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Moving from Generalisations to Specificity about Mangrove –Saltmarsh Dynamics

Kerrylee Rogers¹  · Ken W. Krauss²

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Abstract

Spatial and temporal variability in factors influencing mangrove establishment and survival affects the distribution of mangrove, particularly near their latitudinal limit, where mangrove expansion into saltmarsh is conspicuous. In this paper the spatial variability in mangrove distribution and variability in factors influencing mangrove establishment and survival during the Quaternary period are reviewed, focussing on research at latitudinal limits in Australia and mainland USA. Despite similarities in the response of mangrove to some drivers, the expression of these drivers is both spatially and temporally variable, demonstrating the need for analyses of mangrove-saltmarsh dynamics to move beyond generalisations and incorporate regional and local-scale specificity. We propose i) that precursory recognition that ‘correlation does not mean causation’ is inadequate and assumptions, caveats, and limitations should be clearly articulated in correlative studies; ii) experimental design in manipulative experiments must also articulate the spatial and temporal scale to which the analysis is relevant; and iii) analyses that draw from a range of methods will provide greater confidence. Integrated research programs that transect spatial and temporal scales and incorporate a range of techniques are essential to improve projections. Mangrove-saltmarsh distribution research should move beyond simple models that assume equilibrium between realised and fundamental niches.

Keywords Climate change · Sea-level rise · Frost or freeze · Spatial and temporal variability · Hierarchy theory

Introduction

Mangrove forests, trees and shrubs typically occupy the upper intertidal zone and are regularly inundated by tidal waters. Mangroves thrive where inundation typically occurs daily, often at tidal positions near mean sea level to mean high water. Mangroves reportedly occupy between 83,495–137,760 km² along coastlines in 118 countries and territories (Giri et al. 2011b; Hamilton et al. 2016). Despite this large spatial distribution, it is evident that mangrove forests do not occupy all shorelines globally even where they can climatically, and while they exhibit a close association with sea level, other factors also control the distribution of mangrove on shorelines. Strong spatial patterning in global mangrove

distribution occurs with areal extent greatest in the tropics (Giri et al. 2011b), notwithstanding significant human impacts on mangrove forests in this region (Duke et al. 2007; Richards and Friess 2016).

A corresponding pattern of species diversity also exists with species counts attenuating away from tropical shorelines towards sub-tropical and temperate shorelines (Duke et al. 1998a; Saenger 2002). This strong spatial patterning has long been associated with temperature and at least as early as 1956, it was proposed that mangrove develop best when i) average temperature of the coldest month exceeds 20 °C; ii) development occurs in a fine-grained alluvium substrate; and iii) shorelines are free from strong wave action (West 1956). As a general rule these prerequisites still hold true; however, increasing access to higher resolution temperature data and observations of mangrove health and distribution have demonstrated that mangrove distribution is more nuanced than this rule would present (Quisthoudt et al. 2012; Osland et al. 2013; Cavanaugh et al. 2014; Osland et al. 2016). Exceptions in the global pattern of mangrove distribution are evident on the basis of biotic tolerances to temperature (Stevens et al. 2006; Stuart et al. 2007; Krauss et al. 2008), and variation in physical

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processes such as oceanic currents, rainfall, geomorphic settings and geographic barriers (Ball and Sobrado 1998; Saenger 2002; Quisthoudt et al. 2013; Semeniuk 2013; Saintilan et al. 2014). Consequently, the latitudinal range of mangrove forests is large, extending between 32°N and 38°S (Quisthoudt et al. 2012; Saintilan et al. 2014).

Recent observations of changes in mangrove distribution have motivated debate about controls on mangrove distribution. In southeastern Australia mangrove expansion was initially documented to occur in response to factors relevant at the local-scale and based largely upon comparisons of current and past distribution from aerial photography dating to the 1940s. Through a compilation of 28 independent studies of mangrove expansion across the intertidal zone, Saintilan and Williams (1999) established that the pattern of mangrove expansion into saltmarsh was regional in scale. Proposed mechanisms facilitating mangrove expansion into saltmarsh include changes in rainfall, changing agricultural practices, altered tidal regimes (including eustatic sea-level rise), sedimentation and nutrient addition, and subsidence. A regional pattern of mangrove proliferation has also been established along the Gulf of Mexico following a long period absent of extreme freeze events (Sherrod and McMillan 1985; Osland et al. 2013; Cavanaugh et al. 2014). Evidence of mangrove expansion at latitudinal limits has been compiled, differentiating patterns of change in mangrove distribution across the tidal frame from changes occurring at the latitudinal extremes of mangrove distribution (Saintilan et al. 2014). By necessity, this data compilation was large in spatial extent and identified a pattern of mangrove expansion at poleward limits that applied to both the northern and southern hemispheres and five continents (Asia, Australia, North America, Africa and South America). As per the prior compilation, the authors cautiously presented hypotheses for poleward expansion explaining the changes in distribution, including temperature increases, barriers to propagule dispersal, and elevated atmospheric CO₂ concentrations, which mirrors global patterns of woody shrub encroachment of grasslands (Saintilan and Rogers 2015).

