elements content of saltmarsh and mangrove sediment greater below stormwater outlets in industrial areas compared to residential areas? (2) Does stormwater run-off facilitate exotic plant establishment in saltmarshes? (3) Does stormwater run-off promote mangrove encroachment into saltmarshes?

Methods

Study sites

We assessed environmental conditions (salinity, sediment nutrient and pollutant elements concentrations) and vegetation at coastal wetland sites within the Sydney region and adjacent Central Coast of New South Wales, Australia. Land use adjacent to our study sites included industrial and residential areas. Mangrove forests and saltmarshes of Sydney and the Central Coast area grow on sediment that is derived from highly permeable sandstone (Clarke and Hannon, 1967). The sediment is well drained, acidic and has a sandy surface structure with low nutrient content (Clarke and Hannon, 1967). Average grain size of estuarine sediment of eastern New South Wales ranges from ~63 µm to 500 µm with bigger grain size closer the mouth of the estuary where estuarine silt is replaced by estuarine sand (Kelleway et al., 2017). Salt concentration in wetlands tend to be lower in frequently inundated areas and can vary widely in less inundated areas on the upper shore due to evaporation (Clarke and Hannon, 1967; Saintilan et al., 2009a).

We selected eight study sites where urban run-off is discharged from stormwater outlets located at the saltmarsh / urban land use boundary (Figure A1). Five study sites were located adjacent to current or previous industrial areas within Sydney: Parramatta River, Duck River, Sugarloaf Point, Brays Bay and Lane Cove River. Three sites were located adjacent to non-industrial residential - development: Careel Bay, Empire Bay and Towra Point Nature Reserve (Figure 1, GPS data in table A1).

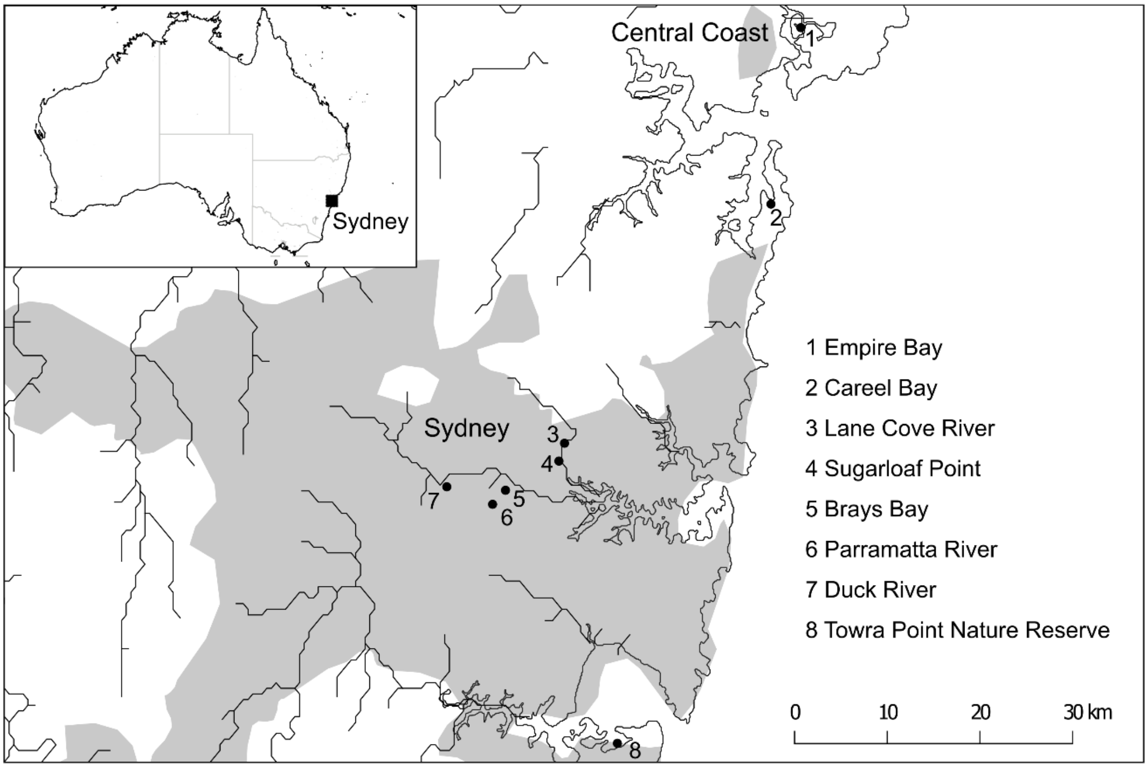

Figure 1 | Map of the study area showing locations of sampling sites within the Sydney region and the Central Coast. Each site consisted of two transects (control and outlet), leading from the landward site into the mangrove boundary (n = 16), where sediment samples were taken and vegetation analysis was performed on five plots per transect.

Study design

Vegetation survey and sediment sampling took place at the eight sites; each site consisting of two 10 - 30 m transects depending on the distance from the stormwater outlet to the mangrove boundary. One transect per site was placed directly below the stormwater outlet leading towards the mangroves. A second transect, which we considered as the control site, was placed at least 50 m away from the stormwater outlet transect to ensure it did not directly receive stormwater discharge. Along each transect we placed five 1 m^2 plots located equidistant apart. Percent foliage cover was visually estimated for all plant species in each plot. Plant species were identified according to Adam (1981), Robinson (2003), Fairley and Moore (2010), Sainty (2012), Johns (2014) and PlantNET (Royal Botanic Gardens and Domain Trust, 2018). Each species was classified into one of three categories: mangrove species, saltmarsh species or exotic species. For this study, an exotic plant is defined as a plant species that is not native to intertidal wetland habitat in Australia. This includes species exotic to Australia as well as freshwater native species that are exotic to intertidal wetlands. Sediment was sampled at five different points within the 1 m^2 plot using a hand-held auger, resulting in sediment cores of 25 mm diameter and 75 mm depth, and then bulked into a single sample per plot. The sediment samples were double-bagged in metal free polyethylene bags and transferred to an ice box to be taken back to the laboratory where they were refrigerated at 4 °C until processed.

Sediment analysis

Sediment samples were split into three sub-samples and tested for pH, salinity, nutrient and pollutant elements content separately. As this study focused on pollutants in stormwater run-off, we analysed for substances that are particularly related to human activities: total nitrogen (N), total phosphorus (P) and potassium (K) (that are derived from fertiliser addition to gardens) and pollutant elements (S, Cl, Ca, Cr, Fe, Ni, Cu, Zn, Cd and Pb) that are derived from pesticides, car fuel spills and car tyre abrasions.

Analysis of sediment pH, and salinity

Prior to analysis, sediment samples were oven dried at 60 ºC for 48 h and sieved to separate particles greater than 1 mm from the sediment. The sediment samples were analysed on a 1:5 sediment:deionised water suspension in the laboratory for pH using a pH meter (Hanna instruments) while salinity was measured using an electrical conductivity meter (EC meter, Hanna instruments). Analysis were carried out following standard procedures by Rayment and Lyons (2011).

Analysis of sediment nutrients

Sediments were analysed for total P and total N including both inorganic and organic compounds to provide a more stable and reliable measure of sediment nutrients than measurement of available P and N. Total N and total P provide a comparable measure as they are used in sediment assessments of other studies focusing on intertidal wetlands (Boto and Wellington, 1984) and urban stormwater run-off (Leishman et al., 2004). The oven dried (60 ºC, 48 h) and sieved samples were analysed at the University of Queensland. Total P analysis was performed by closed vessel microwave assisted digestion using a Milestone Ethos-1 digester and ICPOES analysis on a Varian Vista Pro instrument. Total N was analysed by combustion using a LECO TruSpec analyser.

Analysis of sediment pollutant elements

Pollutant element analysis took place at Macquarie University, NSW, where the sediment samples were oven dried at 103 °C for 48h, sieved, and then milled in a Fritsch Mini Mill II for 10 min at 500 rpm, before being lightly packed into plastic cups with Philips Analytical 3.6 µm polyester X-ray film base. Samples were analysed for S, Cl, K, Ca, Cr, Fe, Ni, Cu, Zn, Cd and Pb using an Olympus Delta 50 kV X-ray fluorescence spectrometer with a tantalum anode tube. Every thirtieth measurement the blank SiO_2 was measured to ensure the measurement area and spectrometer were free of contaminants. Inaccuracy, constrained by repeated measurements (every 30th measurement or at least once a day) of two powdered NIST standards 2710a and 2711a, was generally around 2%, except for Fe and Ni which had -12% and -23%, respectively.

Statistical analysis

The collected data and the code used for analysis is openly available at GitHub (https://github.com/InaGee/stormwater-wetlands, https://doi.org/10.5281/zenodo.1228302).

Sediment analyses

The analysed sediment parameters (i.e. nutrients, pollutant elements) were grouped according to the site location (residential or industrial) and stormwater run-off influence (outlet or control). We calculated the mean and standard deviation and compared the values to given trigger values such as the interim sediment quality guidelines (ANZECC & ARMCANZ, 2000). When concentrations of a certain element exceed the trigger value, risks for the environment and human health can be expected. There were no guidelines available of hazardous concentrations for Ca, Cl, Fe, K and S in Australia. In order to identify significant differences between the site location and stormwater run-off influence, a Wilcoxon rank sum test was employed due to lack of normality using the R package “coin” (Hothorn et al., 2008) of the statistical environment of R (R Development Core Team, 2017).

Impact of nutrients and pollutant elements on vegetation within urban wetlands

An ordination analysis of the percent cover of all species and the measured sediment parameters was applied to assess whether environmental factors were associated with differences in species composition between sites. First, we calculated a detrended correspondence analysis (DCA) to estimate the length of the first DCA axis. The longest gradient was calculated to be 11.67 and Lepš and Šmilauer (2003) suggest applying a canonical correspondence analysis (CCA) if the longest gradient of the DCA is greater than four. This means that species composition is heterogeneous, and species are assumed to have a unimodal distribution along ecological gradients. To account for correlation between sediment parameters, a stepwise variance inflation factor (VIF) selection with a threshold of five was applied (Zuur et al., 2009) sorting out highly correlated parameters. The species data set, which consisted of species cover in percent per sites and plots, was transformed using square root transformation prior to CCA analysis to fulfil assumptions of normality. The CCA was conducted and visualized using the R package "vegan" (Oksanen, 2015).

Due to non-linearity and non-normality of the data, we decided to approach the question of which environmental parameters might drive the cover of the vegetation types (i.e. mangrove forest, saltmarsh and exotic species) at different sites using conditional regression trees. Regression trees explain the variation of the numeric response variable (percentage foliar cover per plot of the three different vegetation types), by repeatedly splitting the data into homogenous groups (De'ath and Fabricius, 2000). Conditional regression trees use p-values ($p < 0.05$) for variable selection and as a stopping criterion (Strobl et al., 2009). The output of a conditional regression tree is an easily interpretable visualisation of the cut points and groups explaining the data in the most homogenous way, and the variables most strongly associated with the response variable (i.e. lowest p-value). The conditional regression trees were calculated and visualised using the R package "partykit" (Hothorn and Zeileis, 2015).

Results

Distribution of pollutant elements concentrations at stormwater outlets in relationship to site location

Overall, we found sediment pollutant elements concentrations were high, with some maximum concentrations exceeding by hundred times (Cd) or nine times (Pb) that of the trigger values. Comparing the pollutant elements concentrations below stormwater outlets to the control transects, we found that average concentrations of Cd, Pb, Ni and Zn exceeded the trigger values (Table 1), but a significant difference ($p < 0.05$) between outlet and control was only found for Ca ($z = -3.147$, $p = 0.002$), Cu ($z = -2.463$, $p = 0.014$) and Zn ($z = -2.151$, $p = 0.031$). We examined industrial and residential sites and found that concentrations of all pollutant elements, except Cu, exceeded the ISQG guidelines at industrial sites. Further, analysis of variance showed that transects at industrial sites contained significantly higher concentrations for all pollutant elements tested compared to transects at residential sites, with the exception of Cd. In particular the industrial sites at Parramatta River and Duck River displayed the highest concentrations of pollutant elements (Figure A2), whereas the residential sites at Empire Bay, Careel Bay and Towra Point showed consistently lower pollutant elements concentrations compared to the industrial sites.

Table 1 | Environmental parameters compared by outlet and control site and by site category (industrialised or residential) using a Wilcoxon rank sum test. Bold values indicate significant differences ($p < 0.05$) between the means for each comparison ($N = 80$). Trigger values indicate interim sediment quality guidelines (ISQG) harmful to health as recommended by the ANZECC guidelines (ANZECC & ARMCANZ, 2000)

		Outlet			**Control**			**Industrial**			**Residential**		
Element measured	**Trigger value**	**Max**	**Mean**	**sd**	**Max**	**Mean**	**sd**	**Max**	**Mean**	**sd**	**Max**	**Mean**	**sd**
Total N (wt%)		1.1	0.5	0.3	1.1	0.4	0.3	1.1	**0.6**	0.3	1.1	**0.3**	0.3
Total P (mg/kg)		1307	644	345	912	668	465	2269	**825**	386	1136	**376**	263
pH		8.2	**6.6**	0.6	7.9	**6.8**	0.6	7.9	**6.6**	0.6	8.2	**6.9**	0.6
Salinity (S/m)		20.8	**5.3**	1.1	36.5	**8.4**	1.6	36.5	8.3	1.6	16.4	4.4	0.7
Ca (%)		2.1	**0.8**	0.6	1.1	**0.4**	0.3	2.1	**0.8**	0.5	1.9	**0.3**	0.5
Cd (mg/kg)	1.5	9.0	3.7	1.7	126.0	8.6	20.4	126.0	7.8	18.3	7.0	3.3	1.1
Cl (g/kg)		51.0	14.8	13.5	98.3	23.5	22.4	98.3	**23.9**	22.1	26.0	**11.2**	6.7
Cr (mg/kg)	80	312	68.3	65.8	324	68.9	69.0	324	**94.3**	73.3	49.0	**25.8**	11.8
Cu (mg/kg)	65	177	**53.6**	49.0	142	**29.6**	30.3	177	**58.7**	43.2	77.0	**13.1**	18.9
Fe (%)		4.4	2.0	1.1	5.8	2.4	1.7	5.8	**2.9**	1.2	1.9	**0.9**	0.5
K (mg/kg)		14.4	7.5	2.8	12.8	7.1	2.8	12.8	**8.1**	2.2	14.4	**6.0**	3.2
Ni (mg/kg)	21	37.0	16.7	10.1	72.0	23.8	17.8	72.0	**28.3**	13.3	15.0	**6.8**	2.2
Pb (mg/kg)	50	449	127	112	466	128	120	466	**186**	108	105	**30.1**	25.5
S (%)		0.6	0.2	0.2	0.5	0.1	0.1	0.6	**0.2**	0.2	0.2	**0.08**	0.04
Zn (mg/kg)	200	854	**321**	263	696	**200**	201	854	**371**	228	448	**75.6**	117

Distribution of pH, salinity and nutrient concentrations at stormwater outlets in relation to site location

The sediment pH (Table 1) was slightly acidic across all sites within the measured wetlands (mean = 6.7, sd = 0.6). We found a significant difference in sediment pH between outlet and control plots (z = 2.315, p = 0.021) as well as between the industrial and residential sites (z = -2.565, p = 0.010) with pH values being more acidic below stormwater outlets compared to controls and in general within industrial compared to residential areas.

Sediment conductivity (Table 1) showed no significant difference between industrial and residential sites (z = 0.112, p = 1.590) but salt concentrations were found to be lower below the stormwater outlet (z = 1.982, p = 0.047) compared to the control sites.

While there was no significant difference in total N or total P between the stormwater outlet and control plots (total N: z = -1.924, p = 0.054; total P: z = -0.269, p = 0.788; K: z = -0.380, p = 0.704), we did find a significant difference between industrial and residential sites, with higher nutrient concentrations in industrial areas (total N: z = 4.151, p < 0.001; total P: z = 5.019, p < 0.001; K: z = 3.926, p < 0.001; Table 1).

Impact of nutrients and pollutant elements on vegetation types within urban wetlands

The ordination analysis (i.e. CCA) illustrates the relative importance of the measured environmental factors in determining species composition of these tidal wetlands (Figure 2). We identified urbanisation (i.e. industrial, residential) as the major driver explaining the vegetation composition at our sites, which can be seen as a division of the data into two groups (Figure 2, black vs. grey point clouds). The factors in order of importance were identified as urbanisation > Ca > pH > total N > distance > transect type (i.e. outlet, control). The arrows indicate environmental parameters that significantly drive the distribution of vegetation within the plots. The longer the arrow, the more important the driver with highest concentrations towards the arrow head. This in mind, figure 2 shows that with increasing distance from the outlet and therefore from the landward site, Ca and total N decline, while pH increases.

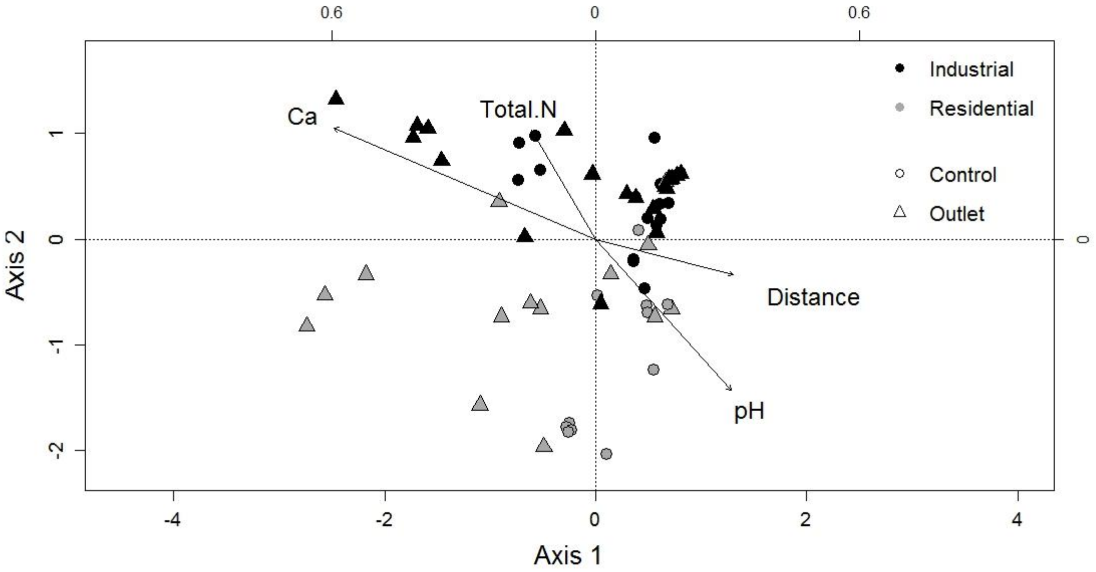

Figure 2 | Canonical correlation analysis (CCA) comparing the species community data set per plot with the environmental sediment data of the sediment within the same plots. Only parameters that had a significant effect ($p < 0.05$) on the vegetation assemblage are shown. Arrow length indicates the strength of the effect of each significant environmental factor.

We applied a conditional regression tree analysis on each group of vegetation type (i.e. saltmarsh, mangrove, exotic) (Figure 3). For mangroves, we found that at a distance of less than 6 m from the outlet, total N concentrations of 0.4 wt% increased the cover of mangroves significantly ($p = 0.041$), while at total N concentrations of less than 0.4 wt% the mangrove cover was found to be 0%. The cover of exotic plants is best explained by Ca concentrations in the sediment. At Ca concentrations above 8840 mg/kg, exotic plant cover is significantly higher ($p = 0.01$) across all sites. Our grouping of exotic species contained 17 species that are exotic to Australia and considered as invader species. Of these 17 non-native species, only three are halophytic plants and 15 are freshwater plants. We also considered 10 native Australian species as exotic, because these were exclusively freshwater plants who cannot survive within intertidal wetlands in natural systems due to their sensitivity to saline sediments and waterlogging (Table A2). Finally, saltmarsh cover is significantly different based on transect type, where plots below stormwater outlets had cover of saltmarsh four times smaller compared to transects that were away from the stormwater outlet (i.e. control), regardless of the land use of the site, i.e. industrial or residential site.

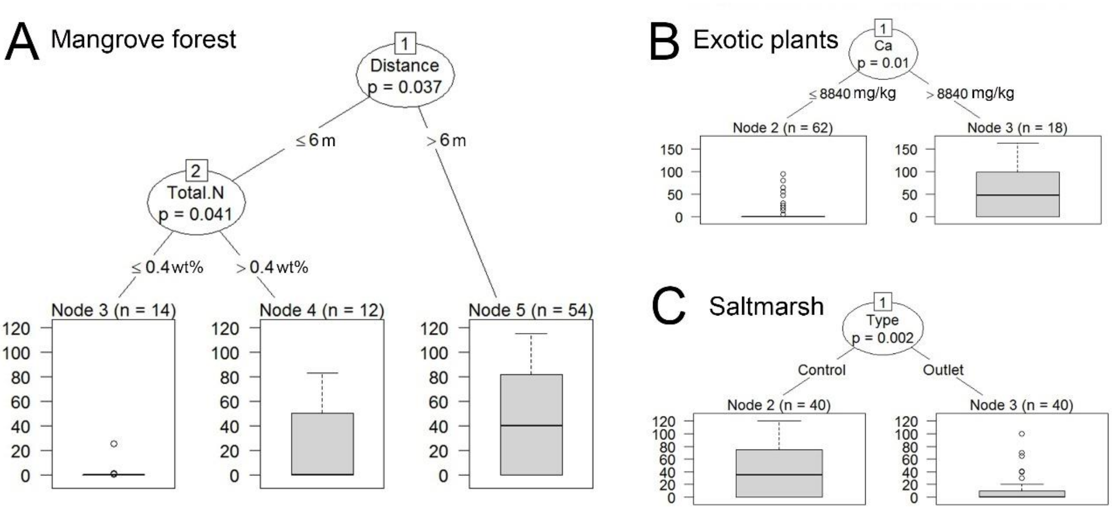

Figure 3 | Conditional regression tree visualizing the best explanatory variables for vegetation type cover in relation to stormwater run-off. The percentage of foliar cover is represented on the y-axis of the box and whisker plots: A = mangrove forest cover, B = exotic plant cover, C = saltmarsh cover.