Coincident with these observations is evidence that increasing atmospheric CO₂ concentrations are elevating air and sea surface temperatures, altering rainfall patterns and increasing sea levels. Due in large part to the correlation between changing mangrove distribution and anthropogenic climate change, studies are focussing on establishing whether climate change is implicated in observed changes in mangrove distribution. As mangroves are closely associated with the position of the sea at local scales, it is not surprising that there has been considerable focus on the relationship between sea-level rise and mangrove distribution changes. More recently, mangrove distribution at the local scale has been associated with temperature and aridity (Osland et al. 2016; Ximenes et al. 2016). Ecophysiological studies have considered the role of elevated CO₂, and the interactions between elevated CO₂,

nutrient additions, water-use efficiency, sea-level rise, salinity changes and mangrove distribution (Famsworth et al. 1996; Ball et al. 1997; Ball and Munns 1992; McKee and Rooth 2008; Langley et al. 2009). Influenced by a need to plan for climate change and promote ecosystem adaptation, research is now being directed towards projecting mangrove distribution. This is typically achieved using modelling techniques, establishing ecosystem niches and applying a range of IPCC scenarios of temperature increases and sea-level rise (Traill et al. 2011; Oliver et al. 2012; Record et al. 2013; Cavanaugh et al. 2015).

Underlying all models is a degree of uncertainty regarding the influence of parameters. For models projecting mangrove distribution, uncertainty increases when processes controlling distribution are poorly understood, or inadequately parameterised (Cowell and Thom 1994). Understanding controls on mangrove distribution becomes even more important when projecting models beyond the spatial and temporal scale that they are based, as uncertainty is compounded by projection (De Vriend 1991; Terwindt and Battjes 1991). Using case studies of mangrove and saltmarsh dynamics near the latitudinal range limit of mangrove from southeastern Australia and the Gulf of Mexico, we specifically discuss the effect of spatial and temporal scaling on mangrove distributions in the context of hierarchy theory. This is achieved by recognising spatial variability, and synthesising literature focussed on mangrove distribution changes over three timescales (i.e. the geological and Holocene, contemporary and observational, and projection timescales). We demonstrate the need for cause and effect models, ecological niche models and subsequent projections to move beyond generalisations of mangrove distribution changes and integrate information across a range of spatial and temporal scales. By adequately addressing how local and regional scale factors mediate mangrove distribution changes, we endeavour to add clarity to the ongoing discussion regarding controls on mangrove distribution and projections of mangrove distribution into the twenty-first century.

Spatial and Temporal Hierarchy of Controls on Mangrove Distribution

Spatial and temporal scaling of processes and effects have been recognised relatively recently by ecologists (Wiens 1989), but is the foundation of other disciplines such as geography and earth science. For coastal sedimentary environments, such as those occupied by mangrove, Wright and Thom (1977) recognised the need to integrate ‘process’ geomorphology with ‘historical’ geomorphology, and proposed that this was best achieved with a conceptual model that reflected the observed variation in coastal geomorphology in time and space, a concept that has also been projected for future scenarios (Woodroffe and Murray-Wallace 2012).

For intertidal wetlands, there is growing awareness that scaling should go beyond considering ecological and morphological processes and integrate other physical processes (Friess et al. 2012). For mangrove, a systematic review of the spatial hierarchy of controls on mangrove distribution was undertaken by Duke et al. (1998a) who distinguished processes relevant at global, regional, estuarine and intertidal scales. In this review, estuarine scales related to the longitudinal distribution of mangrove primarily as salinity gradients diminish along estuaries. Intertidal scales related to position within the tidal frame, which is controlled by the interacting effect of tidal inundation, groundwater additions and rainfall run-off on abiotic factors such as salinity and anoxia, and biotic factors such as propagule dispersal, plant productivity and competition. Spatial and temporal scaling effects were also documented by Twilley et al. (1999) with regard to mangrove structure and function. This study recognised different mangrove distribution patterns at four hierarchical scales. These scales correspond to factors influencing the: i) global distribution of mangrove (i.e. temperature); ii) geomorphological settings (as per Thom (1984) and Woodroffe (1992); i.e. river delta, tidal estuary, lagoon and carbonate reef); iii) ecological forest types (as per Lugo and Snedaker (1974); i.e. riverine, fringe, basin, dwarf); and iv) habitat units within forests at the smallest spatial scale. Processes influencing mangrove were also conceptualised along a temporal scale ranging from an hour to a thousand years. For the Brazilian coastline, Schaeffer-Novelli et al. (2000) proposed four spatial units: i) site functional unit of <0.1 ha (representing individuals or small cohorts of trees); ii) patch level functional unit of 0.1–100 ha (broadly divided into fringing and basin types); iii) mangrove settings of 10–100 km (distinguished on the basis of geomorphology and landform type); and iv) coastal domains representing coastal segments of 500–1000 km length defined on the basis of oceanographic characteristics (e.g. wave- or tide-dominated coastline).

Despite general recognition that a range of factors operating at different spatial and temporal scales influence mangrove distribution, there are few studies that have attempted to integrate multiple factors to model either observed changes in mangrove distribution, or project future changes in distribution. Wright and Thom (1977) propose that development of disciplines focussed initially at macro scales and later at process scales may have limited appropriate integration of knowledge between scales. Wiens (1989) hypothesises that ecologists are intuitively interested in processes operating on anthropocentric scales, and bound by experimental design traditions where perceptual range may be limited. While these reasons may hold true, knowledge gaps and limitations in the availability of data at appropriate scales may also be limiting factors (Friess et al. 2012).

Hierarchy theory provides a useful framework for exploring the spatial and temporal dynamics in processes influencing

mangrove distribution and has been used to conceptualise mangrove restoration trajectories (Twilley et al. 1999). Accordingly, an ecosystem is hierarchical when it operates on more than one spatial and temporal scale, or when different process rates are found in the system (O'Neill 1986; Giampietro 1994). Each level of the hierarchy can be regarded as a whole composed of smaller parts and also part of a higher level. For example, an individual mangrove comprises roots, leaves, trunks, flowers, and so on, but also combines with other individuals to comprise a forest. The influence of a process on any level of the hierarchy must also consider the influence of that process on both higher and lower levels. Extrapolation of this concept means that a process influencing a lower mangrove component, for example flowering, will also influence the higher order component, for example forest regeneration. While the interaction of processes at different levels and across multiple scales adds complexity to ecosystem dynamics, it also acts as a system of filters (Giampietro 1994). For example, poor forest regeneration at the patch scale acts as an indicator of flowering and reproduction problems at the individual level and enables exclusion of other processes operating at larger scales, such as a freeze events.

Application of this theory to models of mangrove distribution requires consideration of two hierarchical scales, space and time, and the interaction of processes operating at higher and lower scales to which the model applies. Consideration of the influence of rainfall on mangrove distribution at annual timescales, for example, requires consideration of the influence of decadal and inter-decadal oscillations, seasonal cycles and inter-annual variability, on rainfall patterns. At this scale global climate change is not as relevant as detection of a global trend and would be confounded by significant variability and error that would be attributed to factors operating at lower temporal scales (e.g. decadal variability).

Figure 1 conceptualises the spatial and temporal scale at which i) climatic/meteorological; ii) hydrological; iii) geomorphological/geochemical; and iv) ecophysiological processes operate, and therefore the spatial and temporal scale that these processes influence mangrove distribution. For simplicity these processes have been separated, and are far from an exhaustive list of processes influencing mangrove expansion. Importantly, interactions between processes are pivotal to ecosystem dynamics, causing both negative and positive feedbacks that can lead to self-organisation and stability, or can trigger a cascade of responses leading to ecosystem collapse (Cowell and Thom 1994). Again, using the rainfall example, the effect of annual changes in rainfall can trigger hydrological changes to groundwater availability and sea-level variability at inter-annual timescales, which can influence soil anoxia and salinity, shrink-swell of sediments, rates of organic matter decomposition, nutrient uptake, plant productivity and ultimately influence the health of mangrove individuals. This example has been demonstrated to influence

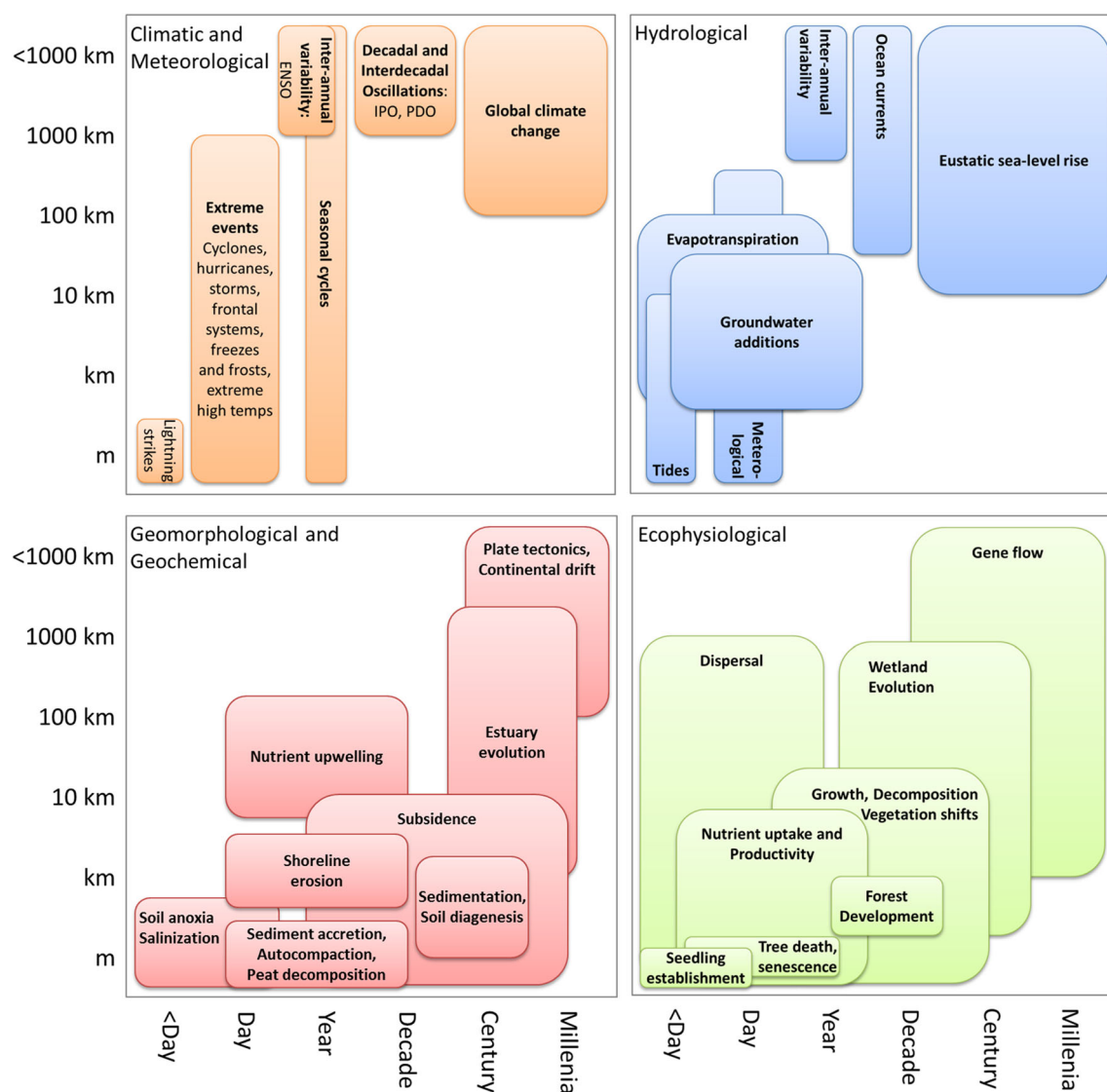


Fig. 1 Spatial and temporal scales over which various climatic and meteorological, hydrological, geomorphological/geochemical and ecophysiological processes operate