Discussion

Our findings suggest that in urban wetlands, native saltmarsh communities in proximity to stormwater outlets are marginalised by exotic plants from the landward edge and by mangroves from the seaward edge. The squeezing of saltmarsh habitat from both sides is likely to result from several factors related to stormwater run-off, but especially nutrients, calcium, pH and freshwater content. This trend is particularly severe in highly urbanised areas, which poses a real threat to this critical habitat as coastal populations continue to grow.

Nutrient and pollutant elements content in urban wetlands

Stormwater run-off can provide a substantial nutrient input to recipient sediments, which may be of particular importance in the generally low sediment fertility systems of eastern Australia (Ehrenfeld, 2000; Leishman et al., 2004). However, in this study we did not find a significant difference in total N, total P and K in the sediments below stormwater outlets compared to control sediments, suggesting that either the amount of nutrient input through stormwater outlets is negligible, or that nutrients might be redistributed in the sediment within sites by the tidal regime. Previous studies on Sydney’s stormwater run-off by Leishman et al. (1990; 2004; 2005) and our studies evidence of decreasing Total N with distance from outlets suggest that the most plausible explanation is dilution or redistribution effect of nutrients within sites due to tidal movement. This also shows that in particular saltmarsh areas are vulnerable to nutrient input due to their landward position in the wetland system. We found that sediment nutrient concentrations were up to twice as high in industrial areas compared to residential areas (Table 1) suggesting that the historical use of the industrial sites and urbanised catchments lead to a built up of nutrients over time.

Significantly greater Ca concentrations below outlets and in industrial areas are consistent with findings by Davies et al. (2010) who linked elevated Ca concentrations in urban areas to concrete wash off from stormwater outlets. High Ca concentrations usually lead to high (alkaline) pH values (Davies et al., 2010), but this contradicts our finding as we consistently measured acidic to slightly acidic pH values at stormwater outlets, turning neutral towards the mangrove boundary. One explanation for the lower sediment pH could be that the saltmarsh sediment was slightly acid, due to oxidation of iron sulphide minerals, particularly pyrite (FeS_2). This explanation can be reinforced by our findings of higher concentrations of S below the outlet, however this effect was only significant in industrial vs. residential sites. Sediment acidification is very common along estuaries in NSW, in particular within mangrove and saltmarsh areas (Powell and Martens, 2005). Apart from Ca, only Cu and Zn showed an increased concentration below stormwater outlets compared to elsewhere within the sites (100% and 70% respectively). These two heavy metals have been linked to stormwater in numerous studies due to being an abrasion product of car tyres and brakes, vehicle emissions and component wear (Birch, 2007; Herngren et al., 2005; McKenzie et al., 2009). The greatest difference in pollutant elements distribution was found on the local scale between highly industrialised and residential areas, where only Cd concentrations did not differ significantly. Generally high pollutant elements concentrations in industrial areas are linked to the historical use of the harbour over the last 150 years, where sewage and industrial contaminants were directly discharged into the waterways of Sydney (Birch, 2007). Only the Clean Waters Act of 1972 controlled discharge into the estuaries and, since 1990, sewage has been dispersed into the ocean about four kilometres from the coast (Birch, 2000). Interestingly, we did not find evidence that pollutant elements - apart from Ca - influenced the vegetation distribution. The ability of saltmarshes and mangroves to tolerate high concentrations of pollutant elements, in particular heavy metals, has been a focus in recent studies (Lutts and Lefèvre, 2015; Nath et al., 2014a). The reasoning is that due to their adaptation to high salt concentrations, halophytes might also be able to exclude and tolerate heavy metals or even eliminate them and therefore function as potential heavy metal bioaccumulator (Lutts and Lefèvre, 2015; Usman et al., 2013). However, pollutant elements concentrations strongly exceeded trigger values stated as harmful for environmental and human health, with concentrations up to ten times higher than those considered to be harmless to human health. Because mangrove forest and saltmarshes provide important habitat and nurseries for fish and invertebrate species, these contaminants can easily end up in the human food chain (Birch, 2007; Lee et al., 2006). One issue in determining the risk of heavy metals and other pollutants in wetland soils is the mobilization of potential toxic elements which can be made available by waterlogging, pH and salinity changes (Shaheen et al., 2017). Historical contamination of sediment can only be reversed by costly remediation processes (DeLaune et al., 2016) and needs to consider the characteristics of the polluted habitat, such as salinity and nutrient availability (Yao et al., 2012). However, to avoid a further build-up of contaminants, management strategies to avoid additional contamination through stormwater run-off would be necessary. Several studies address the filtration of pollutant elements from stormwater sources via media filtration systems, where the contaminants, such as nutrients and heavy metals, can be filtered through different sorbents (Genç-Fuhrman et al., 2007; Takaijudin et al., 2016) or pervious concrete (Holmes et al., 2017) before entering the intertidal wetland system.

Facilitation of exotic plants due to stormwater run-off

In previous studies sediment phosphorus and nitrogen concentrations have been linked to exotic plant establishment below stormwater outlets in terrestrial systems (Leishman et al., 2004). In our study, the cover of exotic plants could not be directly explained by nutrients. In tidal systems the redistribution of soluble elements is probably higher compared to terrestrial systems where only limited redistribution through precipitation occurs. This would also explain why we did not find a significant difference in nutrient concentration between outlet and control sites. However, we found that nutrient concentrations decreased with distance from stormwater outlets and at sediment Ca concentrations above 8840 mg/kg, exotic cover increased from 0 to 50% on average. Additionally, when looking at the saltmarsh cover, we discovered a 40% loss below the outlet sites compared to control sites independent of industrial or residential area. As described above, Ca below stormwater outlets has been linked to Ca washed out from concrete pipes (Davies et al., 2010). We found an increase in exotic plant cover in industrial sites, where Ca levels were highest below stormwater outlets which correlates to the greater abundance of concrete surfaces in highly urbanised and industrial areas. This reflects our hypothesis that in highly industrialised areas, stormwater run-off has a greater impact on urban wetlands and higher pressure of exotic plant establishment. Stormwater run-off is linked to weed encroachment in urban bushland (Leishman and Thomson, 2005), and in intertidal wetlands, the input of freshwater could facilitate establishment of freshwater plants by reducing sediment salt concentrations and even help in seed dispersal through the discharge of water from e.g. gardens. Some of the exotic plants that we found below stormwater outlets can be classified as garden escapes, such as tomato plants (*Solanum lycopersicum)* and nasturtium (*Trapeolum majus)*. The influence of stormwater run-off accounted for a 40% decrease in saltmarsh cover at the site-level. Even though saltmarshes do not depend on saline sediment, they are highly adapted to tolerate high salinities and have evolved three main pathways to cope with it: exclusion, tolerance and elimination (Adam, 1990). Each saltmarsh species is adapted to different salt and waterlogging levels, resulting in a specific zoning of saltmarsh habitat (Saintilan et al., 2009b). The less frequently tidal inundation reaches a certain area within the estuary, the higher the salt content will be due to evaporation. Halophytic adaptations come with an energy cost that makes saltmarsh plants less competitive when growing in freshwater (Crain et al., 2004). Freshwater input from stormwater run-off decreases the salinity below the outlet, which leads to a higher vulnerability of saltmarsh plants to competition by less salt tolerant species, such as some exotic plants (e.g. *Protasparagus aethiopicus*) and mangroves.

Mangrove encroachment and stormwater run-off

Mangroves typically grow in an environment that offers salt concentrations between that of freshwater (0.005 S/m) and seawater (5000 S/m), whereas less frequently inundated saltmarsh habitat can reach up to five times higher sediment salt concentrations than that of sea water. It has been shown previously that mangrove migration into saltmarsh habitat was correlated with an increase in annual precipitation, reducing the sediment salt concentrations within saltmarsh habitat (Saintilan and Williams, 2000). Thus, the decrease of sediment salinity below stormwater outlets could have the same effect as increased precipitation and facilitate mangrove establishment in proximity to outlets. For mangrove cover, we found total N to be a driver of vegetation distribution as mangrove cover increased towards the landward site when total N levels were higher than 0.4 wt%. Similarly, Reef et al. (2016) showed that mangroves react with increased growth and photosynthetic activity to elevated nutrients.

Conclusion

Wetlands are known for their potential to protect coastal areas and filter pollutants, which is why in urban areas they are used as sinks for stormwater run-off. However, the amount of discharge and its effect on a sensitive habitat that provides a multitude of ecosystem services should be carefully considered. We found that uncontrolled discharge of stormwater into inter-tidal wetlands facilitates the establishment of exotic species and the potential encroachment of mangrove forests into saltmarsh habitat. To better understand the impact of singular stormwater components on wetland vegetation, controlled experiments for edaphic parameters such as nutrients and salinity would be necessary. In particular understanding the effect of nutrients on potential mangrove expansion is of great importance due to a global encroachment of mangroves into saltmarshes which has so far been linked mostly to climate change. When stormwater enters wetlands, nutrients and freshwater are flushed into wetlands increasing weed establishment and potentially mangrove encroachment. With expanding urban development, urban wetlands will receive more nutrients and freshwater which could lead to an accelerated decline in saltmarshes. As an already endangered ecological community in Australia, saltmarshes inhabit a vulnerable position in wetlands, between mangroves and competition from freshwater plants and exotic species. We suggest that the use of nutrient filters and maintenance of tidal regimes, such as considering the natural distribution of tidal waters when constructing sea walls and adjacent coastal development, to stabilize sediment salinity should contribute to the resilience of this vulnerable ecological community.

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SUPPLEMENTARY MATERIAL

Table A1 | Name and location of the eight study sites. Categories show the site classification into industrial or residential.

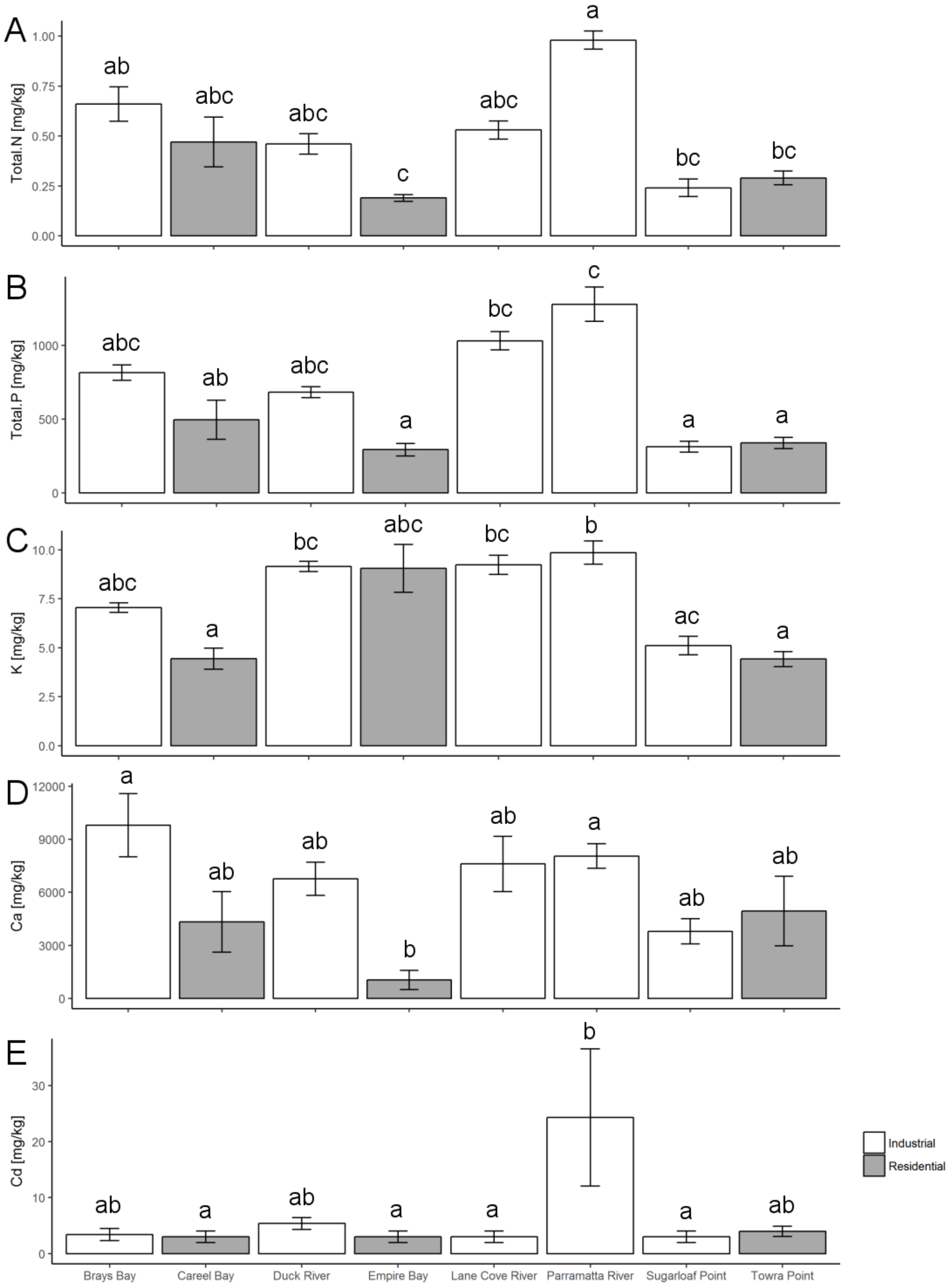
Site Name	Latitude	Longitude	Category	Local Government Area
Brays Bay	-33.83499	151.09361	Industrialised	Rhodes
Careel Bay	-33.62323	151.32973	Residential	Pittwater
Duck River	-33.83242	151.04138	Industrialised	Parramatta
Empire Bay	-33.49239	151.35626	Residential	Gosford
Lane Cove River	-33.80024	151.14606	Industrialised	Chatswood
Parramatta River	-33.84536	151.08212	Industrialised	Homebush
Sugarloaf Point	-33.81288	151.44085	Industrialised	North Ryde
Towra Point	-34.0218	151.19313	Residential	Kurnell

Table A2 | Species list and categorization of the plant species encountered at the sampling sites.

Scientific Name	Common Name	Family	Status	Salt Adaptation
Aegiceras corniculatum	River Mangrove	Myrsinaceae	native	Halophyte
Atriplex australasica	Native Orache	Chenopodiaceae	native	Halophyte
Aurajia sericifera	Moth Vine	Asclepiadoideae	exotic	Glycophyte
Avicennia marina var. australasica	Grey Mangrove	Avicenniaceae	native	Halophyte
Baumea juncea	Bare Twig Rush	Cyperaceae	native	Halophyte
Bidens pilosa	Cobbler's pegs	Asteraceae	exotic	Glycophyte
Casuarina glauca	Swamp She-Oak	Casuarinaceae	native	Halophyte
Commelina diffusa	Native Wandering Jew	Commelinaceae	native	Glycophyte
Conyza parva	Fleabane	Asteraceae	exotic	Glycophyte
Cyperus eragrostis	Umbrella Sedge	Cyperaceae	exotic	Glycophyte
Echinochloa crus-galli	Cockspur, Japanese millet	Poaceae	exotic	Glycophyte
Erharta erecta	Panic veldt grass	Poaceae	exotic	Glycophyte
Geranium solanderi	Native Geranium	Geraniaceae	native	Glycophyte
Hydrocotyle bonariensis	Pennywort	Araliaceae	exotic	Halophyte
Juncus acutus	Spiny Rush	Juncaceae	exotic	Halophyte
Juncus kraussii subsp. australiensis	Sea Rush	Juncaceae	native	Halophyte
Lantana camara	Lantana	Verbenaceae	exotic	Glycophyte
Livistona australis	Cabbage Tree Palm	Arecaceae	native	Glycophyte
Lobelia alata	Angled Lobelia	Lobeliaceae	native	Halophyte

Nephrolepis cordifolia	Fishbone Fern	Davalliaceae	native	Glycophyte
Omalanthus populifolius	Bleeding Heart	Euphorbiaceae	native	Glycophyte
Persicaria decipiens	Slender Knotweed	Polygonaceae	native	Glycophyte
Phragmitis australis	Common Reed	Poaceae	native	Halophyte
Pittosporum undulatum	Sweet pittosporum	Pittosporaceae	native	Glycophyte
Plectranthus parviflorurs	Cockspur Flower	Lamiaceae	native	Glycophyte
Protasparagus aethiopicus	Asparagus Fern	Liliaceae	exotic	Halophyte
Pteridium esculentum	Bracken Fern	Dennstaedtiaceae	native	Glycophyte
Rumex crispus	Curly Dock	Polygonaceae	exotic	Glycophyte
Samolus repens	Creeping brookweed	Theophrastaceae	native	Halophyte
Sarcocornia quinquefolia	Samphire	Chenopodiaceae	native	Halophyte
Senecio glomeratus	Fireweed	Asteraceae	native	Halophyte
Sida rhombifolia	Paddy's Lucerne	Malvaceae	exotic	Glycophyte
Sigesbeckia orientalis	Indian Weed	Asteraceae	exotic	Glycophyte
Solanum avilucarum	Kangaroo Apple	Solanaceae	native	Glycophyte
Solanum lycopersicum	Tomatoe	Solanaceae	exotic	Glycophyte
Sporobolus virginicus	Saltwater Couch	Poaceae	native	Halophyte
Stenotaphrum secundatum	Buffalo Gras	Poaceae	exotic	Glycophyte
Sueda australis	Austral Seablite	Chenopodiaceae	native	Halophyte
Tetragonia tetragonoides	New Zealand Spinach	Aizoaceae	native	Halophyte
Tradescantia albiflora	Wandering Jew	Commelinaceae	exotic	Glycophyte
Triglochin striata	Streaked Arrow Grass	Juncaginaceae	native	Halophyte
Tropaeolum majus	Garden Nasturtium	Tropaeolaceae	exotic	Glycophyte
Zoysia macrantha	Prickly Couch	Poaceae	native	Halophyte