mangrove substrate elevation throughout southeastern Australia where periodic El Niño-Southern Oscillation (ENSO) cycles lead to reduced rainfall, depleted groundwater reserves, weakening sea-level rise and shrinkage of wetland surfaces (Rogers et al. 2005; Rogers et al. 2006; Rogers and Saintilan 2009). In this case disentangling the effect of reduced rainfall on ecosystem dynamics cannot be separated from coincident reductions in sea level over the same period (Rogers et al. 2014).

Temporal Patterns in Mangrove Distribution

Coastlines are highly dynamic and coastal scientists are increasingly aware of the changing environment in which mangrove resides. We know from fossilised mangrove pollen in

the palaeontological record that mangroves have adjusted their geographic position in response to plate tectonics and global climatic change. For example, pollen from the mangrove palm (*Nypa fruticans*), which has evolved on intertidal shorelines for at least 75 million years (Schrank 1987; Gee 2001) and is one of the earliest angiosperms assigned a modern genus, has been documented from the Palaeocene (~66–56 Ma) and Eocene (~56–34 Ma) to have a wide distribution (Saenger 1998). Fossil spores have been found in Tasmania, Australia (Pole and Macphail 1996), Southeast England (Chandler 1978), Texas (Westgate and Gee 1990) and Southern France (Plaziat et al. 2001); where the climate currently contrasts significantly with the climate of extant *Nypa* populations of today. This period coincides with the lead into the Palaeocene-Eocene Thermal Maximum (~56 Ma) and continental shift (Gee 2001), and biogeographic records from

fossil pollen may indicate an influence of global warming and plate tectonics on mangrove distribution. ‘Climate cooling’ in the late Eocene, which coincides with the poleward distribution of mangrove pollen during the Eocene, and closure of the Tethys Sea have been hypothesised as the trigger for differentiation between mangrove in the Indo-West Pacific and Atlantic East Pacific (Plaziat and Cavagnetto 1996; Saenger 1998; Ellison et al. 1999). However, even at the largest of timescales, large-scale processes of climate change and plate tectonics do not adequately explain the presence or absence of mangrove from the fossil record. Loss of available habitat may have resulted in periods of mangrove extinction for some locations in the West and South Pacific (Woodroffe and Grindrod 1991; Ellison 2008). The extent of some mangrove species throughout the Miocene (~23–5.3 Ma) in the Pacific is stated to be greater than current distributions. Localised extinctions are reported to have occurred for *Rhizophora* on Enewetok Atoll in the Marshall Islands (Leopold 1969) and *Sonneratia* on Viti Levu in Fiji (Ladd 1965). Sea-level rise and its effect on accommodation space for mangrove is the hypothesised mechanism for these losses. Unfortunately, assertions related to palaeoclimates and continental drift are limited by incomplete knowledge of the prior position of continents and global temperatures, and it is probable that this hypothesis will remain for some time.

Mangrove Distribution Changes over the Holocene

The distribution of mangrove forests of today is not only an artefact of their evolution with respect to plate tectonics, propagule dispersal and a changing climate, but also associated with their response to sea-level changes and available accommodation space. This is most evident from documented changes in mangrove distribution during the Quaternary (~past 2.5 Ma) (Woodroffe and Grindrod 1991), where evidence of mangrove distribution changes come from fossilised mangrove material in cores extracted from sediments deposited since the last marine transgression and during the Holocene (~past 11.7 ka) (Ellison 2008). Fossil material, including pollen and spores, and mangrove roots and peats, at depths below present mangrove distributions provide an indication of the influence of global eustatic sea-level rise on mangrove distribution and its interaction with regional isostasy. This evidence has been used for two related purposes. The first purpose is as an indicator of sea-level position over time. As mangrove peats and roots develop at depths below the soil surface, the imprecise nature of mangrove organic material as a sea-level indicator is typically recognised, and interpretation is undertaken in the context of evidence from other sea-level indicators such as notches, foraminifera, pollen, diatoms and coral dating (see, for example, McKee et al. 2007).

The second purpose draws from geological principles of uniformitarianism, whereby the present is a key to the past

and by extrapolation, the past is a guide to the future (Woodroffe and Murray-Wallace 2012), with fossil evidence providing an indication of mangrove ecosystem response to sea-level rise. This application presumes that sea level and its interaction with sedimentary processes is the primary control on mangrove distribution, with the distribution of mangrove peats typically interpreted within the context of current geomorphology and enhanced with stratigraphic analyses from multiple cores positioned along a tidal/elevation gradient. This approach does not account for the variable response of species to sea-level rise or other physical processes (e.g. temperature). Figure 2 is the Holocene sea-level curve for southeastern Australia (Sloss et al. 2007) and Florida (Milliken et al. 2008), and demonstrates that there is generally reasonable correspondence between the position of mangrove peats, and other sea-level indicators in both regions. As a consequence of the correlation between multiple sea-level indicators over time, it is therefore reasonable to presume that the position of mangrove organic material within Quaternary sediments does provide a qualitative indication of ecosystem response to sea-level rise and relative sea level position, albeit limited by the imprecise nature of additions of organic material to substrates, and changes to organic material volume caused by peat oxidation, decomposition and CO₂ efflux (Middleton and McKee 2001; Lovelock et al. 2011).