Figure A4 | Photographs of urban saltmarsh and mangroves. Transects were chosen to start at the stormwater run-off outlet (A) and extended through the saltmarsh area across the saltmarsh-mangrove boundary (B) into the mangroves. Invasive species can grow towards saltmarsh habitat and the use of barrier fences to control stormwater run-off and sediment deposition are sometimes used management (C).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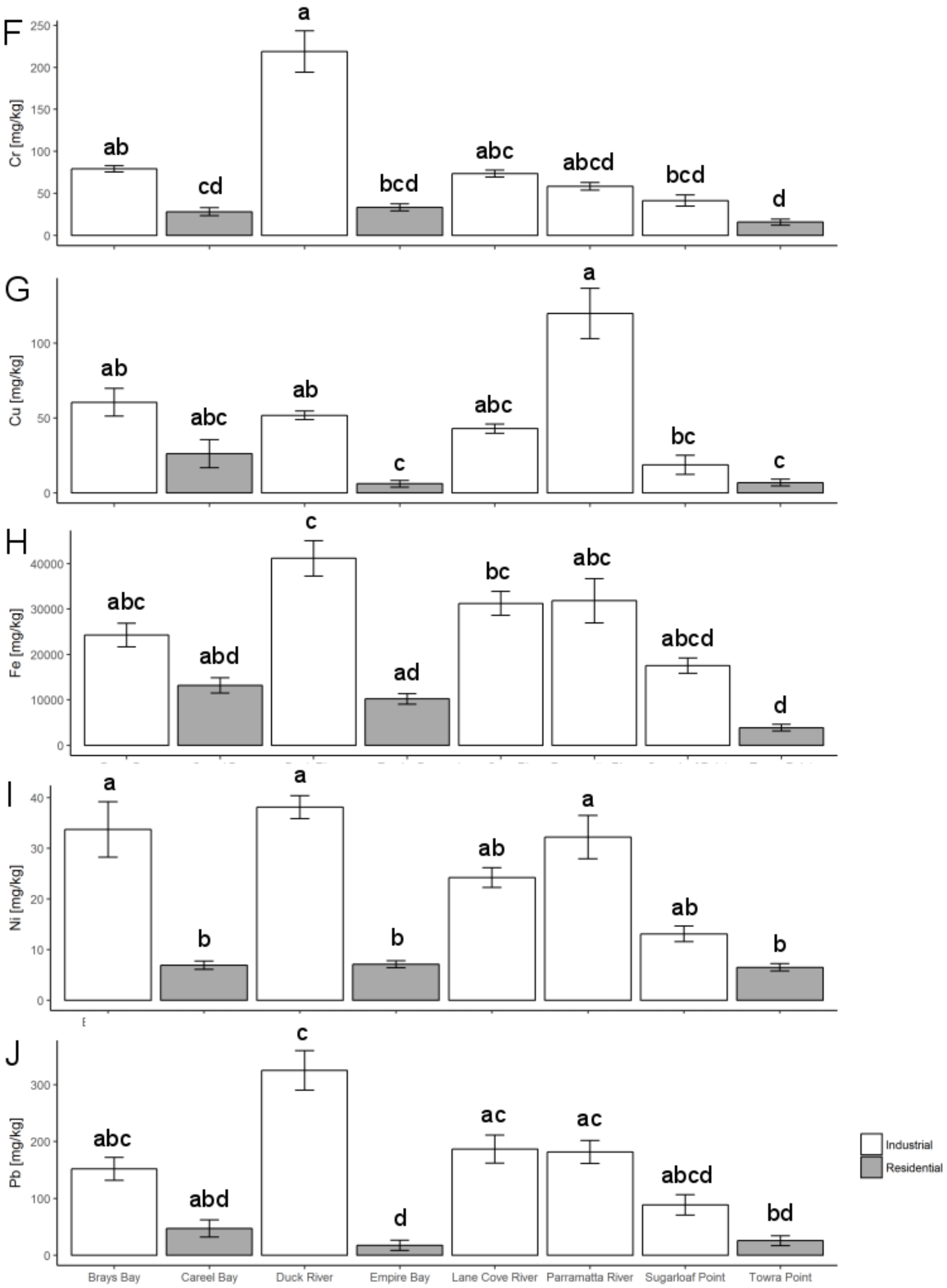
Sugarloaf Point
Towra Point
Industrial
Residential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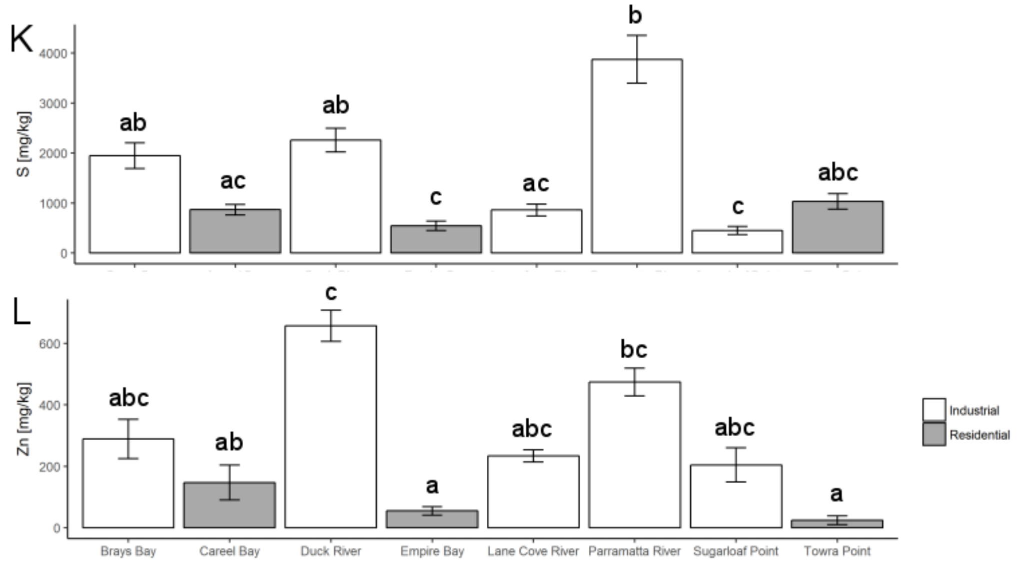

Figure A2 | Average concentrations of nutrients (Total.N, Total.P, K) and heavy metals (Ca, Cd, Cr, Cu, Fe, Ni, Pb, S, Zn) at each sampling site, respectively. The colour of the bars symbolizes whether the site was considered as industrial (white) or residential (grey). The error bars stand for the standard error of the mean and the letters show significant differences ($p < 0.05$) between sites according to Kruskall-Wallis test by ranks.

Chapter 3

Freshwater input drives invasion success of exotic plants in salt-marsh communities

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Abstract

While saltmarsh communities are endangered in many parts of the world due to anthropogenic impact, the risk of invasion by exotic plants is considered to be low because of their saline conditions. However, in urban areas, saltmarshes receive high nutrient freshwater input through stormwater discharge. We tested if invasion of saltmarsh by exotic plant species was facilitated by increased nutrients and reduced salinity associated with urban stormwater input. In a manipulative glasshouse experiment, we grew saltmarsh communities under four treatments: high salinity-low nutrients (control), high salinity-high nutrients, low salinity-low nutrients and low salinity-high nutrients. We then invaded the saltmarsh communities with four common invasive exotic plants. Their survival rates were monitored weekly for seven weeks before final harvesting. All exotic species showed significantly higher survival in the 'low salinity' treatment compared to the 'high salinity' treatment. There was variability among species, with three of four having low survival rates (0-3%) under 'high salinity' conditions, while survival of *Protasparagus aethiopicus* was reduced to only 53-59%. We found a significant increase in biomass under high nutrients for *Acetosa sagittata* ($\chi_{[2,212]} = 8.486$, $p = 0.014$) and *P. aethiopicus* ($\chi_{[3,368]} = 44.021$, $p < 0.001$), but not for *Bidens pilosa* and *Conyza parva.*Our findings suggest that under natural conditions of saltmarshes, the establishment of exotic plant seedlings is restricted. Additional freshwater increased the survival of invading exotic species significantly, whereas adding nutrients increased biomass production but not necessarily survival of exotics. However, the results can be highly species dependant as shown by the unexpected salinity tolerance of *P. aethiopicus*. Reduction in salinity of saltmarsh due to stormwater input facilitates invasion by exotic plant species that would otherwise be unable to tolerate the highly saline environment. This suggests that infrastructure in urban areas should be built to ensure that stormwater is piped directly to the water's edge rather than released into saltmarsh vegetation.

Keywords

Greenhouse; invasive species; nutrients; plant biomass; salinity; stormwater; survival rates; tidal wetlands; urban pollution

Introduction

Exotic species invasions have been identified as the second largest threat to global biodiversity after habitat destruction (Lambertini et al., 2011). An invasive exotic species is defined as a non-native species that has spread beyond its site of introduction, having direct or indirect impacts on recipient communities by, for example, out-competing native species or changes to soil nutrient status or hydrology (Alpert et al., 2000; Gaertner et al., 2017). In particular, urban areas are highly vulnerable to exotic plant invasions because parks and gardens provide high rates of propagule supply for a wide range of exotic species (Hui et al., 2017). In addition, transport linkages (i.e. airports, harbours, roads) support the spread of exotic species through potential dispersal pathways (Gaertner et al., 2017; Štajerová et al., 2017). Disturbances caused by urban development, including fragmentation and nutrient input, further increase the establishment and spread of invasive exotic species (Alpert et al., 2000; Lake and Leishman, 2004) by reducing native biodiversity and decreasing biotic resistance (Cheng and Hovel, 2010).

Much urban development globally is concentrated in coastal regions (Elmqvist et al., 2013), where the remaining natural wetland ecosystems are particularly threatened. Approximately 62-63 % of coastal wetlands have been destroyed in the last century (Davidson, 2014). This loss is largely attributable to anthropogenic habitat destruction resulting from urbanisation and agriculture (Van Asselen et al., 2013). One wetland ecosystem that has been particularly affect by anthropogenic habitat destruction is saltmarshes (Adam, 2002; Matthews, 1993). Globally, saltmarsh communities occur in subtropical to temperate regions and inhabit areas between the lower and upper tidal range (Adam, 2009). Periodical inundation by the tide coupled with evaporation between tides means that the soil salt concentrations can be up to five times that of seawater (Adam, 2009). Due to their ability to tolerate high salinity and waterlogging, saltmarsh plants are well adapted to survive these harsh conditions (Adam, 1990).

Urban development along coastal zones adds numerous disturbing factors, such as land reclamation and pollution through stormwater or agricultural run-off (Adam, 1990; Geedicke et al., 2018; Saintilan et al., 2009), which can ultimately lead to a decline in saltmarsh habitat (Lee et al., 2006). In recognition of the multitude of services that saltmarshes provide, such as coastal stabilization and habitat for bird, invertebrate and fish species (Alongi, 2002; Hughes, 2004; Mitsch and Gossilink, 2000), regulations such as the Ramsar Convention (Ramsar Convention, 2016) have been put in place to conserve these important ecosystems.

It has been suggested that the harsh environmental conditions in saltmarsh make them less vulnerable to exotic plant invasions than more benign systems (Adam, 2009). However, for saltmarsh species there is a trade-off between tolerance of high salinity conditions and growth rate. That is, they are generally slow growing which makes them less competitive when salinity levels are reduced (Crain et al., 2004). Therefore, in highly urbanised areas saltmarshes may become more vulnerable to invasion due to increased stormwater runoff entering these systems (Geedicke et al., 2018). Urban stormwater reduces soil salinity and contains high concentrations of nutrients; both factors which are likely to facilitate the growth and reproduction of exotic plant species. For example, in a previous study of urban saltmarshes and mangroves in the Sydney region, Australia, we showed that the cover of invasive exotic species increased by 40% below stormwater outlets and that this was correlated with reduced salinity and increased nutrient concentrations of the soil (Geedicke et al., 2018).

In the present study, we used a manipulative experimental approach to test the effect of salinity and nutrients on the invasion success of exotic plant species over native saltmarsh species, using species that commonly co-occur in saltmarsh communities in the greater Sydney region, Australia. We grew model saltmarsh communities in mesocosms in a fully factorial glasshouse experiment with salinity and nutrient concentration as the treatment factors. These mesocosms were then invaded with seedlings of common invasive exotic plant species whose survival and growth were assessed. We hypothesised that (i) the survival and growth (biomass) of the invasive exotic species will be lowest under undisturbed saltmarsh conditions (high salinity – low nutrients) because saltmarsh species will be competitive relative to exotic species under these harsh conditions, and (ii) that highest survival rates and growth of the exotic species will occur under disturbed saltmarsh conditions (low salinity - high nutrients) due to the relatively greater competitive ability of exotic species under these freshwater and high nutrient conditions.

Methods

Species selection

We selected four native saltmarsh species (*Tetragonia tetragonoides* (Pall.) Kuntze, *Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) A.J.Scott, *Suaeda australis* (R.Br.) Moq. and *Selliera radicans* Cav.) and four invasive exotic species (*Protasparagus aethiopicus* L. (asparagus fern), *Acetosa sagittata* (Thunb.) (turkey rhubarb), *Conyza parva* Cronquist and *Bidens pilosa* L. (cobbler's pegs)) that commonly co-occur in saltmarsh communities within the greater Sydney region. The four selected native saltmarsh species have similar waterlogging and salt tolerance capacities and typically co-occur within saltmarshes in south-east Australia (Sainty, 2012). The four exotic species (Table 1) are listed as introduced invasive species to south-east Australia (Royal Botanic Gardens and Domain Trust, 2018) and were also found to be abundant in a previous vegetation survey of urban saltmarsh communities of the Sydney region (Geedicke et al., 2018).

Table 2 | Information on the taxonomy, native range, growth form and average height of the invasive exotic species used in this study

Name	**Family**	**Native range**	**Growth form**	**Maximum height [cm]**
Acetosa sagittata	Polygonaceae	South Africa	perennial climber	100
Bidens pilosa	Asteraceae	South America	annual herb	100
Conyza parva	Asteraceae	South America	annual herb	50
Protasparagus aethiopicus	Asparagaceae	South Africa	perennial shrub	200

Seedlings of the native saltmarsh species were obtained from commercial nurseries (Bunya Native Nursery, Dural, NSW and Indigo Native Nursery, Ingleside, NSW, Australia) who had sourced the seeds from the Sydney suburbs of Hammondville, Ingleside and Ermington. Seeds of each exotic species were collected from a minimum of 50 different individual plants growing along the dunes of Umina Beach, NSW, Australia (Lat: -33.526632, Long: 151.315770). In the laboratory, the seeds were germinated on moist paper towels in aluminium trays sealed with plastic wrap. Prior to germination, *P. aethiopicus* seeds were soaked for six hours in warm water and scarified to increase the germination rate. The sowing of the different exotic species was timed so that their germination occurred within a 24-hour time period, enabling them to all be planted into the mesocosms at the cotyledon emergence stage.

Experimental Design and Treatments

We established 28 mesocosms containing native saltmarsh plants in the Plant Growth Facility glasshouse at Macquarie University. The mesocosms consisted of 60 L tubs (43 cm wide, 34.5 cm deep, 63 cm long) filled with 80:20 sand-soil mix (Australian Native Landscape Ltd., North Ryde, NSW, Australia). The sand-soil mix consisted of screened river sand and compost, resulting in nutrient levels of 150 mg/kg total nitrogen and 100 mg/kg total phosphorus. These soil nutrient concentrations are comparable to concentrations obtained at saltmarsh communities within the Sydney area in a previous study by Geedicke et al. (2018). At the time of planting, the native saltmarsh plants were about one year old and selected to be of similar height (approximately 15 cm). Three replicates of each species (12 plants) were planted in each mesocosm in three rows of four, spaced approximately 10 cm apart (Fig. A1). The 28 mesocosms were randomly allocated to locations in the glasshouse and watered for three minutes twice a day using an automatic watering system. The water level was dynamic because the mesocosms were inundated and drained through punctures in the bottom of the mesocosms twice a day. The temperature in the glasshouse was maintained at 25 ºC during the day and 18 ºC at night, which represents the average summer temperatures of the Sydney region.

We used a standard two-way factorial design for the experiment, with the two factors being nutrient concentration and salinity. Immediately after planting the saltmarsh species we applied one of four different treatments to the mesocosms (seven mesocosms per treatment): high salinity + high nutrients (HSHN), high salinity + low nutrients (HSLN), low salinity + high nutrients (LSHN), low salinity + low nutrients (LSLN). We applied the salinity treatment every two weeks by adding 1 L 0.5 M NaCl to all ‘high salinity’ mesocosms which represents the NaCl concentration of seawater while the ‘low salinity’ mesocosms received 1 L of freshwater. These salinity treatments were selected as they represent the salinity range measured in the field (Geedicke et al., 2018) where we tested soil salinity levels in natural undisturbed saltmarshes and saltmarshes below stormwater outlets in the greater Sydney region. Soil salinity was measured weekly using a HI98196 electrical conductivity meter (Hanna Instruments, Castle Hill, NSW, Australia) to confirm that the salinity treatments were being maintained at the appropriate levels. On the weeks when the salinity treatments were not applied, the nutrient treatments were applied. For the high nutrient treatment, we added 1 L 0.4g/L Aquasol soluble fertilizer (Yates Australia, Wetherill Park, NSW, Australia; 23 N:3.95 P:14 K) while the ‘low nutrient’ mesocosms received 1 L of freshwater. Nutrient treatment was derived from the field data collected in a previous study on urban saltmarsh soils (Geedicke et al., 2018). The saltmarsh mesocosms were then grown and treated using this regime for 12 weeks until the plants were well established and resembled a saltmarsh community. Once established, 15 individuals from each of the four exotic plant species (60 seedlings total at cotyledon stage) were randomly planted into each mesocosms in a 6 x 10 grid design. The high density of exotic plant seedlings was chosen because propagules generally enter wetland systems in high densities via point pollution sources, such as stormwater run-offs (Zedler and Kercher, 2004). The survival of the exotic plant seedlings was then recorded on a weekly basis. To ensure surviving exotic plants for biomass harvesting, we terminated the experiment after seven weeks. The most critical life stage for seedling survival lies within the first two months after emergence, which is why we assumed that survival of seedlings will follow the Deevy curve type III after seven weeks (Fenner, 1987). All the plants within the mesocoms were harvested, separated into above- and below-ground biomass, washed, oven dried at 60 °C for 72 h and weighed using an analytical electronic balance (Sartorius AG, Göttingen, Germany). The exotic plants were harvested and separated at the individual-level, while the saltmarsh species were harvested at the species-level due to root entanglement.

Data analysis

Because the survival data contained censored data and the distribution of survival times was highly skewed, multiple regression analyses were not appropriate for our data. Therefore, we used Cox regression for our survival analyses (Cox, 1958) to investigate the effect of salinity and nutrients on the survival rate of the exotic plant seedlings per species. The significant differences between the treatments were analysed with Dunnett’s multiple comparison test (Dunnett, 1955) where we assigned the high salinity – low nutrients treatment as the control group. For visualization we used the Kaplan-Meier estimator (Fig. 1), which evaluates censored data (i.e. the surviving plants) (Efron, 1988). Survival rates were calculated using the R packages ‘*survival*’ (Therneau and Grambsch, 2000), ‘*survminer*’ (Alboukadel et al., 2018) and ‘*multcomp*’ (Hothorn et al., 2008).

The effect of the four treatments and the native saltmarsh species on the biomass of the exotic plant species was analysed using a factorial generalized linear model (GLM) with a gamma distribution and log link. The gamma distribution was used due to the continuous, strictly positive response data with large variances and the log link to achieve homoscedasticity of the residuals. For each exotic species' total biomass, we built GLMs separately, taking the treatments (HSHN, HSLN, LSLN and LSHN) and the native saltmarsh biomass as fixed effects. Because there was no significant interaction between all treatments and native saltmarsh biomass, we simplified the model by adding native saltmarsh biomass as an additive effect (Supplement A1). An analysis of deviance was then applied to the model which computes the reductions in the residual deviance as each term of the formula is added in turn. Differences between treatment groups were tested with a post-hoc Tukey test using the '*multcomp*' package in R. Multiple comparison after Dunnett, as performed on the survival data, was not possible because three of the four exotic species did not have enough surviving seedlings within the control group to test for significant biomass differences.

All statistical analyses were performed within the R statistical environment (R Development Core Team, 2018). The code and data of this analysis is openly available at GitHub (address and doi added after acceptance).

Results

Survival rates

Overall survival rates were significantly higher across all four exotic species in the two ‘low salinity’ treatments compared to the control treatment (HSLN) (LSLN: z = -19.080, p < 0.001, LSHN: z = -17.213, p < 0.001; Fig. 1). However, there was no significant difference in survival of the exotic species between ‘high salinity, low nutrient’ and ‘high salinity, high nutrient’ treatments (z = -1.715, p = 0.467). At the individual species-level, all exotic species had significantly higher survival in the ‘low salinity’ treatment compared to the ‘high salinity’ treatment. In contrast, there was no significant nutrient effect on the survival of any of the exotic species. It should be noted that *A. sagittata* and *B. pilosa* seedlings experienced 100% mortality in the HSLN control treatment after seven weeks while *C. parva* seedlings had 100% mortality in both ‘high salt’ treatments.

For all treatments, an initial mortality of all exotic species occurred during the first week after planting of seedlings (Fig. 1 a-d). However, the range of the initial mortality rates differed strongly between species and treatment. After one week of treatment, *A. sagittata* (Fig. 1a) showed a mortality of 44 % and 43 % in the high salinity treatment HSHN and HSLN, respectively, but only 3 % in low salinity. At the end of the study, 7 % (HSHN) and 0 % (HSLN) of *A. sagittata* plants survived in high salinity but 86 % and 95 % survived under low salinity with high (LSHN) and no added nutrients (LSLN), respectively. The survival of *A. sagittata* was significantly higher without added salinity (LSLN: z = -9.449, p < 0.001, LSHN: z = -11.554, p < 0.001) compared to the control group (HSLN) but no significant difference between nutrient treatments at high salinity (z = -2.362, p = 0.0527) was observed.

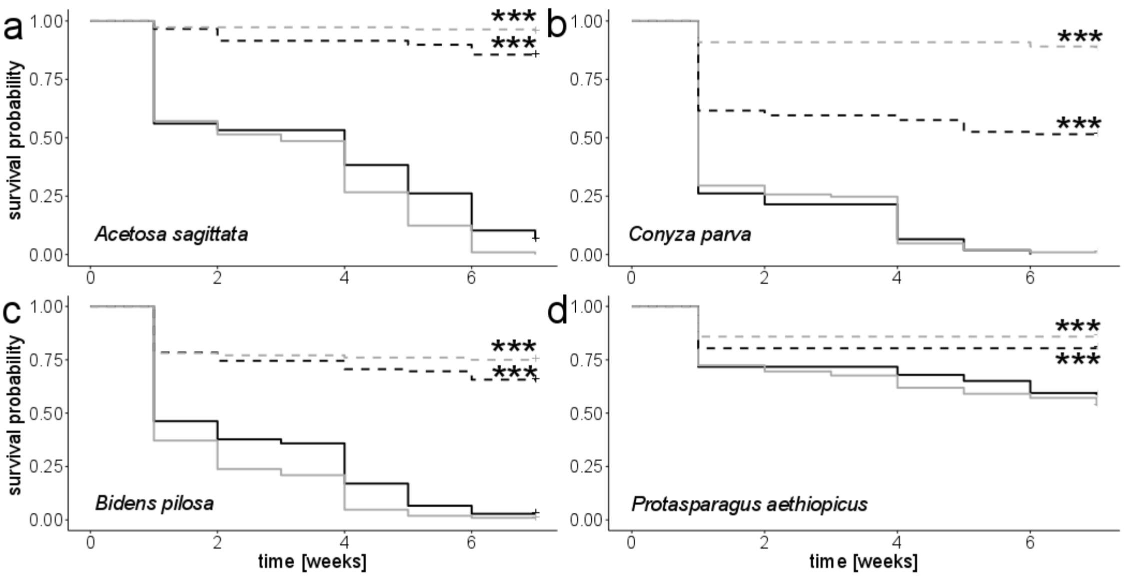

Fig. 1 | Kaplan-Meyer survival curves of the four different exotic species within the saltmarsh mesocosm communities and their survival rates within seven weeks under four different treatments: high salinity + low nutrients (HSLN/control, grey solid line), high salinity + high nutrient (HSHN, black solid line), low salinity + low nutrient (LSLN, grey dashed line), low salinity + high nutrients (LSHN, black dashed line). The asterisks symbolise significant differences of the treatment against the control group HSLN: *p < 0.05, **p < 0.01, *** p < 0.001.