Australia

The generalised model of mangrove response to sea-level rise during the Holocene for tide-dominated estuaries in Australia (Woodroffe 1995), initially presented by Woodroffe et al. (1985), and substantiated by evidence of similar sequences of estuary infill for the Adelaide, Daly, Mary, Ord, King, and Hawkesbury Rivers (Thom et al. 1975; Chappell 1993), includes three phases (Woodroffe et al. 1993), though the exact timing of the phases varies between sites on the basis of rates of sediment supply. For the tide-dominated estuaries of northern Australia, these phases largely include the i) transgressive phase of sea-level rise (8000–6800 y BP) when mangrove encroached landward into terrestrial ecosystems; this was followed by the ii) big swamp phase (6800–5300 y BP) when sea level stabilised and mangrove was abundant, establishing throughout the current area of estuarine plains; and iii) sinuous/cuspate phase (since 5300 y BP) when mangrove retreated to meandering channels, point bars and shoals following significant vertical sedimentation during the prior phase.

The response of mangrove on wave-dominated southern coastlines of Australia differs from the northern tide-dominated systems. Broad-scale mangrove colonisation would have been triggered by the development of low-energy environments and substrate development. Precursory to these conditions was the formation of coastal barriers that

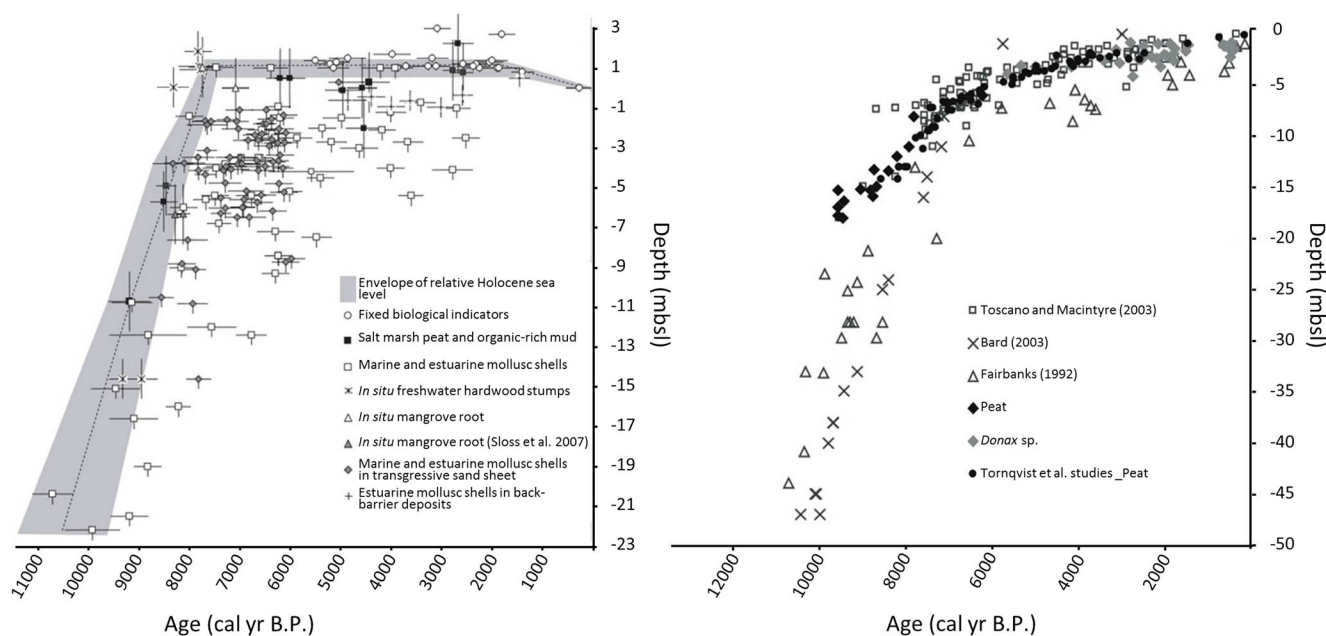


Fig. 2 Holocene sea-level curves from (a) southeastern Australia (as per Sloss et al. 2007) and (b) northern Gulf of Mexico (as per Milliken et al. 2008). Note the correspondence between mangrove peats and other sea level indicators in both regions

bounded estuary entrances of shallow embayments as sea levels stabilised approximately 7000 y BP (Roy et al. 2001). Evidence of mangrove colonisation is primarily based on mangrove root material as pollen of *Avicennia marina* does not preserve well in sediments, unlike the pollen of more tropical species (e.g. *Rhizophora stylosa*). For example, pollen analysis at Minnamurra River (34.63°S, 150.86°E) indicated a transition from a tidal flat to saltmarsh ecosystem between 4300 and 2500 y BP (Jones 1990). Subaerial barrier development in deep embayments became the trigger for mangrove colonisation of low-energy substrates associated with flood-tide and fluvial deltas as sea level stabilised within drowned river valleys. The position of fossil mangrove root material from the region corresponds to Holocene sea-level rise in the region (Saintilan and Hashimoto 1999; Hashimoto et al. 2006; Sloss et al. 2007), with a mangrove stump located near Bulli (34.33°S, 150.91°E) with an elevation of 2.2 m above present mean sea level (PMSL) providing some evidence of a sea level high stand 2 m above PMSL (Jones et al. 1979).