We observed a similar pattern in *Bidens pilosa* and *Conyza parva* (Fig. 1b and c): high initial mortality of 63 % -54% and 74-70% in the control group (HSLN) and HSHN, respectively. After seven weeks of treatment only 1-3 % of B. pilosa and and 0-1 % of C. parva survived high salinity.

Only *Protasparagus aethiopicus* (Fig. 1b) showed high survival rates overall, with higher initial survival of 72 % under both high salt treatments and 80 % and 85 % of survival under freshwater conditions with high (LSHN) and low (LSLN) nutrients, respectively. By the end of the experiment 59% and 53% of the initial population survived the salinity treatment (HSHN, HSLN) and there was no further mortality observed within the freshwater treated mesocosms. The survival in low salt treatments was significantly higher (LSLN: z = -4.535, p < 0.001, LSHN: z = -3.720, p < 0.001) compared to the control group and no significant difference could be observed between nutrient treatments under high salinity conditions (HSLN) and HSHN (z = -0.630, p = 0.883).

Exotic plant biomass

After seven weeks of treatment, the three exotic species apart from *P. aethiopicus* showed high mortality (97-100%) within the control group HSLN and so there were insufficient data to enable a statistical comparison of biomass between the control and other treatments. Similarly, *C. parva* showed 100 % mortality under the HSHN treatment so that there was only sufficient biomass to enable comparison of the two freshwater treatments (LSLN, LSHN).

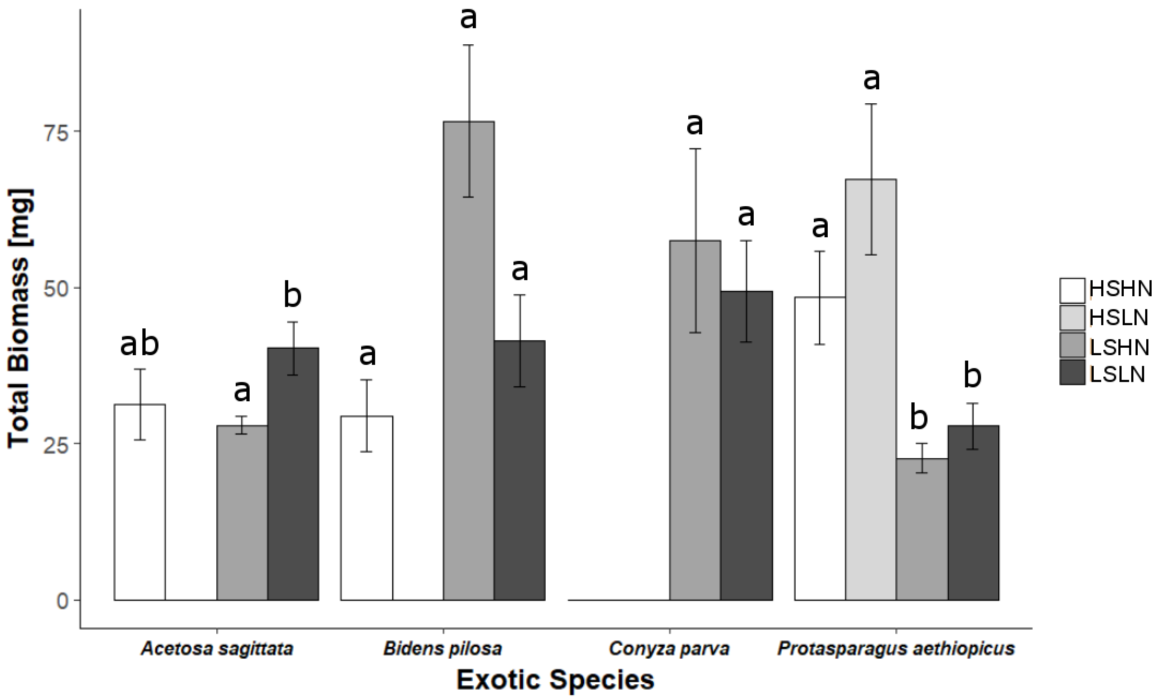

Fig. 2 | Total biomass of the four different exotic species after seven weeks of growth in the mesocosm under the four different treatments: HSHN, HSLN, LSLN, LSHN. The bars show the average total biomass and the standard deviation of the data. Letters symbolize significant differences between treatments for each species and were calculated from the model data including the fixed effect of native saltmarsh biomass on the exotic species.

A positive significant effect of the native saltmarsh biomass on the biomass of three of the four exotic species was found (*B. pilosa:* $\chi[1,149] = 4.868$, $p = 0.014$; *C. parva:* $\chi[1,146] = 4.440$, $p = 0.035$; *P. aethiopicus:* $\chi[1,368] = 5.684$, $p = 0.017$). However, due to the high variability of saltmarsh biomass between the mesocosms we could not identify which treatment or treatment combination had a significant effect on the saltmarsh species growth and therefore on the exotic plant biomass. The analysis of deviance showed a significant effect of the treatments on the biomass of *A. sagittata* ($\chi_{[2,212]}$ = 8.486, p = 0.014) and *P. aethiopicus* ($\chi_{[3,368]}$ = 44.021, p < 0.001).

Post-hoc comparisons using the Tukey HSD test (Fig. 2) for *A. sagittata* showed that under the LS treatments, seedlings treated without additional nutrients (LSLN) accumulated significantly more biomass than seedlings in mesocosms with nutrient addition (LSHN) (z = 2.939, p = 0.008). No other treatment differences existed for *A. sagittata* (LSHN – HSHN: z = -0.360, p = 0.925; LSLN – HSHN: z = 0.330, p = 0.936). Post-hoc comparisons for *P. aethiopicus* showed significantly greater biomass of seedlings in the HS treatments compared to the LS treatments (LSHN – HSHN: z = -4.563, p < 0.001; LSLN – HSHN: z = -2.990, p = 0.015; LSHN – HSLN: z = -5.860, p < 0.001; LSLN – HSLN: z = -4.314; p < 0.001), regardless of nutrient treatment.

Discussion

Although saltmarshes are listed as a threatened ecological community under national and state legislation in Australia (Saintilan and Rogers, 2013), invasion by exotic species is not generally identified as a threat (Deegan et al., 2012). Previous research in the field has shown a correlation between reduced soil salinity and increased soil nutrients with an increase in exotic species invasion in urban saltmarsh communities of eastern Australia (Geedicke et al., 2018). The present study was designed to test these field observations, using a manipulative experimental approach.

The first hypothesis tested was that survival and growth of exotic species will be lowest under high salinity and low nutrient availability (i.e. natural environmental conditions typical of saltmarshes) compared to all other treatment combinations. Our experiment provided strong support for this hypothesis. Across all exotic species, survival was lowest under high salinity, low nutrient conditions. However, there were differences among the four species, with three of the four species having almost no survival under high salinity, while the survival of *P. aethiopicus* was more than twenty times higher under high salinity compared to the other exotic species. Surprisingly, biomass of *P. aethiopicus* was significantly higher under high salinity compared to low salinity mesocosms. *Protasparagus aethiopicus* is listed as a declared noxious weed in eastern Australia (Royal Botanic Gardens and Domain Trust, 2018) and as invasive in Florida (Langeland, 2008). Although, it is known to invade a wide range of ecosystems, such as exposed headlands, rainforests, woodlands, coastal dunes and heathlands (Bowden and Rogers, 1996), we could find no studies reporting salt adaptation or occurrence in saline environments for this species in the literature. However, germination studies on *P. aethiopicus* have reported that it has a 73.3% germination success on average under a wide range of treatments, i.e. different light conditions and temperatures (Vivian-Smith and Gosper, 2010), however, none were saline. Furthermore, we observed higher frequency of bare patches within our high salinity mesocosms compared to the freshwater ones (Fig. A1 B-E) which may have indirectly enhanced the growth of *P. aethiopicus* by increasing light availability. The higher frequency of bare patches in wetlands as a facilitation to wetland invasion has also been discussed by Zedler and Kercher (2004). However, there was no significant difference in saltmarsh biomass between the salinity treatments due to high variability of the biomass data. Our findings suggest that *P. aethiopicus* should be considered a potential invader of halophytic environments, especially when competition with other species is low due to bare patches from disturbances, such as trampling or the inflow of materials such as plant debris and soil (Zedler and Kercher, 2004).

Our second hypothesis was that exotic invasive species would have highest survival and growth under the low salinity and high nutrient treatments compared to all other treatment combinations. This is because in high resource environments, particular high nutrient conditions, invasive exotic species tend to have traits that enable rapid growth (Grotkopp and Rejmánek, 2007; Leishman et al., 2010; Leishman and Thomson, 2005). This is consistent with previous studies on terrestrial urban systems that have shown enhanced invasion success of exotic species under high nutrient conditions associated with urban stormwater runoff (Lake and Leishman, 2004; Leishman and Thomson, 2005). In our study however, highest survival of all tested exotic species was found under the low salinity and low nutrient treatment. It was expected that the exotic species would be most responsive under low salinity, however we also expected that this would be most evident under high nutrient conditions rather than low nutrient conditions as exotic invasive plants are often efficient in nutrient uptake (Mozdzer and Megonigal, 2012). Because we tested against the control group, it was not statistically tested if highest survival was significantly greatest under low salinity-low nutrient treatment. At the species-level, we found that the biomass of *A. sagittata* grown under low salinity was significantly greater in the low nutrient treatment compared to the high nutrient treatment. Furthermore, we found that the biomass of native saltmarsh species had a significant negative competitive effect on the other three exotic species (*B. pilosa, C. parva, P. aethiopicus*) across all treatments. We assume that competition is suppressing the biomass of some exotic species at seedling stage when growing in between adult saltmarsh species. By providing additional freshwater and nutrients, we created optimal conditions for the exotic species to establish with mortality remaining constant after the initial first stage. This suggests that the most important time in the establishment of exotic plants in saltmarshes is just after germination when they are most vulnerable. However, to draw this conclusion longer term studies are needed to determine if mortality truly remains constant or fluctuates through time.

Regardless of the nutrient treatment, our results show that under freshwater conditions, survival and growth of exotic species is very high and that the invasion of saltmarsh communities is facilitated. In undisturbed areas, a large decrease in soil salinity could only be achieved through extreme precipitation events. Such events have been shown to cause vegetation change in saltmarshes such as the encroachment of less salt tolerant mangroves (Saintilan and Rogers, 2015) and/or the germination of exotic species within the seedbank of saltmarshes (Callaway and Zedler, 2004). Zedler and Kercher (2004) propose that wetlands in particular are sensitive to plant invasions as they often function as a sink to terrestrial as well as maritime and/or freshwater disturbances due to their lowland position. In urban areas, disturbances which increase freshwater input into saltmarshes are much more regular, because the impervious surfaces of roads and buildings lead to the accumulation of stormwater run-off, which is collected and channelled into the adjacent pervious surfaces, such as urban parklands, remnant vegetation or, in coastal areas, wetlands (Al Bakri et al., 2008; Grella et al., 2018). Stormwater input is not the only freshwater input into coastal wetlands, with other anthropogenic influences through manipulation of the hydrologic system (e.g. importing water for agricultural and urban uses), influencing salinity in these systems (Zedler and Kercher, 2004). For example, in southern California, it has been shown that these freshwater inputs facilitate the invasion of exotic species into saltmarshes (Callaway and Zedler, 2004). Typically, species that invade coastal wetlands tend to be exotic or native saltmarsh species (Zedler and Kercher, 2004), such as *Phragmitis australis* in the United States (Hazelton et al., 2018). However, *Spartina anglica* and *Spartina alterniflora,* two exotic saltmarsh species in China, can also tolerate a wide range of salinity and waterlogging levels. Li (2018) proposed that sea level rise will facilitate the invasion of *S. anglica* into native *P. australis* communities in China due to their high salinity tolerance. Thus, saltmarshes may be threatened by invasion by freshwater exotic species on the landward site and from salt tolerant exotic species on seaward side, resulting in substantial changes in saltmarsh assemblages with flow-on effects to native fauna and ecosystem processes.

Conclusion

Saltmarsh communities are endangered worldwide due to urban development, agriculture and coastal infrastructure, and increasingly from sea level rise. An additional stress in urban areas is the influx of nutrient-rich freshwater through stormwater systems. This is likely to result in a compositional species shift in coastal wetlands towards more terrestrial species, including exotic species, being present. This study has shown that exotic plants have better survival and growth in low salinity conditions compared to the high salinity conditions typical of saltmarshes, suggesting that invasion of urban saltmarshes is facilitated by stormwater input. Wetlands are in general thought of as resilient to plant invasion and additional nutrient input. Therefore, wetlands are often used or constructed as a sink for stormwater run-off. Our results show however, that saltmarshes are particularly vulnerable to be invaded by exotic plants when treated with freshwater. We suggest that management of stormwater input into these threatened coastal wetlands should be a high priority. However, even with maintenance of high salinity conditions, some exotic species such as *P. aethiopicus* will be able to thrive and therefore require targeted management.

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SUPPLEMENTARY MATERIAL

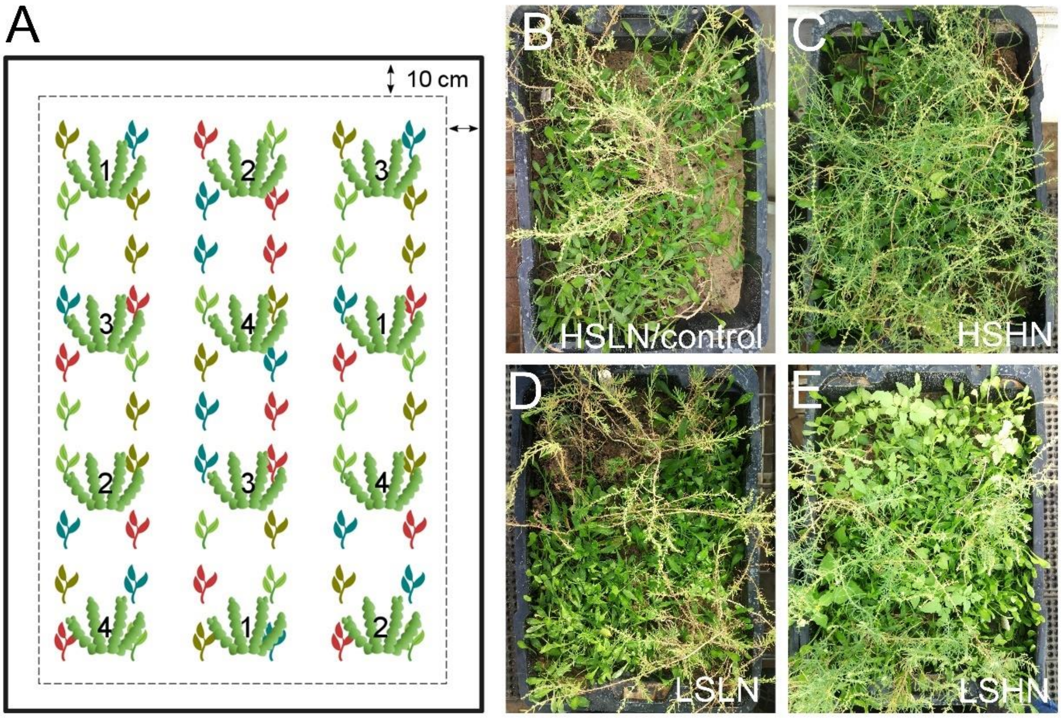

Fig. A1 | Experimental design and overview of plant density after 7 weeks of growing the exotic species within the mesocosms. (A) shows the planting design of the mesocosms. Twelve saltmarsh plants were grown per tub and planted in a 3x4 grid with random selection of the four different species (saltmarsh symbol 1-4). After 12 weeks, 60 exotic plants were planted between the saltmarsh plants in a grid of 6x10, with random selection of the four exotic species (exotic plant symbol in 4 different colours). B-D shows a mesocosm under each treatment just before harvesting.

Chapter 4

Elevated carbon dioxide and seawater salinity enhances mangrove seedling establishment in a model saltmarsh community

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Abstract

The global phenomenon of mangrove encroachment into saltmarshes has been observed across five continents. It has been proposed that this encroachment is driven in part by rising atmospheric CO_2 concentration and reduced salinity in saltmarshes resulting from rising sea levels enhancing the establishment success of mangrove seedlings. However, this is yet to be empirically tested at the community-level. In this study, we examined the effect of CO_2 and salinity on seedling growth of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, grown individually and in a model saltmarsh community in a glasshouse experiment. We found that the shoot (210%) and root (91%) biomass of the saltmarsh species was significantly greater under elevated CO_2. As a result, both mangrove species experienced a stronger competitive effect from the saltmarsh species under elevated CO_2. Nevertheless, *A. marina* seedlings produced on average 48% more biomass under elevated CO_2 when grown in competition with the saltmarsh species which they used to grow taller suggesting they were light limited. In contrast, *A. corniculatum* growth did not significantly differ between CO_2 treatments. However, it had on average 36% greater growth under seawater salinity compared to hypersaline conditions. *Avicenna marina* seedlings were not affected by salinity. From these results, we suggest that although CO_2 and salinity are not universal drivers determining saltmarsh-mangrove boundaries, it is likely that rising atmospheric CO_2 concentration and reduced salinity associated with sea level rise will enhance the establishment success of mangrove seedlings in saltmarshes, which may facilitate mangrove encroachment in the future.

Keywords

Aegiceras corniculatum, *Avicennia marina*, climate change, wetland, woody plant encroachment

Introduction

Saltmarsh and mangrove communities provide critically important habitat and feeding grounds for a range of invertebrates, shore-birds and fish as well as other important ecosystem services including coastal stabilisation, filtration and trapping of pollutants (Kathiresan, 2012; Spencer et al., 2009). Economic modelling of the value of goods and services provided by saltmarsh and mangrove communities to coastal fisheries production, coastal protection, carbon sequestration and biodiversity conservation is estimated to be on average $USD 194 000 ha^{-1} yr^{-1} (Costanza et al., 2014). Given that the global area of saltmarsh communities is estimated to be greater than two million hectares and mangrove communities is greater than 18 million hectares (Saintilan and Rogers, 2013), we can calculate their total value at ~$USD 4 trillion annually. Therefore, significant changes to the structure and distribution of saltmarsh and mangrove communities will not only impact the natural processes that they mediate but also have a profound effect on human activities that utilise these communities.

Within the subtropics, an ecotone of 2-3° of latitude occurs where mangrove and saltmarsh communities co-exist and compete for dominance, with saltmarshes usually found landwards of mangroves (Osland et al., 2013). Recently, the expansion of mangroves into saltmarsh communities has been observed worldwide (Saintilan et al., 2014) with examples from North America (Comeaux et al., 2012; Krauss et al., 2011), Central America (López-Medellín et al., 2011) and Australia (Saintilan and Williams, 1999; Williamson et al., 2011). It has been suggested that this expansion of mangroves into saltmarsh communities is a result of changes in environmental factors associated with climate change such as increasing temperatures, rising atmospheric CO_2 concentration and reduced salinity levels resulting from sea-level rises (Alongi, 2015; Cavanaugh et al., 2014; Reef and Lovelock, 2014; Saintilan and Rogers, 2013). This is unsurprising considering the highest velocity of climate-driven change is occurring in the coastal zone (Loarie et al., 2009), where mangrove and saltmarsh ecosystems serve as sentinels of temperature, CO_2 and sea-level impacts (McKee et al., 2012).

In terrestrial systems, it has been proposed that rising atmospheric CO_2 concentration over the last 200 years may be a potential driver of woody plant encroachment in grasslands (Archer et al., 2017; Bond and Midgley, 2000). This is because the growth of woody plants that utilise the C_3 photosynthetic pathway is promoted under elevated CO_2, while the co-occurring C_4 grass species obtain little or no benefit from additional CO_2 (Ainsworth and Long, 2004; Leakey et al., 2009). Despite the obvious parallels between terrestrial woody plant and mangrove encroachment, there has been limited research on the role of CO_2 in determining saltmarsh-mangrove boundaries (Saintilan and Rogers, 2015). The studies that have tested the response of mangrove species to elevated CO_2 have shown that responses tend to be species-specific (Alongi, 2015). For example, a study testing the growth responses of four Caribbean mangrove species reported that three of the species were not affected by elevated CO_2 while the remaining species (*Laguncularia racemosa*) had a decline in biomass (Snedaker and Araújo, 1998). Although CO_2 is likely to be a key driver of woody plant encroachment in terrestrial grasslands, it is not yet clear if a similar mechanism will drive mangrove encroachment in saltmarshes. This is due to several additional factors in saltmarsh-mangrove systems: the unpredictable responses of mangrove species to elevated CO_2, the relative abundance of C_3 and C_4 species in saltmarsh communities (Arp et al., 1993; Drake et al., 1989; Rozema et al., 1991), and the effect of salinity on mangrove recruitment (Alongi, 2015).

Mangrove species tend not to cope with the high salinity levels that can exist in saltmarsh communities, but rising sea-levels may reduce salinity in these communities making conditions more favourable for mangroves (Adam, 2009; Rogers et al., 2006). Furthermore, increased water use efficiency under elevated CO_2 may also increase the tolerance of mangroves to high salinity levels as has been shown to be the case for *A. germinans* (Reef et al., 2015). However, a previous study showed that the mangrove species *Rhizophora apiculata* and *R. stylosa* were only responsive to elevated CO_2 under 25% seawater salinity but not 75% seawater salinity (Ball et al., 1997). Therefore, it is likely that mangrove responses to the interactive effects of CO_2 and salinity will be complex, with some species thriving while others decline or show no change (Alongi, 2015).

Currently, there is a critical gap in our knowledge of how climate change associated environmental factors will interact to influence saltmarsh-mangrove boundaries. The first step in addressing this knowledge gap is to determine the effect these environmental factors have on the establishment success of mangrove seedlings, which is the crucial first step in mangrove encroachment. Therefore, the aim of this study was to determine the effect CO_2 and salinity has on the establishment success of mangrove seedlings in saltmarsh communities. To test this, we established model saltmarsh communities under different CO_2 (ambient=400 ppm, elevated=600 ppm) and salinity (seawater=50 ds m^{-1}, hypersaline=100 ds m^{-1}) treatments, then planted propagules of two mangrove species (*Aegiceras corniculatum* (L.) Blanco and *Avicennia marina* (Forssk.) Vierh.) into the established communities. The mangrove species were also grown individually. The saltmarsh and mangrove species used in the study are commonly co-occurring species along the entire coast of New South Wales (NSW), Australia, and all are C_3 species. We predicted that (1) the mangrove species will increase their growth under elevated CO_2 and seawater salinity when grown individually; (2) the C_3 saltmarsh species will also respond positively to elevated CO_2 thus increasing their competitive effect on the mangrove species and preventing them from establishing, particularly in hypersaline conditions.

Materials and methods

Species selection

We selected three C_3 species that commonly co-occur in saltmarsh communities along the entire coast of NSW, Australia (Daly, 2013). The selected species were *Ficinia nodosa* (Rottb.) Goetgh., Muasya & D.A.Simpson (family: Cyperaceae), *Juncus kraussii* Hochst. (family: Juncaceae) and *Selliera radicans* Cav. (family: Goodeniaceae). It should be noted that *Sarcocornia quinqueflora* (Bunge ex Ung.Sternb.) A.J.Scott was initially included as a fourth saltmarsh species but did not respond well to transplanting due to poor quality tube stock so was removed from the experiment after 6 weeks. Seeds for *F. nodosa* and *J. kraussii* and runners of *S. radicans* were obtained from commercial suppliers (seeds from Nindethana Seed Service, Albany, WA, Australia; runners from Bunya Native Nursery, Dural, NSW, Australia). The *F. nodosa* and *J. kraussii* seeds were germinated on freshwater moistened paper towels within aluminium trays that were sealed with plastic wrap. For the mangrove species, *A. corniculatum* propagules were collected from Mickeys Point, NSW, Australia (33°97'79.4"S, 151°02'30.4"E) while *A. marina* propagules were collected from Empire Bay, NSW, Australia (33°29'32.0"S, 151°21'22.0"E)

Experimental design and treatments

Four individuals from each saltmarsh species were grown together in mesocosms (12 plants/mesocosm) using a fully factorial experimental design with two factors: CO_2 (ambient and elevated) and salinity (seawater and hypersaline). The mesocosms consisted of 70 L tubs (60 cm long × 40 cm wide × 30 cm deep), with each tub containing 65 L of commercially obtained 80:20 sand soil mix (Australian Native Landscapes, North Ryde, NSW, Australia). This mix was selected for the experiment because the sand was obtained from sieved estuary sediment which is appropriate to our study system. The nutrient properties of the mix were 150 mg kg^{-1} total N and 100 mg kg^{-1} total P. *Ficinia nodosa* and *J. kraussii* seedlings were transplanted from the germination trays into the mesocosms at the stage of cotyledon emergence. For *S. radicans*, 5 cm cuttings of belowground runners were transplanted into the mesocosms. All seedlings and runners were planted within 10 hours of each other in two rows of six with positions being randomly allocated. The seedlings and runners were then allowed to establish in the mesocosms within a single glasshouse for 4 weeks after which the CO_2 and salinity treatments were imposed beginning January 2018.

The CO_2 treatments were set to ambient (400±20 ppm) and elevated (600±20 ppm). These CO_2 concentration ranges were maintained and monitored continuously by a CO_2 dosing and monitoring system (Canary Company Pty Ltd, Lane Cove, NSW, Australia). The elevated CO_2 treatment represents the predicted atmospheric CO_2 concentration by 2060 under the RCP 4.5 emissions scenario (IPCC, 2014). Each CO_2 treatment (consisting of 12 mesocosms) was represented by one 55 m^2 glasshouse with the glasshouses located next to each other (sharing a common wall). The temperature of the glasshouses was set for a minimum of 18°C and a maximum of 25°C and was continuously maintained by a fan coil unit using a water cooling and heating system. The fan coil unit was also responsible for circulating the air and evenly distributing the CO_2 within each glasshouse. Relative humidity (RH) and photosynthetically active radiation (PAR) of the glasshouses was continuously monitored using a Multi-grow Controller System (Autogrow Systems, Auckland, New Zealand). The readings taken at 14:00 (time of maximum RH and PAR in the glasshouses) each day were then analysed using paired t-tests to show that RH (GH1=87%, GH2=86%; p=0.283) and PAR (GH1=818 mol $m^{-2}s^{-1}$, GH2=779 mol $m^{-2}s^{-1}$; p=0.260) did not significantly differ between the glasshouses.

Salinity treatments were set to seawater (50±5 ds m^{-1}) and hypersaline (100±5 ds m^{-1}). We selected these treatments to represent the natural salinity range (20-95 ds m^{-1}) reported for saltmarsh communities within the greater Sydney region, NSW, Australia (Sydney Environmental & Soil Laboratory, 2018). These treatments were monitored weekly using a HI98196 electrical conductivity meter (Hanna Instruments, Castle Hill, NSW, Australia) and maintained by dissolving the necessary amount of NaCl in 1 L of water which was then added to the mesocosms (1 ds m^{-1} = 550 mg l^{-1} of NaCI). At each salinity treatment application, the amount of NaCl added to each mesocosm within a treatment was kept consistent.

Each treatment combination (CO_2 × salinity) was replicated six times with treatments randomly assigned to mesocosms. This design resulted in a total of 24 mesocosms (two CO_2 treatments x two salinity treatments x six replicates). The mesocosms were mist watered for 3 minutes per hour between 06:00-10:00 and 18:00-22:00. Watering was concentrated at these times to simulate tidal movements. That is, by 10:00/22:00 the mesocosms were inundated with water which would typically take 3 hours to drain. Mist watering was used as the watering method to ensure inundation occurred gradually so NaCl was not flushed out of the mesocosms at a rapid rate.

The model saltmarsh communities were grown for 12 weeks after which three propagules from each of *A. corniculatum* and *A. marina* were planted into each mesocosm. Mangrove propagules were selected based on their fresh weight with *A. corniculatum* propagules having a weight of 4.3±0.3 g and *A. marina* propagules having a weight of 0.8±0.2 g. The mangrove propagules were planted in one row, between the two rows of saltmarsh plants, equidistant from each other in a random order. The propagules were then allowed to grow within the mesocosms for a period of 20 weeks. It should be noted that the cotyledons dropped off the mangrove seedlings ~4 weeks after planting. To minimise any glasshouse effect, the mesocosms along with the CO_2 treatment were switched between the two glasshouses after 6 weeks (mid-way through the growth period before the mangrove propagules were planted) and 22 weeks (mid-way through the growth period after the mangrove propagules were planted). Throughout the duration of the experiment volumetric soil water content (VSWC) of the mesocosms was measured on a weekly basis at a depth of 15 cm using a Hydrosense II Portable Soil Moisture System (Campbell Scientific Australia Pty Ltd, Garbutt, QLD, Australia). As the soil was always at saturation point (~40%) due to being inundated daily we have not reported the VSWC data in the ‘Results’ section below. In addition to the mangrove propagules planted in the model saltmarsh communities, three propagules of each species for each CO_2 × salinity treatment combination were planted individually in 12 L pots containing 11.5 L of the same sand soil mix used for the mesocosms.

At the conclusion of the experiment (32 weeks) every plant (both mesocosm and individually grown plants) was individually harvested and washed free of soil. The exception to this was the root biomass of the saltmarsh species, which was too intertwined to separate into individual plants. For the mangrove seedlings grown in the mesocosms, shoot height and root length were measured for each individual plant. The biomass components were then oven-dried at 70°C for 72 hours and weighed using an analytical electronic balance (Mettler Toledo, Port Melbourne, VIC, Australia).

Data analysis

To test the effect of the CO_2 and salinity treatments on the shoot biomass of the model saltmarsh communities we used a three-way mixed model ANOVA. CO_2 and salinity were treated as fixed factors while species was treated as a random factor. The same analysis was conducted for root biomass with the exception of species being removed from the model as we were unable to separate roots on an individual plant basis.

We then tested effects of the CO_2 and salinity treatments on the total biomass, shoot height and root length of each mangrove species using two-way ANOVAs. CO_2 and salinity were treated as fixed factors. This analysis was conducted for mangrove seedlings grown in the mesocosms and repeated for the mangrove seedlings grown individually.

All statistical analyses were performed using R version 3.2.4. (R Development Core Team, 2018) with the significance level set at 0.05. When necessary to satisfy requirements for normality and fulfil the assumptions of ANOVA, a $\log_{10}$ transformation was used.

Results

There was no significant interactive effect between any of the factors on the biomass (total, shoot and root) of the saltmarsh communities. The shoot ($F_{1,60}$=45.40, p=0.021) and root ($F_{1,20}$=21.34, p<0.001) biomass of the model saltmarsh communities were significantly greater under elevated compared to ambient CO_2 (Fig. 1). In contrast, there was no significant effect of salinity (shoot: $F_{1,60}$=0.86, p=0.453; root: $F_{1,20}$=0.15, p=0.701; Fig. 1) or species (shoot only: $F_{2,60}$=40.56, p=0.058) on either the shoot or root biomass of the model saltmarsh communities.

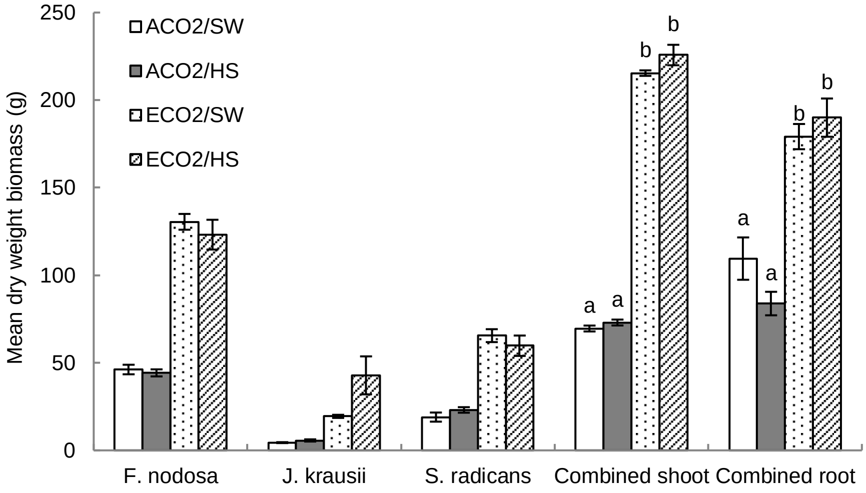

Figure 1 | Mean shoot dry weight biomass of each saltmarsh species and their combined shoot and root dry weight biomass under all treatment combinations (ACO_2-ambient CO_2, ECO_2-elevated CO_2, SW-seawater salinity, HS-hypersaline). Mean dry weight biomass values are at the mesocosm-level. Letters indicate significant differences at p<0.05.

There was no significant interactive effect between CO_2 and salinity on the biomass (total, shoot and root), shoot height and root length of the mangrove species grown individually and in mesocosms. The total biomass of *A. corniculatum* seedlings grown in mesocosms was significantly reduced under elevated CO_2 ($F_{1,20}$=8.43, p=0.009; Fig. 2) while shoot height ($F_{1,20}$=0.19, p=0.668; Fig. 3) and root length ($F_{1,20}$=2.45, p=0.133; Fig. 3) did not differ between the CO_2 treatments. In contrast, the total biomass of the *A. corniculatum* seedlings grown individually did not significantly differ between CO_2 treatments ($F_{1,8}$=0.35, p=0.569; Fig. 2). The total biomass of *A. corniculatum* seedlings grown in mesocosms ($F_{1,20}$=7.30, p=0.014; Fig. 2) and individually ($F_{1,8}$=10.91, p=0.011; Fig. 2) were significantly greater under seawater salinity. Their shoot height was also greater under seawater salinity ($F_{1,20}$=20.00, p<0.001; Fig. 3) while their root length did not differ between the CO_2 treatments but only marginally ($F_{1,20}$=4.29, p=0.052; Fig. 3).

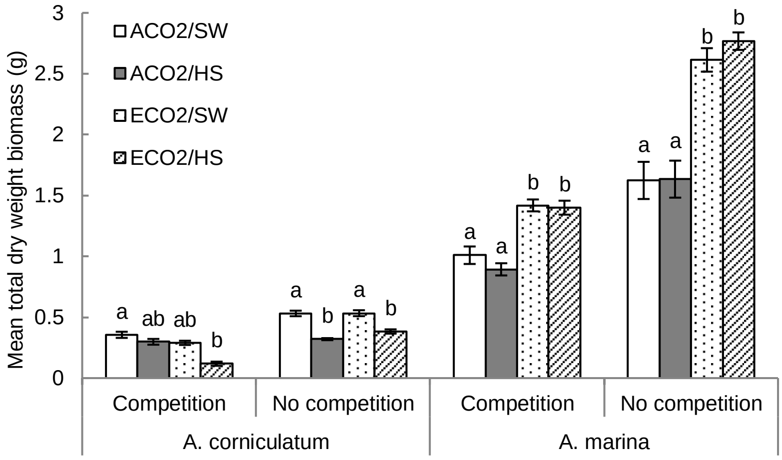

Figure 2 | Mean total dry weight biomass of each mangrove species when grown in mesocosms (competition) and individually (no competition) under all treatment combinations (ACO_2-ambient CO_2, ECO_2-elevated CO_2, SW-seawater salinity, HS-hypersaline). Letters indicate significant differences within species × competition groups at $p<0.05$.

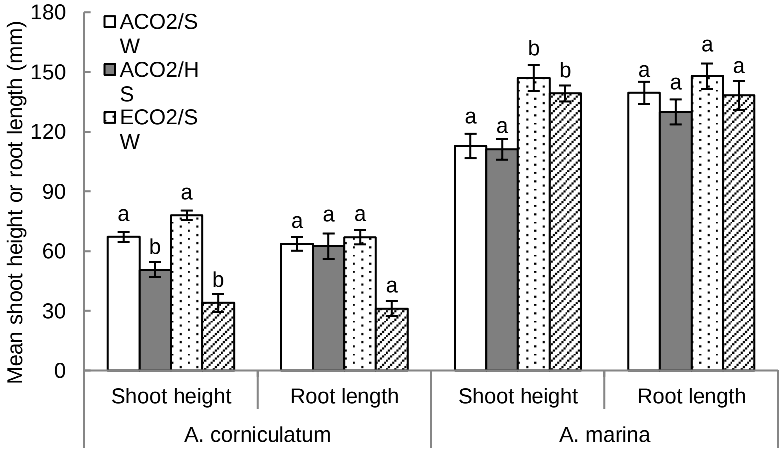

Figure 3 | Mean shoot height and root length of each mangrove species when grown in mesocosms (competition) under all treatment combinations (ACO_2-ambient CO_2, ECO_2-elevated CO_2, SW-seawater salinity, HS-hypersaline). Letters indicate significant differences at $p<0.05$.

The total biomass of *A. marina* seedlings grown in mesocosms ($F_{1,20}=15.71$, $p=0.001$) and individually ($F_{1,8}=9.26$, $p=0.0.016$; Fig. 2) was significantly greater under elevated CO_2. Their shoot height was also greater under elevated CO_2 ($F_{1,20}=7.72$, $p=0.012$; Fig. 3) while root length did not differ between the CO_2 treatments ($F_{1,20}=0.42$, $p=0.524$; Fig. 3). In contrast to *A. corniculatum,* salinity did not have a significant effect on the growth of *A. marina* irrespective of whether it was grown in mesocosms or individually.

Discussion

The expansion of mangroves into saltmarsh communities has been observed worldwide (Saintilan et al., 2014), with a range of different environmental factors associated with climate change considered as drivers of this encroachment (Alongi, 2015). More specifically, rising atmospheric CO_2 concentration and reduced salinity levels as a result of rising sea-levels have been identified as potential key drivers of mangrove encroachment (Alongi, 2015). The crucial first step in mangrove encroachment is the successful establishment of mangrove seedlings, when they are most vulnerable to biotic and abiotic stresses, in saltmarsh communities (McKee and Rooth, 2008). Therefore, the aim of this study was to determine the effect CO_2 and salinity has on the establishment success of mangroves seedlings in saltmarsh communities.

Both shoot and root biomass of our C_3 saltmarsh species increased, by an average of 210% and 91% respectively, when grown under elevated CO_2. All three saltmarsh species had at least a 180% increase in shoot biomass under elevated CO_2 with this increase being most pronounced in *J. kraussi* (520% on average). Previous studies have shown similar strong growth responses to elevated CO_2 in a number of different C_3 saltmarsh species (Arp et al., 1993; Drake et al., 1989; Rozema et al., 1991). This suggests that the competitive effect of saltmarsh species on mangrove seedlings will likely increase under future CO_2 conditions, reducing any direct positive effect of elevated CO_2 on mangrove growth in mixed saltmarsh-mangrove assemblages. The strong response of C_3 saltmarsh species to elevated CO_2 may also help saltmarsh communities respond to other pressures associated with climate change (Saintilan and Rogers, 2015). For example, a two-year study of a saltmarsh community at Chesapeake Bay in the United States found that increased belowground biomass production in the C_3 species *Schoenoplectus americanus* under elevated CO_2 accelerated soil elevation gain by 3.9 mm yr^{-1} (Cherry et al., 2009; Langley et al., 2009), providing a counterbalance against rising sea-levels (Langley et al., 2009; see Lovelock et al., 2015 for exeptions). It is worth noting that, similarly to terrestrial systems, the responsiveness of saltmarsh communities to elevated CO_2 has been shown to be dependent on ample nutrient supply (Langley et al., 2013). As our model saltmarsh communities experienced a strong response to elevated CO_2, we can suggest that they were not nutrient limited.

From what we have learnt of woody plant encroachment in terrestrial grassland systems (Manea and Leishman, 2015), it would be expected that an increase in saltmarsh community biomass under elevated CO_2 would suppress the growth of co-occurring mangrove seedlings. This was the case for the mangrove species *A. corniculatum*, which produced on average 24% less total biomass under elevated compared to ambient CO_2 when grown in competition with the saltmarsh species. This is despite it producing marginally more total biomass (10% on average) under elevated CO_2 when grown individually. In contrast, the mangrove species *A. marina* produced on average 48% more total biomass when grown in the model saltmarsh communities under elevated CO_2. However, this was also a reduction from the average 78% increase in total biomass it had when grown individually. Despite both mangrove species experiencing a similar strong competitive effect from the saltmarsh species under elevated CO_2, the relatively stronger effect of CO_2 on *A. marina* seedlings compared to *A. corniculatum* seedlings suggests they are more likely to 'escape' competition from saltmarsh species and become established in saltmarsh communities in the future. This suggestion is supported by a historical reconstruction of *A. marina* growth response in the Indo-Pacific region over the last two centuries which showed that the greater biomass gains in this species over this time period were a result of rising atmospheric CO_2 concentration (Reef and Lovelock, 2014).