Mainland USA

Parkinson (1989) presented a somewhat similar mangrove response model for carbonate settings in southwest Florida, which also has broad agreement throughout the Caribbean (Evans et al. 1985; Hine et al. 1988; Stapor et al. 1988; Parkinson et al. 1994; McKee 2011). This region is ideal for extracting evidence of the Holocene response of mangrove to sea-level rise as peat building is primarily influenced by biotic processes, rather than abiotic processes such as sediment supply. In this model i) rates of sea-level rise were initially too

rapid for broadscale development of coastal wetlands (15000~7000 y BP); followed by a ii) deepening phase (>3500 y BP) with rapid sea-level rise, shoreline retreat and development of transgressive facies sequences; and a iii) shallowing phase when the rate of sea-level rise was slower and shoreline stabilisation occurred. This was evident by relatively thick peat sequences on mainland shorelines, and when landscapes had a low gradient, mangrove transgressed inland (e.g., Krauss et al. 2011).

Along the northern coastline of the Gulf of Mexico where allochthonous sediment input is the primary source of material for substrate development there remains little evidence of mangrove colonisation over the Holocene (Sherrod and McMillan 1985), despite suitable accommodation space (Twilley et al. 2016). In this region, eradication of mangrove during the cooler conditions of the Pleistocene and early Holocene was proposed, with retreat of mangrove towards warmer shorelines closer to the equator (Sherrod and McMillan 1985). Evidence of mid to late-Holocene mangrove peats from Texas and Louisiana remain elusive from the abundant sediments of the region, despite periods of warm or warmer sea surface temperatures than current temperatures during the late-Holocene (Richey et al. 2007). The late-Holocene was marked by climatic variability, and colonisation from the genetically disparate populations of the east coastline (i.e. Florida) and the west coastline (i.e. Texas) of the Gulf of Mexico (McMillan 1986) may have been periodically halted; this climatic variability was proposed to facilitate natural selection for chill tolerant strains of *Avicennia germinans* (Sherrod and McMillan 1985). Substrate deterioration along the Mississippi River Deltaic Plain following avulsion, river abandonment and decreases in sediment input facilitated submergence and

reworking of delta sediments during the Holocene (Twilley et al. 2016), potentially eroding any evidence of mangrove peats and organic material from delta lobes.

Synthesis of Holocene Distribution Changes

Despite similarities in the response of mangrove to sea-level rise, two primary differences emerge between Holocene mangrove development in Australia and mainland USA. First, the initiation of the transgressive phase in Australia occurred earlier (8000–6800 y BP) than Florida (>3500 y BP), which was followed by a longer period of shoreline stability in Australia when sea levels may have been up to 2 m higher than PMSL. Temporal variation in the timing of mangrove distribution changes can be partly explained by the variation in Holocene sea-level curves between the two regions in response to external glacio-isostatic processes of lithosphere deformation associated with ice sheet growth and melt that causes varying degrees of subsidence or uplift of the basement upon which wetland sediments accumulate and which influence global patterns of relative sea-level rise over the Holocene (Clark et al. 1978; Murray-Wallace and Woodroffe 2014). More specifically, Australia had a longer history of sea-level stability and evidence of a high stand during the Holocene, whilst in Florida the rate of sea-level rise declined over the mid to late-Holocene, but never exhibited an extended period of stability (Cronin 2012) (See Fig. 2).

Second, the influence of other climatic factors on mangrove distribution has varying importance between the two regions. In Australia, divergence of *Avicennia marina* eastern (var. *eucalyptifolia*), western (var. *marina*) and southern (var. *australasica*) varieties appears to have occurred during the Pleistocene (~2.5 Ma - 11.7 ka) when lower sea levels isolated populations (Duke 1995; Duke et al. 1998b; Maguire et al. 2000). Southern populations have more ancient origins (Duke et al. 1998b), with evolution for cold tolerance potentially commencing in the mid-Cretaceous (~100 Ma) (Duke 1995). There is little evidence that Holocene climatic variability influenced mangrove distribution in Australia. Current distributions are likely relicts from warmer climates and unlikely to reflect populations recovering from extreme events during the Holocene; *Avicennia marina* propagule buoyancy is relatively short (Clarke and Myerscough 1991), and markedly less than the buoyancy period for *Rhizophora stylosa* and *Aegiceras corniculatum* (Clarke et al. 2001), significantly limiting dispersal of propagules through constricted entrances of barrier estuaries along this coastline (Clarke 1993). Conversely, climatic variability in the northern Gulf of Mexico throughout the Late Holocene was significant, with sea surface temperatures reported to vary by approximately 3 °C over the past 1400 years (Richey et al. 2007). This variability may have prevented widespread mangrove establishment and the development of chill tolerance, despite available accommodation

space. Propagule dispersal is evidently not a limitation for recovery with observations of propagules of *Rhizophora mangle* and *Avicennia germinans* in beach drift along the northern Gulf Coast (Sherrod and McMillan 1985). Given the propensity for mangrove dispersal throughout the Gulf of Mexico, early written accounts of mangroves in Mississippi and Louisiana in the 1700s and 1800s (Moldenke 1960; Chapman 1975) may correspond to a warming period following the Little Ice Age (~1300–1850) minima.