In terrestrial grassland systems, there are two mechanisms by which woody plant seedlings can utilise their additional biomass gains under elevated CO_2 to 'escape' competition from co-occurring grasses. They can grow taller which allows them to overtop the grass canopy and 'escape' any shading effect from the grasses (Bond and Midgley, 2000) and/or they can send their roots deeper, giving them access to water and nutrient resources that the grasses cannot reach (Polley et al., 1997). For *A. marina*, it is likely that the 'escape from shade' scenario is true as it grew on average 30% taller under elevated CO_2 but did not send its roots deeper. This increase in height enabled it to overtop the extremely dense lower *S. radicans* layer (~10 cm in height) in the mesocosms thus giving it access to more light. This result contrasts with the findings of a previous study that found belowground competition was more important in the establishment and growth of *A. germinans* seedlings when grown in competition with the C_4 saltmarsh species, *Spartina alterniflora* (Howard et al., 2018). A possible explanation for these differing results is that because our model saltmarsh communities were not nutrient limited, it is likely that light was the most limiting growth resource which made it more advantageous for *A. marina* seedlings to use the additional CO_2 to grow taller. This explanation is supported by the findings of previous studies that found *A. germinans* growth is only stimulated under elevated CO_2 when nutrients is not limiting (McKee and Rooth, 2008; Reef et al., 2016). Furthermore, these studies reported that the majority of this increased growth occurred in aboveground biomass (Reef et al., 2016) and resulted in increased shoot height (McKee and Rooth, 2008) which is consistent with our findings for *A. marina*.

Salinity tends to be higher in saltmarsh communities compared to mangrove communities due to a higher evaporation rate in the higher intertidal zone (Adam, 2009). Consequently, saltmarsh species are generally adapted to cope with higher levels of salinity than mangrove species (Adam, 2009). Consistent with the findings of Clarke and Hannon (1970), we found that *A. corniculatum* seedlings produced more total biomass under seawater salinity irrespective of competition (on average 36% in mesocosms and 51% individually). Surprisingly, the growth of *A. marina* seedlings was not influenced by salinity despite previous studies reporting the contrary (Clarke and Hannon, 1970). These results suggest that the encroachment of certain mangrove species into saltmarsh communities will be favoured by rising sea-levels in the future. However, as discussed above, the soil elevation gains in saltmarsh communities that may occur in the future may negate this to some extent (Saintilan and Rogers, 2015).

From our study, we can suggest that rising atmospheric CO_2 concentration and reduced salinity as a result of sea-level rise are likely to enhance the establishment success of mangrove seedlings in saltmarsh communities thus facilitating mangrove encroachment. Having said that, it is important that we acknowledge the caveats of this study that need to be considered when applying our results to natural environments. Firstly, as our study was conducted in an enclosed glasshouse the impact from herbivores was non-existent. This is important to note because in the field it has been shown that herbivory greatly reduces the survival of *A. germinans* seedlings (McKee and Rooth, 2008). It has been suggested that this herbivory could negate any positive effect elevated CO_2 may have on mangrove seedling growth in saltmarsh communities (McKee and Rooth, 2008). Secondly, it would have been ideal to have included C_4 or CAM species in our model saltmarsh communities (seed sourcing problems for *Sporobolus virginicus* and poor-quality *S. quinqueflora* tube stock prevented this from happening), considering mangrove encroachment is most prevalent in C_4 and CAM saltmarsh communities. Because of this our results may be viewed as conservative when applied to C_4 and CAM saltmarsh communities due to these species having less of a competitive effect on mangrove seedlings than C_3 species under elevated CO_2. Finally, the salinity treatments we used were above the natural salinity range (<50 ds m^{-1}) which some of our species typically thrive in (e.g. *J. kraussii*; see Clarke and Hannon 1970). Despite this, no individuals of these species experienced mortality with *J. kraussi* actually preferring higher salinity levels under elevated CO_2. This suggests the salinity treatments we imposed were not unreasonable for the survival and growth of our study species Irrespective of these caveats, this study provides a valuable insight into how climate change associated environmental factors may influence saltmarsh-mangrove boundaries in the future.

In terms of management implications for the future, the encroachment of mangroves into saltmarsh communities can be relatively easy to manage through simple intervention at local scales (Laegdsgaard, 2006). For example, in Australia, the removal of encroaching mangroves, using natural barriers on the seaward side and allowing the natural regeneration of saltmarsh species has proven to be a successful restoration technique (Laegdsgaard, 2006). However, at a broader scale, it largely remains unknown whether artificially maintaining current mangrove-saltmarsh boundaries into the future will be beneficial or not to ecosystem functions and service provisions (Kelleway et al., 2017). It has been suggested that mangrove encroachment is beneficial in terms of carbon and nutrient storage and coastal protection but detrimental in terms of habitat availability for fauna as well as the recreational and cultural activities associated with this fauna (Kelleway et al., 2017). However, many of these impacts will be site specific and depend on the species involved (Kelleway et al., 2017). Therefore, it is important that the strategy implemented for the management of mangrove encroachment is considered on a site by site basis.

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Chapter 5

Changes in saltmarsh area over the last 42 years in coastal New South Wales, Australia

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Abstract

Landward mangrove expansion has been observed globally and at large spatial scales is thought to be associated with climate change drivers such as rising sea level and temperature. In south-east Australia, where mangrove forest and endangered saltmarsh communities co-occur, the expansion of mangroves is associated with a decline in areas of saltmarsh. However, differences in encroachment rates suggest that additional factors that are associated with catchment modification, such as input of nutrients and freshwater, may be important at local to regional scales. In this study we tested if encroachment of mangroves and a consequent loss of saltmarsh is greater in extensively modified catchments compared to largely unmodified catchments. Using a supervised classification of aerial images from 1970 and 2012, we analysed wetland vegetation change of four estuaries in south-east Australian catchments with different levels of modification (i.e. largely unmodified, extensively modified). The images were classified with an accuracy of 77 - 90 % for the historical images and 90 - 96 % for the modern images. Our analysis showed that large areas of saltmarshes have been lost in these estuaries since 1970, and that the vegetation type “*Casuarina/Melaleuca*” has greatly increased, indicating seaward encroachment into saltmarsh communities. However, the loss of saltmarsh was not associated with mangrove expansion and patterns of change in vegetation class were not associated with intensity of catchment modification for these estuaries.

Keywords

mangrove encroachment, freshwater, nutrients, aerial images, classification, remote sensing

Introduction

Mangrove and saltmarshes are important coastal wetland vegetation communities that co-occur in subtropical regions. Mangroves cover 83,495-137,760 km^2 of coastal areas (Giri et al., 2011b; Hamilton and Casey, 2016) and are found in tropical to subtropical regions, while saltmarsh is estimated to have a total area of 54,950 km^2 (Mcowen et al., 2017), occurring from the poles to the subtropics. The global distribution of mangroves is mainly limited by cold temperatures (Hogarth, 2007; Stuart et al., 2007), so that at latitudes above 32°N and 40°S they are completely replaced by saltmarshes (Stuart et al., 2007). The co-occurrence of these two plant communities within subtropical regions is driven by complex physico-chemical dynamics, typically resulting in sharp boundaries between saltmarshes and mangroves (Adam, 2009). When co-occurring with mangroves, saltmarshes are restricted to the upper intertidal environment, in general between the elevation of the mean high tide and mean spring tide (Saintilan et al., 2009a). Mangroves, however, occupy the regularly inundated areas within the upper intertidal zone, usually near mean sea level to mean high tide, on the seaward site of saltmarshes (Rogers et al., 2017).

Landward encroachment of mangroves has been documented globally (Saintilan et al., 2018, 2014) and is widely thought to be associated with climate change and its consequence of sea level rise and increased sea surface temperature (Osland et al., 2013; Saintilan et al., 2014; Saintilan and Rogers, 2015). Where freezing events occur, mangroves are limited, yet inconsistencies in the expansion rate suggest that additional environmental factors are important in determining saltmarsh-mangrove boundaries, particularly at local to regional scales (Saintilan et al., 2014). Recent experimental studies have shown that high nutrient loads and high atmospheric CO_2 concentration lead to significantly greater mangrove biomass, chlorophyll activity and stronger root systems compared with control systems (Reef et al., 2016; Alongi, 2015). However, a study on the competition effect of mangrove-saltmarsh communities under elevated CO_2 and nutrient treatment suggested that saltmarsh curtail mangrove growth under these conditions (McKee and Rooth, 2008). Additional disturbances will be required, such as herbivory or anthropogenic destructions, to alter the competitive balance between the two communities (McKee and Rooth, 2008). In a previous study within urbanised catchments in the Sydney region, Geedicke et al. (2018) found greater mangrove abundance in areas receiving nutrient enriched urban stormwater run-off compared to areas that did not. In addition to a high nutrient-load, urban stormwater also provides freshwater input, resulting in reduced salinity in these coastal wetlands. Fluctuations in salinity are typical in intertidal wetlands, but long-term changes, such as changes in the tidal inundation, heavy rain or freshwater input through storm-water or agricultural run-off, can reduce soil salinity (Adam, 2009; Hogarth, 2007). This is likely to affect mangrove-saltmarsh boundaries as although both mangrove and saltmarsh species are halophytic, saltmarshes tend to cope with higher salt concentrations than mangroves (Adam, 2009).

Several studies have evaluated mangrove expansion and associated saltmarsh loss at regional to continental scales e.g. in Louisiana (Giri et al., 2011a) and Florida (Stevens et al., 2006) in the U.S.A., Mexico (López-Medellín et al., 2011), Taiwan (Hsu and Lee, 2018) and New Zealand (Morrisey et al., 2010). Krauss et al. (2011) even went as far back as 1927 to measure the extent of mangrove expansion in Florida from aerial photographs, finding a 35% increase of mangrove area at the expense of saltmarsh communities. Mangrove expansion does not necessarily lead to saltmarsh loss, for example in the gulf coast of Texas mangrove expansion of 74% and saltmarsh loss of 24% within 30 years was recorded by Armitage et al. (2015) but only 6% of saltmarsh loss could actually be associated with mangrove expansion. In south-east Australia, saltmarsh loss of 30% due to mangrove expansion has been recorded by Saintilan and William (2000) and Wilton (2001) from survey data, but there is also evidence that saltmarsh loss is less towards the southern limit of mangrove range in Victoria (5-15%) (Rogers et al., 2005).

Given that saltmarsh-mangrove vegetation within modified catchments may be subject to environmental factors such as increased nutrients and reduced salinity due to stormwater or agricultural run-off, we might expect to see higher rates of mangrove expansion at the expense of saltmarsh in extensively modified catchments compared to largely unmodified catchments.

In this study, we aimed to assess the impact of catchment modification on wetland vegetation of these systems. We compared aerial images of highly modified versus largely unmodified estuaries over a time period of 40 years to assess changes in mangrove and saltmarsh areas independent of urban development. We hypothesize that (i) mangrove encroachment of saltmarsh has occurred in all estuaries; (ii) mangrove expansion has been greater in highly modified estuaries compared to largely unmodified estuaries; and consequently (iii) the decline in saltmarsh area has been greater in highly modified estuaries.

Methods

We chose two estuaries along the New South Wales coast of Australia which were categorized by the National Land and Water Recourses Audit (NLWRA, 2002) as extensively modified and two that were classified as largely unmodified. Each extensively modified estuary was paired with a largely unmodified estuary that experienced similar climate and geology. The criteria for 'extensively modified' estuaries were: less than 33 % natural land cover, major changes to tidal flow, extractive activities such as dredging, extensive agriculture and habitat modifying fisheries (NLWRA, 2002). The criteria for 'largely unmodified' estuaries were: 65-90 % of natural land cover, no significant impediments to tidal flow or changes from natural morphology and limited activities from sustainable commercial and recreational fisheries (NLWRA, 2002). The two extensively modified estuaries (Hastings River (Lat: -31.42/Long: 152.86) and Shoalhaven River (Lat: -34.86/Long: 150.74), Figure 1), occur within the urban regions of Port Macquarie and Nowra, respectively. The catchments for these estuaries are influenced by agricultural and urban land use. The two largely unmodified estuaries were Karuah River (Lat: -32.64/Long: 151.99) and Currambene Creek (Lat: -35.01/Long: 150.66), (Figure 1). For each of the four estuaries, two species of mangrove comprised the mangrove vegetation class along the water's edge (*Avicennia marina* and *Aegiceras corniculatum)*. At the lowest elevation in the saltmarsh vegetation class, which receives relatively frequent inundation, the dominant species was *Sarcocornia quinqueflora*. The mid-level saltmarsh was typically dominated by *Sporobolus virginicus* and *Juncus kraussii*, while *Baumea juncea* usually dominates the drier plant communities at higher elevations (Adam, 1981). Further landwards, in the supratidal zone, the vegetation is characterized by stands of *Casuarina* and *Melaleuca* species (Rogers et al., 2017; Sainty, 2012).

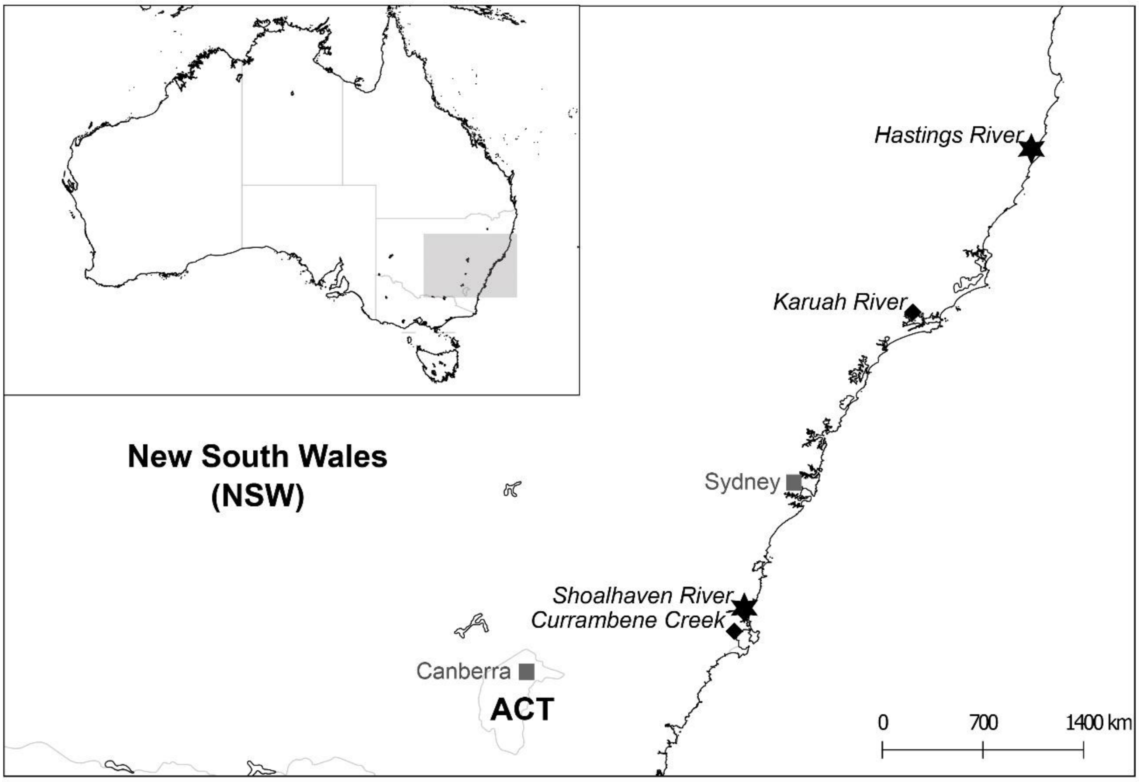

Figure 1 | Map of the study sites along the coast of New South Wales, Australia. The star symbols stand for the extremely modified sites and the square symbols for largely unmodified estuaries.

Aerial imagery analysis

Aerial images from 1970 and 2012 for each of the four estuaries (n = 8) were obtained from the NSW Department of Finance, Services and Innovation. The images had a resolution of 0.6 m x 0.6 m per pixel for the recent images and 0.9 m x 0.9 m per pixel for historical images. The images were georeferenced (15 ground control points) using the OpenLayers plugin in Quantum GIS (QGIS Development Team, 2019). The root mean square error (RMSE) measures the difference of the predicted versus the observed values of the control points and showed little error being below ± 8 cm to ensure high quality of the georeferencing process. To minimize data processing time, we limited the area in the images to encompass wetland areas only. Our hypothesis focused on the vegetation changes by replacement of other vegetation types. Thus, we excluded urban development areas from the analysis. To analyse the changes in wetland vegetation type for each of the four sites, the pre-processed images were classified into seven different land cover classes (i.e. mangrove, saltmarsh, water, sand, soil, Casuarina/Melaleuca, grass). For verification, the vegetation classes were compared to digital vegetation classification maps provided by the NSW Department of Primary Industries (http://www.dpi.nsw.gov.au/content/research/areas/aquatic-ecosystems/estuarine-habitats-maps) and a field inspection at each site in September 2017. Earlier studies have shown that mangroves can be easily identified using aerial images displaying an emergent canopy above saltmarshes usually at the water's edge (Figure 2a and b) (Saintilan et al., 2014).

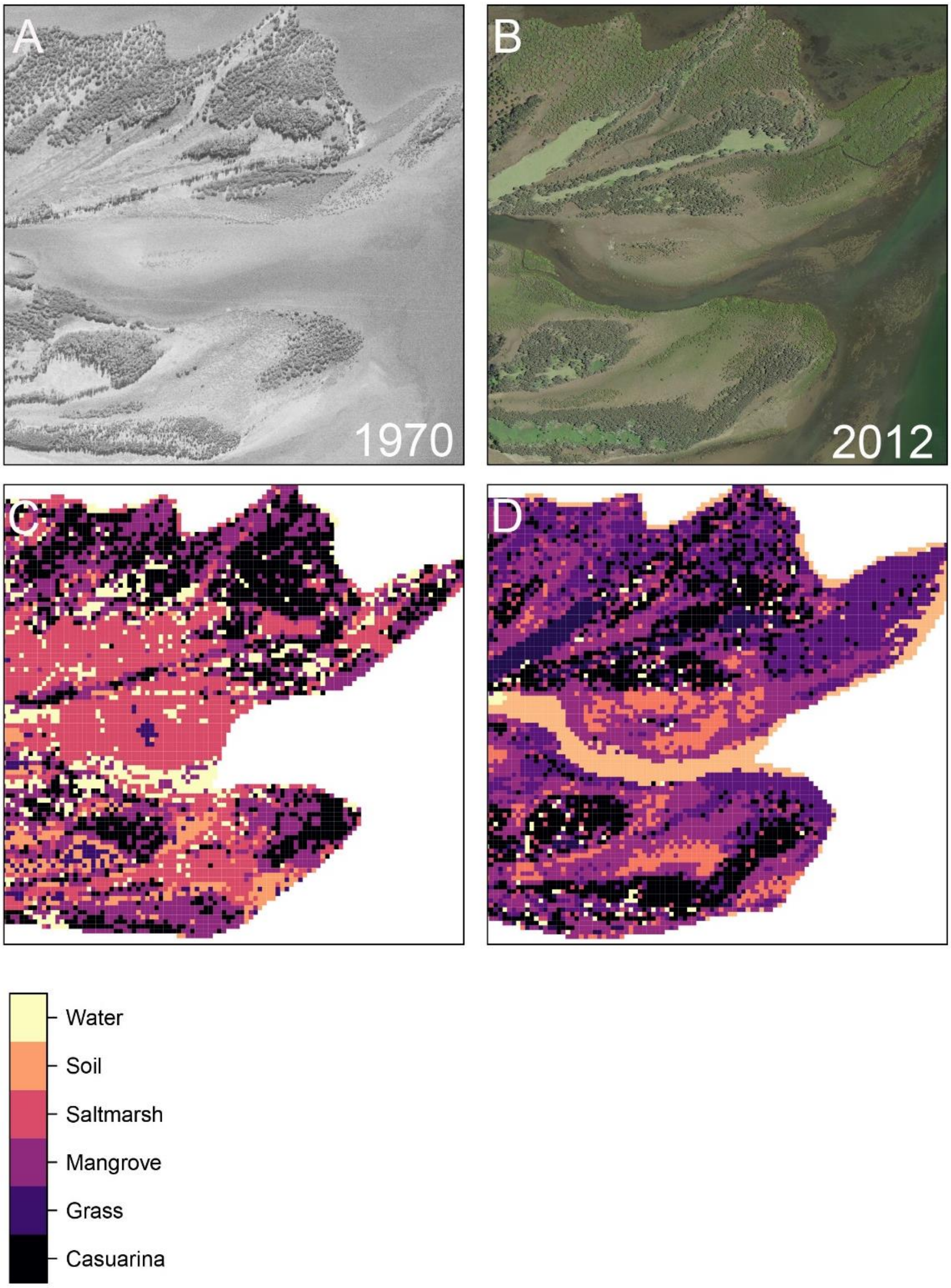

Figure 5 | Historical image (A) and modern aerial image (B) of Karuah River with the resulting classification map of vegetation classes shown beneath (C and D)

Although the boundaries of wetlands can be sharp, they may also be less delineated due to the occurrence of saltmarsh species growing amongst the mangroves. Thus, a manual classification of the different land use classes would not be feasible, we chose to analyse the images using a supervised classification algorithm. A supervised classification uses selected pixel values and associates them with a certain land use class. The algorithm is "trained" to recognize these pixel values on a training data set. The training data set made up 75 % of the whole data set and 25 % were later used as a test data set to classify the whole area. Within each land cover class, ten training polygons were set for homogenous classes (i.e. water, soil, sand, shadow) and twenty training polygons were set for vegetation classes as they are more heterogenous (i.e. mangroves, saltmarsh, Casuarina/Melaleuca). To ensure a balanced classification, the pixel number of the training polygons per class were down-sampled to fit the class containing the least number of pixels (Kuhn and Johnson, 2013a). The recent images consisted of three bands (red, green and blue), resulting in three predictors for the classification. However, the historical images were grey-scale only and therefore consisted of one band. To add more information/predictors to the classification, a Grey Level Co-occurrence Matrix (GLCM) was calculated for all images as a representation of image texture. The GLCM is a tabulation of how often different combinations of pixel brightness values (grey levels) occur in an image. The pixel brightness values are calculated by considering a set area of neighbouring pixels (alias window size). We tried different window sizes (3 x 3 – 41 x 41) and we chose the window size to be set to 21 x 21 pixels because it showed the clearest and most recognizable pattern of the images. We chose two GLCM parameters, i.e. GLCM contrast and GLCM variance. GLCM contrast represents the amount of local grey level variation in an image; a high value of this parameter may indicate the presence of edges, noise, or wrinkled textures in the image. The second parameter, GLCM variance measures the dispersion (with regard to the mean) of the grey level distribution and is commonly used for enhancement of visual edges of land-cover patches (Hall-Beyer, 2017).

We used a random forest classifier (Breiman, 2001) as image classification algorithm which uses a series of binary decision trees to assign thematic classes (i.e. mangrove, saltmarsh, Casuarina/Melaleuca, sand, soil water, grass) to each image pixel. Random forest classifiers use multiple decision trees (Hastie et al., 2009) and we repeated the process 500 times, after which the mean accuracy over the repetitions was calculated. Previous studies showed that classification using decision tree algorithms result in higher accuracies of wetland classification compared to maximum likelihood algorithms (Mccarthy et al., 2018). To evaluate the performance of the prediction, several accuracy metrics were calculated based on a confusion matrix. A direct interpretation offers the overall accuracy (OA) because it reflects to what percentage the reference classes from the training data set and the predicted classes from the testing data set coincide. However, OA represents the accuracy of all classes but does not provide information as to whether one class performed particularly well or poorly (Kuhn and Johnson, 2013b). Therefore, the producer accuracy (PA) and user accuracy (UA) were calculated to indicate class specific errors (Congalton and Green, 2009). PA represents the percentage of a correctly classified class according to the reference data given by the producer. It is calculated as the number of correctly classified references for a class divided by the total number of references of that class. UA is the percentage of the correctly classified class according to the prediction algorithm. It divides the number of correct classifications (predictions) for a class by the total number of classifications (predictions) for that class.

The best random forest classification model was applied to the test data set and was converted into a classification map (Figure 2 c and d). From the classification map the number of pixels for each class were extracted. The total area for each class was calculated by multiplying pixel size of each image times frequency of pixel per land use class and compared the areas of heavily modified vs largely unmodified estuaries (Table 2).

Classification analysis was performed in the statistical environment of R (R Development Core Team, 2018) using the “caret” packages (Kuhn et al. 2017) and the “glcm” package (Zvoleff, 2016).

Results

Classification

The supervised classification of the trainings data set resulted in an overall accuracy for the modern images of 90 – 96% and for the historical images of 77 – 90%. However, looking at the specific classes, the most heterogenous classes “mangroves” and “*Casuarina/Melaleuca”* resulted in the lowest producer accuracies of only 50% (Hastings River 1970, class “*Casuarina/Melaleuca”*, Supplementary table A6) and 71% (Currambene Creek 2012, class “mangrove”, Supplementary table A3). In addition, the user accuracy showed lowest values within the “*Casuarina/Melaleuca”* class of 62% (Hastings River 1970, Supplementary, table A6) and 73% (Currambene Creek 2012, Supplementary table A3). For a better understanding, we present the complete accuracy table for 2012 Karuah River image (Table 1). Here, the overall accuracy was 96%, but looking at producer and user accuracy, we get a more detailed look at the classification performance per class. If we take “*Casuarina/Melaleuca”* as an example, the algorithm predicted that of 1234 trainings pixel, 210 pixel belonged to the class “*Casuarina/Melaleuca”*. However, according to the polygons that we set as a reference of these 210 pixels, 11 belonged to the class “mangrove” and 6 pixels to the class “shadow”, resulting in a user accuracy of 92%. The producer accuracy was calculated to be 90% for the class “*Casuarina/Melaleuca”*, of 215 pixels that we set as a reference in the image, the algorithm would have classified 13 pixels as class “mangrove” and 9 pixels as class “shadow” resulting in 193 pixels to be truly classified as class “*Casuarina/Melaleuca”*.

Table 1 | Classification accuracies for the modern image of Karuah River. The percentage in the lower right corner represents the overall accuracy of the classification. Numbers represent the number of pixel per class of the trainings data set. UA = user accuracy, PA = producer accuracy.

Karuah River 2012		*Reference*							
		Casuarina/Melaleuca	**Mangrove**	**Saltmarsh**	**Sand**	**Shadow**	**Water**	**Total**	**UA**
Prediction	**Casuarina/ Melaeuca**	**193**	11	0	0	6	0	210	92%
	Mangrove	13	**188**	0	0	1	0	202	93%
	Saltmarsh	0	0	**215**	0	0	0	215	100%
	Sand	0	0	0	**215**	0	0	215	100%
	Shadow	9	15	0	0	**208**	0	232	90%
	Water	0	1	0	0	0	**215**	216	100%
	Total	215	215	215	215	215	215	**1234**	
	PA	90%	87%	100%	100%	97%	100%		**96%**

Vegetation Change

Over a time period of 42 years, total vegetation cover at each of the sites was stable with a maximum variation of 0.2 km^2. Any changes recorded can be attributed to changes within the tidal system due to new wetlands forming (i.e. Currambene Creek, Shoalhaven River) or being lost (i.e. Hastings River), as urban development was excluded from the image classification. According to the supervised classification, the wetlands at the four estuaries showed variation in the relative cover of the vegetation classes (Table 2). All estuaries with the exception of Shoalhaven River experienced saltmarsh loss of 26% to 47% from 1970 to 2012. A small increase of mangrove area could only be observed at Shoalhaven River (12%) and Currambene Creek (12.5%). Largest changes were observed in *Casuarina* / *Melaleuca* stands, with increases of 109% at Karuah River and 32% and 31% at Hastings River and Currambene Creek, respectively. Only at Shoalhaven River, where both mangroves and saltmarshes increased by 12%, a decrease in *Casuarina* / *Melaleuca* was found. Overall there was no clear difference in vegetation class changes between the two estuary types, extensively modified or largely unmodified.

Table 2 | Vegetation class area change at the four studied estuaries determined from comparison of aerial images from 1970 and 2012.

Site	***Estuary Class***	***Vegetation Type***	***Area 1970 [km²]***	***Area 2012 [km²]***	***ΔArea [km²]***	***ΔArea [%]***
Shoalhaven River	extensively modified	Mangroves	2.48	2.77	0.30	11.97
		Saltmarshes	2.20	2.46	0.26	11.67
		Casuarina/ Melaleuca	1.90	1.73	-0.17	-9.11
Hastings River	extensively modified	Mangroves	1.00	0.94	-0.06	-6.32
		Saltmarshes	1.24	0.73	-0.51	-41.44
		Casuarina/ Melaleuca	0.92	1.22	0.29	31.89
Karuah River	largely unmodified	Mangroves	1.28	1.28	0.00	0.30
		Saltmarshes	1.20	0.63	-0.57	-47.20
		Casuarina/ Melaleuca	0.48	1.01	0.53	109.28
Currambene Creek	largely unmodified	Mangroves	0.67	0.75	0.08	12.50
		Saltmarshes	0.57	0.42	-0.15	-25.93
		Casuarina/ Melaleuca	0.64	0.84	0.20	30.85

Discussion

Wetlands in anthropogenic modified estuaries are exposed to numerous disturbance factors, such as nutrient input and changes in salinity through agricultural or stormwater run-off. In this study, we tested if changes in wetland vegetation cover of extensively modified and largely unmodified estuaries can be detected by comparing aerial images of 1970 and 2012 across four estuaries in New South Wales, Australia. Using a supervised classification algorithm, we analysed the images with an accuracy of 77 - 90% for the historical images and of 90 - 96% for the modern images. However, we could not find a consistent trend of vegetation class changes between the extensively modified and largely unmodified estuaries. Interestingly though, large areas of saltmarshes were lost, associated with a strong increase of the "*Casuarina/Melaleuca*" class, indicating pressure from the landward side onto saltmarsh communities.

Our first hypothesis was that mangrove encroachment will be detected at all estuaries, consistent with studies on mangrove encroachment globally (Feller et al., 2017; Saintilan and Rogers, 2015) We analysed changes in mangrove cover in the four estuaries over the observation period of 50 years. Two estuaries showed an increase in mangrove area while the other two showed a small decrease or no change at all. Saintilan and Williams (1999) observed a general increase in mangrove encroachment along the whole south-east coast of Australia occurring since the 1950s, which has been mainly attributed to temperature increase over the past century (Saintilan et al., 2014) and concomitant sea level rise (Rogers et al., 2006). Increases in mangrove encroachment have also been attributed to an increase in sediment availability (Feller et al., 2010; Morrisey et al., 2010), as well as to higher rainfall, which was observed in northern Queensland (Eslami-Andargoli et al., 2009). At a more local scale, factors that influence rate of mangrove encroachment are availability of land to expand onto and potential for mangrove propagules to reach those sites (Saintilan et al., 2014). Factors inhibiting the establishment of mangrove propagules include unfavourable currents, rocky coasts and closed estuary entrances (Saintilan et al., 2009b). At Hastings River, where we detected a decrease in mangrove area, the entrance at the ocean is partially blocked and frequented by boat usage, which might prevent propagules from establishing. On the other hand, at Shoalhaven River, a large artificial island (Comerong Island) is situated directly at the mouth of the estuary, also partially blocking its entrance and here we observed an increase in mangrove area which might also be attributed to the higher sedimentation rates close to Shoalhaven Heads. High sedimentation occurs here because the river was artificially diverted to exit instead at Crookhaven Heads, after a channel construction in 1822 (Carvalho and Woodroffe, 2013). This suggests that estuary type, i.e. wave dominated delta or tide dominated delta, may be an important factor in mangrove encroachment due to its influence on sedimentation rates and tidal fluctuations which in turn affect mangrove establishment (Woodroffe, 1990).

For our second hypothesis we suggested that extensively modified estuaries should experience greater mangrove encroachment compared to largely unmodified estuaries. However, we found no evidence of this across the four estuaries, with changes in mangrove area not related to intensity of catchment modification. However, assessment of vegetation change for a larger number of estuaries is necessary to clearly confirm whether such an association exists. We used the National Land and Water Resources Audit (2002) to classify estuaries as extensively modified or largely unmodified, which is based on criteria including catchment natural cover, estuary-use, land-use and tidal regime. However, in order to assess the relative importance of the environmental drivers of mangrove encroachment in estuaries, additional data on factors known to affect mangrove growth should be included, such as nutrient availability, salinity and sedimentation rates (Lovelock et al., 2011; Reef et al., 2016). These additional parameters could provide us with is a more detailed picture of the modification state of the estuary and thus reduce variability when comparing by category.

Our third hypothesis was that the greater expansion of mangroves in extensively modified estuaries would be associated with a greater decline in saltmarsh area. We did not find that saltmarsh decline was greater in estuaries and associated with increased mangrove area in extensively modified catchments. However, we did find an overall loss of saltmarsh area of 26-47% in three of the four estuaries, consistent with the findings of Saintilan and Williams (2000) and Saintilan (2014) of an average 30 % decline in saltmarsh. However, rather than a decline in saltmarsh associated with mangrove encroachment, our study found a decline in saltmarsh associated with an increase in the area of *Casuarina*/*Melaleuca* vegetation. The seaward encroachment of *Casuarina*/*Melaleuca* has been observed previously by Chafer (1998) and Saintilan and Wilton (2001), who associated the expansion of *Casuarina*/*Melaleuca* to changes in hydrology. Several *Casuarina* and *Melaleuca* species show slight tolerances to salinity and waterlogging but are categorized as terrestrial freshwater plants (Robinson, 2003; Sainty, 2012). A seaward encroachment by *Casuarina* / *Melaleuca*, in addition to a landward encroachment by mangroves as observed in other studies, would drastically increase the squeeze effect of saltmarsh vegetation in coastal regions.

Conclusion

Using a supervised classification on historic and modern aerial images, we confirmed saltmarsh loss over a period of 50 years in four estuaries of south-east Australia that experienced different levels of catchment modification. Although changes in mangrove area varied and thus a mangrove driven squeezing effect could not be supported; the area of *Casuarina* / *Melaleuca* communities increased markedly. This indicates seaward encroachment of these communities as an additional threat to saltmarsh vegetation. This study represents a first step in assessing the changes in wetland vegetation cover across estuaries subject to varying levels of catchment modification, but more estuaries and specific data on nutrient, sediment and salinity status will be needed to confirm the generality of these changes and the likely drivers.

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SUPPLEMENTARY MATERIAL

Table A3 | Classification metrics for the classification of the 2012 images from Karuah River. The lower right cell contains the overall accuracy (96.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (1234).

Karuah River 2012		Reference							
		Casuarina	Mangrove	Saltmarsh	Sand	Shadow	Water	Total	UA
Prediction	Casuarina	**193**	11	0	0	6	0	210	92%
	Mangrove	13	**188**	0	0	1	0	202	93%
	Saltmarsh	0	0	**215**	0	0	0	215	100%
	Sand	0	0	0	**215**	0	0	215	100%
	Shadow	9	15	0	0	**208**	0	232	90%
	Water	0	1	0	0	0	**215**	216	100%
	Total	215	215	215	215	215	215	**1234**	
	PA	90%	87%	100%	100%	97%	100%		**96%**

Table A4| Classification metrics for the classification of the 1970 images from Karuah River. The lower right cell contains the overall accuracy (91.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (6521).

Karuah River 1970		Reference						
		Casuarina	Mangrove	Saltmarsh	Sand	Water	Total	UA
Prediction	Casuarina	**1148**	369	8	0	2	1527	75%
	Mangrove	290	**1066**	6	0	0	1362	78%
	Saltmarsh	3	5	**1427**	0	0	1435	99%
	Sand	0	0	0	**1441**	0	1441	100%
	Water	0	1	0	0	**1439**	1440	100%
	Total	1441	1441	1441	1441	1441	**6521**	
	PA	80%	74%	99%	100%	100%		**91%**

Table A5 | Classification metrics for the classification of the 2012 images from Currambene Creek. The lower right cell contains the overall accuracy (90.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (4068).

Currambene Creek 2012		Reference							
		Casuarina	Mangrove	Saltmarsh	Sand	Shadow	Water	Total	UA
Prediction	Casuarina	**567**	178	5	0	22	3	775	73%
	Mangrove	143	**539**	0	0	12	2	696	77%
	Saltmarsh	5	0	**746**	0	0	13	764	98%
	Sand	0	0	0	**756**	0	0	756	100%
	Shadow	40	38	0	0	**722**	0	800	90%
	Water	1	1	5	0	0	**738**	745	99%
	Total	756	756	756	756	756	756	**4068**	
	PA	75%	71%	99%	100%	96%	98%		**90%**

Table A6 | Classification metrics for the classification of the 1970 images from Currambene Creek. The lower right cell contains the overall accuracy (88.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (2997).

Currambene Creek 1970		Reference						
		Casuarina	Mangrove	Saltmarsh	Sand	Water	Total	UA
Prediction	Casuarina	**471**	142	5	0	11	629	75%
	Mangrove	187	**514**	4	0	3	708	73%
	Saltmarsh	18	9	**670**	2	10	709	94%
	Sand	0	0	3	**682**	0	685	100%
	Water	8	19	2	0	**660**	689	96%
	Total	684	684	684	684	684	**2997**	
	PA	69%	75%	98%	100%	96%		**88%**

Table A7| Classification metrics for the classification of the 2012 images from Hastings River. The lower right cell contains the overall accuracy (95.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (14298).

Hastings River 2012		Reference								
		Casuarina	Grass	Mangrove	Saltmarsh	Shadow	Soil	Water	Total	UA
Prediction	Casuarina	**1913**	1	261	26	60	0	2	2263	85%
	Grass	0	**2132**	0	1	0	10	0	2143	99%
	Mangrove	152	0	**1844**	0	10	0	0	2006	92%
	Saltmarsh	31	1	0	**2096**	0	28	0	2156	97%
	Shadow	43	0	36	0	**2071**	0	0	2150	96%
	Soil	1	7	0	18	0	**2103**	0	2129	99%
	Water	1	0	0	0	0	0	**2139**	2140	100%
	Total	2141	2141	2141	2141	2141	2141	2141	**14298**	
	PA	89%	100%	86%	98%	97%	98%	100%		**95%**

Table A8 | Classification metrics for the classification of the 1970 images from Hastings River. The lower right cell contains the overall accuracy (77.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (4841).

Hastings River 1970		Reference						
		Casuarina	Grass	Mangrove	Saltmarsh	Water	Total	UA
Prediction	Casuarina	**624**	9	266	20	89	1008	62%
	Grass	4	**1087**	1	132	11	1235	88%
	Mangrove	474	0	**923**	2	45	1444	64%
	Saltmarsh	28	119	3	**1094**	0	1244	88%
	Water	128	43	65	10	**1113**	1359	82%
	Total	1258	1258	1258	1258	1258	**4841**	
	PA	50%	86%	73%	87%	88%		**77%**

Table A9 | Classification metrics for the classification of the 2012 images from Shoalhaven River. The lower right cell contains the overall accuracy (94.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (5032).

Shoalhaven River 2012		Reference									
		Casuarina	Grass	Mangrove	Saltmarsh	Shadow	Soil	Water	Water_fresh	Total	UA
Prediction	Casuarina	**585**	0	90	18	17	0	0	3	713	82%
	Grass	0	**668**	0	2	0	0	0	0	670	100%
	Mangrove	32	0	**543**	4	4	0	2	0	585	93%
	Saltmarsh	8	2	4	**614**	0	29	0	0	657	93%
	Shadow	41	0	33	0	**646**	0	0	0	720	90%
	Soil	0	0	0	32	0	**641**	0	0	673	95%
	Water	0	0	0	0	0	0	**668**	0	668	100%
	Water_fresh	4	0	0	0	3	0	0	**667**	674	99%
	Total	670	670	670	670	670	670	670	670	**5032**	
	PA	87%	100%	81%	92%	96%	96%	100%	100%		**94%**

Table A10 | Classification metrics for the classification of the 1970 images from Shoalhaven River. The lower right cell contains the overall accuracy (79.0%). Class specific accuracies can be found in the lower marginal row (producer accuracy, PA) and outer right marginal column (user accuracy, UA). Values shown in diagonal cells contain correctly classified pixel samples for each class and the total number of pixel samples (7262).

Shoalhaven River 1970		Reference							
		Casuarina	Grass	Mangrove	Saltmarsh	Soil	Water	Total	UA
Prediction	Casuarina	**1073**	0	509	13	0	32	1627	66%
	Grass	0	**1313**	0	6	203	0	1522	86%
	Mangrove	407	0	**891**	17	9	82	1406	63%
	Saltmarsh	27	2	24	**1369**	10	118	1550	88%
	Soil	1	220	9	5	**1313**	0	1548	85%
	Water	27	0	102	125	0	**1303**	1557	84%
	Total	1535	1535	1535	1535	1535	1535	**7262**	
	PA	70%	86%	58%	89%	86%	85%		**79%**

Chapter 6

Discussion

Ina Geedicke

Discussion

Approximately 85% of Australia's population lives within 50 km of the coastline (Trewin, 2004). The predicted growth of global urban population by another 13% until 2050 (United Nations, 2018), will lead to an increased impact on coastal wetlands by anthropogenic effects. Such effects entail pollution associated with stormwater run-off and changes in salinity due to rising sea levels (UNEP, 2014). This thesis examined different anthropogenic effects on the mangrove and saltmarsh communities of south-east Australia (Figure 1). First on a local scale, where we analysed the direct effect of stormwater discharge and its consequences on vegetation (Chapter 2 and 3). This was followed by an extension to elevated CO_2 and changes in salinity associated with anthropogenic climate change (Chapter 4). Finally, at the regional scale, a remote sensing approach (Chapter 5) was used to assess if the changes in vegetation pattern observed in Chapter 2 can be detected in aerial images of extremely modified catchments across a 42-year period.