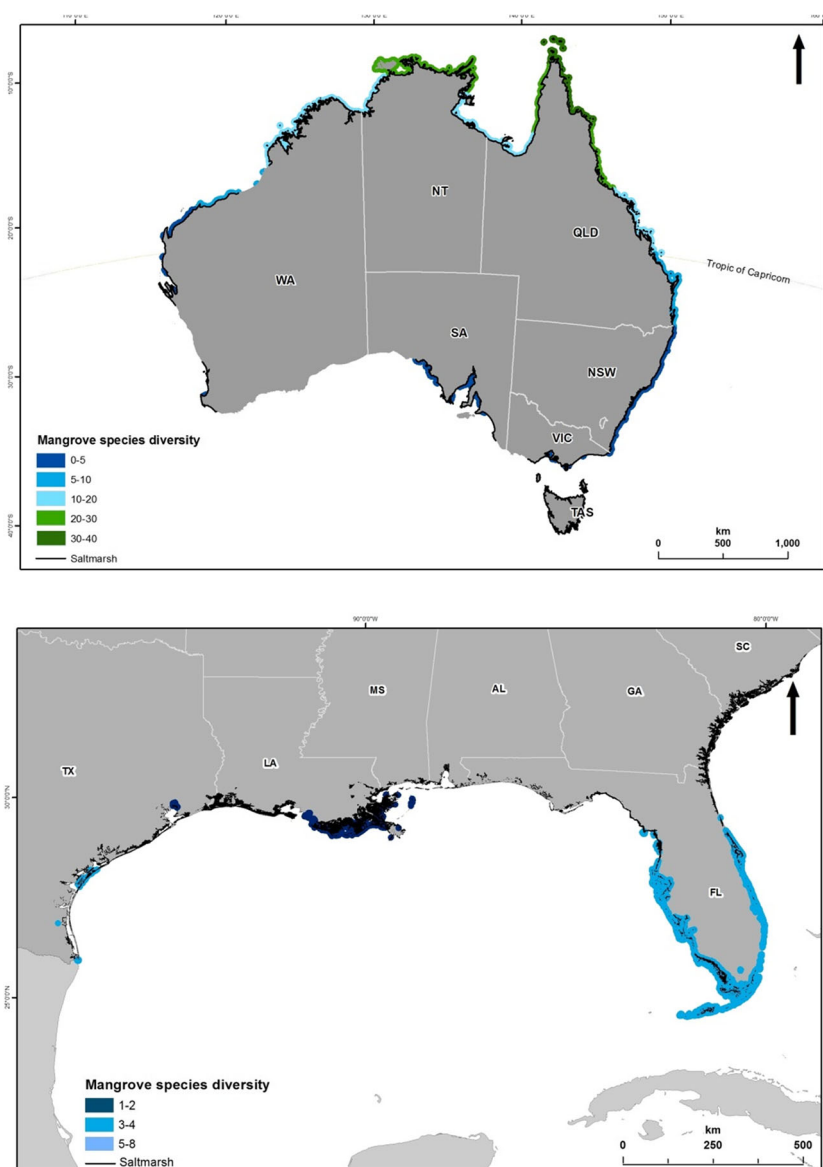
Contemporary Mangrove Distribution Changes

Mangrove dynamics during the Holocene provide the foundation upon which contemporary observations of ecotone dynamics occur. The most pervasive control on mangrove distribution since industrialisation has been the effect of humans directly through land cover conversion and indirectly through the alteration of coastal processes. A recent review documented the decline of mangrove and saltmarsh in Australia, primarily through the conversion of wetlands for flood mitigation purposes and achieved through drainage, ditching and dyking (Rogers et al. 2016). Along the Northern Gulf of Mexico within the influence of the Mississippi River delta, where wetland maintenance is dependent upon supply of sediment to offset deep subsidence, sediment autocompaction and sea-level rise, river management decisions, such as floodplain containment and reductions in sediment supply from upstream damming, have had the greatest influence on rates of wetland loss (Twilley et al. 2016). Excluding the direct influence of humans, observations in both Australia and mainland USA reveal a pattern of mangrove expansion, typically into adjoining saltmarsh (Saintilan et al. 2014).

Australia

Low-energy intertidal zones of coastal mainland Australia are occupied by both mangrove and saltmarsh, and mangrove species diversity typically decreases with increasing latitude, whilst the inverse pattern is evident for saltmarsh (Galloway 1982; Wells 1983; Rogers et al. 2016) (Fig. 3a). Mangrove is absent from the most southern state. Mangrove generally occupies lower elevations of the upper intertidal zone, while saltmarsh is restricted to higher elevations of the upper intertidal; rarely, and in particularly brackish conditions, *Phragmites australis* may seasonally grow as a narrow band in front of mangrove (Fig. 4a). At approximately the Tropic of Capricorn (23°30'S) on both the eastern and western Australian coastlines, rainfall correlates with the relative proportion of mangrove and saltmarsh within the intertidal zone. Where rainfall is high, mangrove occupies a greater proportion of the intertidal and saltmarsh species may be restricted to a narrow zone that merges with adjoining hinterland habitats

Fig. 3 Distribution of saltmarsh and mangrove, including number of mangrove species around the (a) Australian coastline and (b) northern Gulf of Mexico. Mangrove and saltmarsh are restricted to low energy environments and do not occur contiguously along the coastline. Based in information from (a) Duke (2006) and Rogers et al. (2016); and (b) Giri et al. (2011b), IUCN Red List (2017) and Mcowen et al. (2017)



or freshwater wetlands (Bucher and Saenger 1994). In the intertidal zone of arid northwestern Australia, mangrove habitats give way to expansive salt flats dominated by cyanobacterial mats (Lovelock et al. 2010).