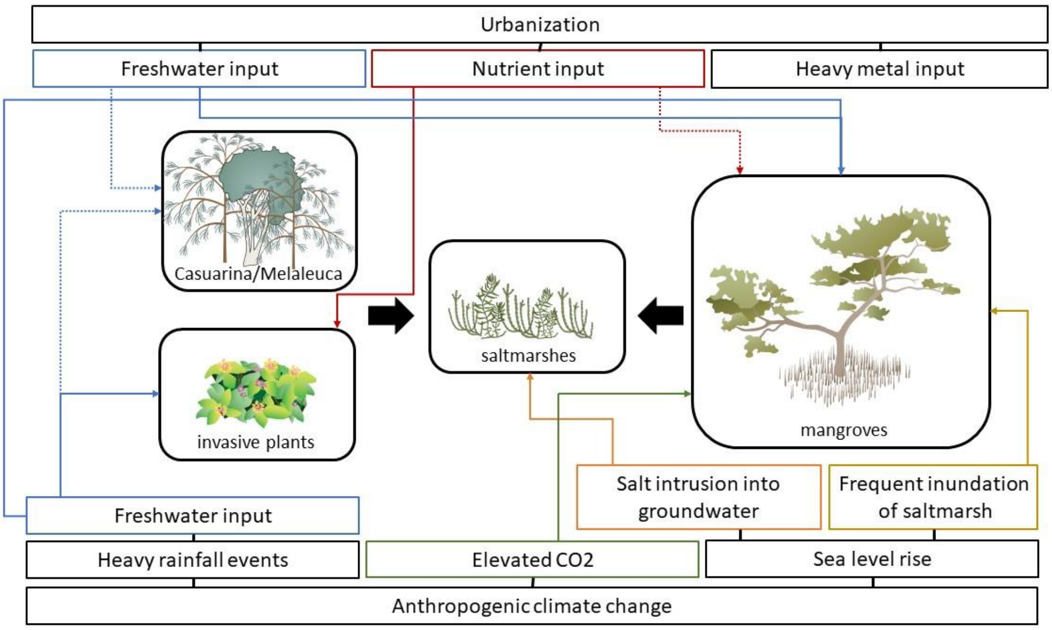

Figure 6| Concept map of parameters influencing the vegetation pattern of Australian coastal wetlands discussed in this thesis. Black arrows indicate positive influence on vegetation growth and dashed arrows indicate assumed positive influence on vegetation growth.

Impact of stormwater run-off on urban wetlands

Natural vegetation in proximity to urban and agricultural development is influenced by pollutants associated with roads and vehicles, urban gardening (nutrients and pesticides) and industrial sites (heavy metals and organic chemicals) (Leishman and Thomson, 2005; Sharley et al., 2017). Especially after high rainfall, stormwater outlets may flush the additional rainwater into adjacent coastal wetlands. In a first field study (Chapter 2, Geedicke et al., 2018), we showed that stormwater input alters the vegetation pattern of coastal wetlands by facilitating the growth of exotic freshwater plants into saltmarsh vegetation downslope of stormwater outlets and the expansion of mangroves into saltmarsh vegetation from the seaward side. This results in a squeezing effect of the saltmarsh communities that occur between urban development and mangrove forest. At industrial sites this effect was stronger, where greater areas of impervious surfaces can be expected, resulting in larger amounts of stormwater and pollution (Davies et al., 2010; Davis et al., 2001; Wright et al., 2011).

Urban stormwater carries litter and numerous chemical components, such as nutrients and heavy metals, after flowing over impervious surfaces and managed areas, such as gardens or parks (Davies et al., 2010; Semadeni-Davies et al., 2008). Even though we found alarming concentrations of heavy metals in the soil, we could not detect an effect of metal concentration on the vegetation composition below stormwater outlets. However, our models showed that decreased soil salinity and total nitrogen concentration explained the high abundance of invasive species and mangroves, compared to saltmarsh species, below stormwater outlets the most. Our findings align with laboratory (Reef et al., 2016) and fieldwork studies (Ribeiro et al., 2015) that showed that mangrove growth and photosynthetic activity is accelerated with nutrient input. Though, some studies showed no improvement of survivorship of mangrove seedlings after fertilisation (Saintilan, 2010). In regards to exotic species, invasion success was shown to be facilitated by stormwater run-off in terrestrial urban vegetation as shown by Leishman and colleagues in a series of field and manipulative glasshouse experiments (Lake and Leishman, 2004; Leishman et al., 2004; Leishman and Thomson, 2005). They showed that nutrient concentration was key factor driving exotic species success. Our study provides a first overview of anthropogenic drivers that shape coastal wetland communities influenced by urban stormwater run-off. However, we captured a single point in time only. In a dynamic tidal wetland, seasonality might change the concentration of environmental parameters considerably. Therefore, and due to the complexity of natural systems, a multitude of factors can be correlated and in order to determine the drivers of the observed vegetation pattern of mangroves, saltmarshes and exotic plants, it is essential to undertake manipulative experiments that may validate our findings. Overall, the results of this study are important for the management of saltmarsh and mangrove vegetation in urban areas. In Australia, 'Subtropical and temperate coastal saltmarsh of Australia' has been listed as an endangered ecological community under the Commonwealth Environmental Protection and Biodiversity Conservation (EPBC) Act. Understanding the key threatening processes to saltmarsh vegetation is essential to ensure its effective conservation management.

Impact of freshwater and nutrients on saltmarsh communities

Due to the limitations (i.e. correlation of environmental parameters, no repeated sampling) of correlative field studies, we decided to conduct a mesocosm glasshouse experiment to test the hypotheses that increased nutrients and reduced salinity facilitated exotic species invasion into saltmarsh vegetation (Chapter 3). Our results showed that reduced salinity in saltmarsh communities facilitated exotic plant success and that - contrary to our hypothesis - additional nutrients increased biomass production but not necessarily the survival of exotics. Surprisingly, one exotic species, *Protasparagus aethiopicus*, showed high survival rates even under high salinity conditions. *Protasparagus aethiopicus*, however, was not originally reported as being tolerant to high salinity conditions (Bowden and Rogers, 1996; Langeland, 2008; Royal Botanic Gardens and Domain Trust, 2018).

Under natural conditions, saltmarsh communities are thought to be resilient to invasion by exotic plant species, with the exception of exotic saltmarsh species (Zedler and Kercher, 2004). However, the lowland position of saltmarshes in the landscape makes them the recipient of propagules from a wide catchment (Callaway and Zedler, 2004; Zedler and Kercher, 2004). In urban areas, saltmarshes are regularly disturbed by freshwater. Impervious surfaces of roads and buildings lead to the accumulation of stormwater run-off, which is collected and channelled into the adjacent pervious surfaces, such as wetlands which has been described in Chapter 2 (Al Bakri et al., 2008; Grella et al., 2018). Stormwater is not the only freshwater input into coastal wetlands. Other anthropogenic influences manipulate the hydrologic system (e.g. importing water for agricultural and urban uses) which changes the salinity in these systems (Zedler and Kercher, 2004). Interestingly, in non-urban regions, without freshwater input from engineered stormwater run-off areas, a large decrease in soil salinity can be achieved through extreme precipitation events. These events are predicted to increase in frequency with the changing climate (IPCC, 2014) and can cause vegetation change in saltmarsh communities by the encroachment of less salt tolerant mangroves (Saintilan and Rogers, 2015) or the germination of exotic species within the seedbank of saltmarshes (Callaway and Zedler, 2004). Our findings strongly support the findings from the previous field study (Geedicke et al., 2018), that saltmarshes experience a squeezing effect from the landward site from exotic plants in proximity to stormwater run-off. To investigate the squeezing pattern from the seaward side onto the saltmarsh community, it would be interesting to test if mangrove establishment into saltmarsh is facilitated by reduced salinity and increased nutrients. This could be accomplished in a similar manipulative experiment to the one in chapter 3 by replacing exotic species with mangrove propagules.

Management implications

Intertidal wetlands are, in general, not considered as threatened by exotic species invasion due to their adaptation to saline environments (Adam, 2009; Deegan et al., 2012). Our observations from the field (described in chapter 2) and the manipulative experiment (described in chapter 3) showed that intertidal wetlands are not always resilient to plant invasion. In particular, saltmarsh communities that occupy a vulnerable area between mangrove forests on the seaward site and freshwater plant communities on the landward site, are threatened by exotic plant invasion when there is a greater input of freshwater. The freshening of intertidal wetlands has already been noted as a problem for saltmarsh in other regions, which is enhanced when in proximity to urban and agricultural development (Alldred et al., 2017; Harty, 2004; Lee et al., 2006). We suggest that management of stormwater input into these threatened coastal wetlands should be a high priority. For planning strategies to be effective however, it is important to recognise that one of the main threats to coastal wetland vegetation is clearing due to land use change and changes to the hydrological system. Thus, policies should first seek to protect mangrove and saltmarsh vegetation from further destruction (Harty, 2004). The main cause to wetland destruction is still the active removal through urban and agricultural development or passive destruction through pollution and changes to the hydrological system by e.g. construction of channels (UNEP, 2014). Thus, by explicitly protecting mangroves and saltmarshes globally from destruction, new construction projects would need to consider their direct impact on them before further harm is done.

There are a number of techniques that can be used to reduce urban stormwater input to coastal wetlands in order to lessen the freshening and eutrophication of wetlands. This includes trapping of sediment through the construction of vegetated buffer zones and uptake of nutrients by plants in the buffer zone, thus reducing the input of nutrients into the tidally influenced areas where saltmarsh occurs. Sediment traps have also been proven to retain heavy metal and nutrients such as sediment-bound phosphorus (Genç-Fuhrman et al., 2007; Tondera et al., 2018; Walker and Hurl, 2002), but need to be cleaned out regularly with sediment removed off-site. However dissolved nitrogen and phosphorus compounds are not retained through sediment traps and must be managed by other methods such as phytoremediation (Tondera et al., 2018). It should be noted that the construction and maintenance of such traps is expensive, and it should also be considered how much damage the construction would cause to existing vegetation.

Beyond engineering solutions, other approaches could include educational programs that increase people's awareness of the vulnerability and importance of wetlands and easy steps to contribute to their protection, such as not allowing detergents or fertilisers to enter the stormwater system (Harty, 2004). For new constructions, several planning strategies should be considered. The minimization of impervious surfaces or the reuse and retention of rainwater, e.g. green roofs, through innovative architectural design and water-sensitive urban design could reduce stormwater run-off drastically (Berger et al., 2015; Goonetilleke et al., 2005; Harty, 2004). In addition, consideration of climate change effects, such as sea level rise, should promote the planning and development of buffer zones to enable landwards shifting of wetlands. These could include the prohibition of landfilling adjacent to wetlands (Harty, 2004) or active planning of possible retreats for coastal vegetation as demonstrated by Rogers et al. (2019). However, even with maintenance of high salinity conditions, some exotic species such as *P. aethiopicus* will be able to thrive and therefore require targeted management. Additionally, awareness and monitoring of potential halophyte invaders that are able to tolerate a wide range of soil salinity conditions should be prioritised. Halophytic invasive species often transform the invaded area into a monospecific habitat, suppressing native species and reducing biodiversity not only of the plant community but also of the faunal community (Zedler and Kercher, 2004).

Impact of CO_2 on mangrove and saltmarsh communities

Anthropogenic climate change, driven by elevated greenhouse gases such as CO_2, is anticipated to lead to reduced soil salinity in wetlands due to sea level rise and a higher frequency of rainfall events (IPCC, 2014). This effect might be further enhanced in urban environments, where atmospheric CO_2 and the input of freshwater is elevated due to combustion of fossil fuels (Idso et al., 1998) and stormwater run-off from impervious surfaces (Davies et al., 2010), respectively. It was hypothesized that elevated CO_2 and reduced soil salinity would facilitate mangrove encroachment into saltmarsh communities. In a glasshouse experiment (Chapter 4), we examined the effect of CO_2 and salinity on seedling growth of two mangrove species grown individually and in a model saltmarsh community. Our results suggest that CO_2 and salinity are not universal drivers determining saltmarsh-mangrove boundaries. It is likely that rising atmospheric CO_2 concentration and reduced salinity associated with sea level rise or freshwater input in urban areas, will enhance the establishment success of some mangrove species in saltmarshes. This in turn, would result in facilitation of mangrove encroachment in the future. Nevertheless, we showed that our saltmarsh communities experienced enhanced growth under elevated CO_2 as well as slowing mangrove growth through competition when grown together. This is consistent with findings by McKee and Rooth (2008), who also showed mangrove growth was curtailed when grown together with the saltmarsh plant *Spartina alterniflora* under elevated CO_2. When grown alone, three mangrove species showed vigorous growth under elevated CO_2 and reduced salinity (Ball et al., 1997; McKee and Rooth, 2008). However, as for all experimental greenhouse work, there may be limitations in applying our results to natural environments. For example, as our experiment was conducted in a closed environment, herbivory impact was non-existent. A field study by (McKee and Rooth, 2008) showed that herbivory reduced the survival of the mangrove *Avicennia germinans* seedlings and it was suggested that herbivory could negate any positive effect elevated CO_2 may have on mangrove seedling growth in saltmarsh communities. Our study thus implies that the competition effect of saltmarsh species onto mangroves should not be underestimated in prospect of future climate change effects. We only tested C_3 saltmarsh and mangrove species, however it would be interesting to test the competition effect of C_4 saltmarsh species on the C_3 mangroves under the same treatments because C_3 plants are expected to use CO_2 in a more effective way than C_4 plants.

Impact of catchment modifications

As we could show in the previous chapters, wetlands in anthropogenically modified estuaries are exposed to numerous factors, such as nutrient input and changes in salinity through agricultural or stormwater run-off. In the final data chapter of this thesis (Chapter 5), we tested if changes in wetland vegetation cover of heavily modified and largely unmodified estuaries can be evaluated by comparing aerial images of 1970 and 2012 across four estuaries in New South Wales, Australia. By using a supervised classification on historic and modern aerial images, we confirmed saltmarsh loss over a period of 42 years across four estuaries of south-eastern Australia that experienced different levels of anthropogenic modifications. We did not find a uniform trend of vegetation change within the two estuary categories (extensively modified and largely unmodified). Following the results from chapters 2 and 3, we expected to see expansion of mangroves into saltmarsh from the seaward side and expansion of terrestrial vegetation from the landward side into saltmarsh. This was not observed from the imagery. However, the area of *Casuarina* and *Melaleuca* communities, that were defined in our land cover classification, increased drastically. This might indicate seaward encroachment of these communities as an additional threat to saltmarsh loss. Similar findings by Saintilan and Wilton (2001) confirm our suggestion of seaward encroachment of saltmarsh fringing *Casuarina* and *Melaleuca* species. They observed the encroachment at Jervis Bay, NSW, using aerial imagery from 1944 – 1999 and associated it with increased freshwater and nutrient input. Also, in riparian systems, it has been shown that *Casuarina cunninghamiana* responds with increased growth under elevated CO_2 (Lawson et al., 2017). If this is also true for *Casuarina glauca*, which inhabits the saltmarsh fringes of south-eastern Australia, encroachment might also be linked to elevated CO_2, particularly in urban regions where CO_2 concentrations can be very high (Idso et al., 1998). The opposite has been observed in tropical Australia, where saline intrusion as a consequence of sea level rise has resulted in *Melaleuca* dieback, as well as mangrove encroachment (Saintilan et al., 2018). The biggest caveat of the chapter 5 study lies with the number of estuaries analysed. To detect changes in a complex system, it is likely that a greater number of estuaries per class is needed. Also, by categorizing the estuaries (NLWRA, 2002), we assume that environmental conditions such as nutrient or freshwater input are fairly consistent within modification classes. The categories of the estuaries we studied were based on land-use and disturbance within the catchment however additional data on nutrient, sedimentation or freshwater input to the system could refine the categorization and therefore lead to better understanding of any vegetation changes. This should be tested by verifying the nutrient concentrations and salinity of the water and wetland soil of the estuaries. The earliest images we acquired that covered all our sites were from 1970, however, adding older images or even vegetation maps, could provide an insight on the mangrove and saltmarsh boundaries prior to large-scale catchment modifications of the 20th century. The successful use of vegetation maps and aerial images to detect changes in saltmarsh cover was shown by Allen (2014) within the Severn Estuary in the United Kingdom. Adding these additional data to our study could help us understand what impact catchment modification have on intertidal wetland vegetation of south-eastern Australia.

Conclusions

This thesis has examined environmental drivers of saltmarsh / mangrove boundaries at scales from local, i.e. impacts of stormwater input on urban wetland systems (chapter 2 and 3) to regional (chapter 5) and global scales (chapter 4). We showed that freshwater input threatens the sensitive tidal wetland ecosystem and facilitates its invasion by exotic plants. However, our data showing the squeezing effect of mangroves from the seaward side and freshwater exotic species from the landward side was at local scales only. A remote sensing study using high resolution aerial images could reveal if mangrove forests tend to grow in closer proximity to the landward site when there is input of freshwater from stormwater outlets. This future study would need to be conducted on a bigger scale including a large number of stormwater outlet pipes throughout urban regions. Increasing the number of sites to detect a clear pattern, is also the lesson learned from chapter 5, where we tested if the degree of catchment modification has resulted in substantial vegetation change in coastal wetlands. We detected interesting changes, however these were not consistent within the two categories of heavily modified and largely unmodified estuaries. Analysing ten estuaries per category along the east coast of New South Wales, as well as assessing control sites, i.e. pristine estuaries, should provide us with an adequate representation of vegetation changes. The comparison of historical and modern aerial images to detect long-term changes in vegetation distribution is a simple analysis of a complex system. However, linking these observations to particular parameters is often difficult because measured environmental data over longer time periods may not be available or measured using a consistent technique. The set-up of long-term manipulative experiments, such as the open top chambers by Drake et al. (1989), are particularly useful to answer questions related to slow vegetation change under a wide range of disturbances, such as nutrient input or elevated CO_2. The open top chambers were set up in 1987 in wetlands of Chesapeake Bay, an estuary in the U.S. states of Maryland and Virginia, to deliver an elevated CO_2 treatment to saltmarsh vegetation (Drake et al., 1989; Erickson et al., 2013). Such installations would be useful to analyse the effect of elevated CO_2 on mangrove and saltmarsh plants as an extension to chapter 4, but also with the inclusion of C_4 grasses, as they are assumed to fare less well under high atmospheric CO_2 concentrations.

By studying mangrove and saltmarsh communities of south-eastern Australia under anthropogenically disturbed conditions, we showed that the reduction of salinity and changes in soil nutrient concentration facilitates the establishment of exotic species and the potential encroachment of mangrove forests into saltmarsh habitat. Especially the abundance of exotic species encroaching into saltmarshes below stormwater run-off is an alarming finding, because saline wetlands were thought to be resilient to invasion by freshwater plants. We also found that a plant, *Protasparagus aethiopicus*, which is listed as an invasive exotic freshwater plant possesses tolerance to elevated soil salinity. These findings will be useful to wetland management in proximity to urban development. On a regional scale, we can suggest that rising atmospheric CO_2 concentration and reduced salinity as a result of sea-level rise are likely to enhance the establishment success of mangrove seedlings in saltmarsh communities thus facilitating mangrove encroachment. Additionally, by using a supervised classification on historic and modern aerial images, we confirmed saltmarsh loss over a period of 42 years in estuaries of south-east Australia across four estuaries that experienced different levels of anthropogenic changes. We provided input to management actions at local scales as well as contributed to the understanding of regional and global drivers on the sensitive saltmarsh-mangrove boundaries.

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Declaration

Certificate of Originality

English: I hereby declare that the contents of this thesis entitled “Anthropogenic impacts on mangrove saltmarsh communities in eastern Australia” are a record of my own original work, except where other contributors are named. In detail, my contributions and those of others are listed in the below statement.

German: Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen verwendet habe. Mein Anteil an Konzeption, Durchführung und Berichtsabfassung, sowie die Beiträge Anderer sind im „Contribution Statement“ im Einzelnen dargelegt.

Ina Geedicke

Hamburg, March 2019

Contribution Statement

Chapter 1 | Introduction

Conceptualization: Ina Geedicke (IG); Investigation: IG; Writing – Original Draft Preparation: IG; Writing – Review & Editing: Michelle R. Leishman (MRL), Jens Oldeland (JO); Visualization: IG

Chapter 2 | Urban stormwater run-off promotes compression of saltmarshes by freshwater plants and mangrove forests

Conceptualization: MRL, JO and IG; Methodology: MRL, JO and IG; Formal Analysis: IG and JO; Investigation: IG; Data Curation: IG; Writing – Original Draft Preparation: IG; Writing – Review & Editing: MRL and JO; Visualization: IG; Supervision: MRL and JO

Chapter 3 | Freshwater input drives invasion success of exotic plants in saltmarsh communities

Conceptualization: MRL, JO and IG; Methodology: MRL, IG and Anthony Manea (AM); Formal Analysis: IG; Investigation: IG and AM; Resources; Data Curation: IG; Writing – Original Draft Preparation: IG; Writing – Review & Editing: MRL, JO, AM and IG, Supervision: MRL and JO

Chapter 4 | Elevated carbon dioxide and seawater salinity enhances mangrove seedling establishment in a model saltmarsh community

Conceptualization: MRL, AM; Methodology: MRL, AM and IG; Formal Analysis: AM; Investigation: AM and IG; Writing – Original Draft Preparation: AM; Writing – Review & Editing: MRL, IG and AM; Visualization: AM

Chapter 5 | Changes in saltmarsh area over the last 42 years in coastal New South Wales, Australia

Conceptualization: MRL, JO and IG; Methodology: JO, IG; Formal Analysis: IG and Rene Hans-Juergen Heim (RHJH); Investigation: IG and RHJH; Data Curation: IG and RHJH; Writing – Original Draft Preparation: IG; Writing – Review & Editing: MRL, JO, RHJH and IG, Supervision: MRL and JO

Chapter 6 | Discussion

Conceptualization: IG; Investigation: IG; Writing – Original Draft Preparation: IG; Writing – Review & Editing: MRL and JO; Visualization: IG