The southern coastlines of Australia are particularly suited for determining controls on mangrove distribution both within and between estuaries; here mangrove, particularly *Avicennia marina*, has occupied the intertidal zone for thousands of years (as discussed above) and theoretically has had sufficient time following 7000 y of relative sea-level stability (See Fig. 2), to occupy their fundamental niche following major disruptions during the Quaternary period (as proposed by Woodroffe and Grindrod 1991). Geomorphic constraints on propagule dispersal and availability of suitable habitat are significant controls on the distribution of mangrove, particularly between

estuaries where estuary entrance closure and associated small tidal prism reduce the available habitat for mangrove establishment and growth (Roy et al. 2001). Known regionally as intermittently closed or open lakes and lagoons, or ICOLLs, intermittent entrance closure of estuaries has been associated with restricted mangrove distribution in Australia, Brazil and South Africa (Haines et al. 2006; Adams et al. 2016; Saintilan et al. 2016). In addition to reduced habitat availability in the absence of notable tides, dispersal of propagules through intermittent estuary entrances may be limited, periodic flushing of salts which is essential for mangrove survival is diminished, and/or soils become anoxic when water levels are elevated following catchment rainfall. Lower air temperatures in southern Australia minimise the influence of evapotranspiration on soil physiochemical conditions; soil salinity and waterlogging

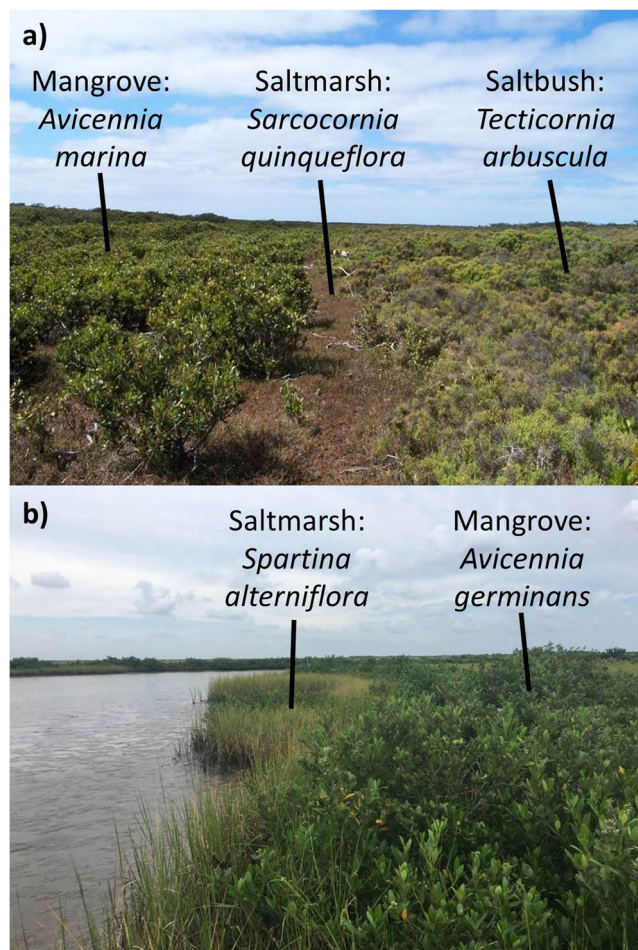


Fig. 4 Zonation of mangrove and saltmarsh at (a) Westernport Bay, southeastern Australia and (b) Port Fourchon, Louisiana. Lower elevations shown on left of each image, with the *Avicennia marina* typically positioned at lower elevations than saltmarsh in (a) southeastern Australia, and *Spartina alterniflora* typically positioned at lower elevations than *Avicennia germinans* in (b) Louisiana

controlled by position in the tidal frame appears to have a greater influence on propagule establishment and survival (Clarke and Myerscough 1993).

The southeastern coastline supports approximately 10 mangrove species (Duke 2006). Of those with the most southerly distribution, *Rhizophora stylosa* and *Bruguiera gymnorhiza* (Wilson 2009) are reported to be increasing latitudinal range (Wilson and Saintilan 2012). Frosts or freezes are absent from the coastline near their southern limit and expansion correlates with a pattern of rising temperatures over the twentieth century (Nicholls and Collins 2006). On the basis of leaf phenology and longevity, *Rhizophora stylosa* has potentially not realised its thermally-defined niche with little difference in leaf phenology between southerly individuals and tropical counterparts (Wilson and Saintilan 2012). If true, and on the basis of suitable mangrove habitat within estuaries immediately south of the current extent, biotic factors may be an important determinant on range expansion

between estuaries. Clarke et al. (2001) found a negative correlation between patterns of adult distribution of 14 mangrove species at macro-scales and propagule dispersal properties, proposing that factors influencing establishment may be a better predictor of adult distribution. Salinity did not limit shoot initiation or growth of *Rhizophora stylosa* (Clarke et al. 2001), but light may limit its establishment and growth, particularly at lower elevations where *Rhizophora stylosa* co-dominates with *Avicennia marina* (Smith III 1987), a species known for rapidly filling a regeneration niche (Clarke and Allaway 1993).

Aegiceras corniculatum does not occur south of Lake Merrimbula (36.88°S, 149.90°E); its current range and intertidal distribution have remained relatively stable over the observational record, unlike *Avicennia marina* (Clarke 1995). Investment into reproduction is greater in *Avicennia* than *Aegiceras*, evident by larger propagules; fruit predation is higher in *Aegiceras* than *Avicennia*; and the establishment phase is longer for *Aegiceras*, thereby increasing opportunities for herbivory in early life stages (Clarke et al. 2001). Sinking of propagules at low salinities partly explains the zonation of *Aegiceras*, which is known as the River Mangrove as it favours lower salinities occurring in the upper estuary and across the intertidal zone when run-off or groundwater contributions are high (Clarke 1995). Zonation is also facilitated by growth and water use efficiencies at lower salinities (Clarke and Hannon 1970; Ball and Farquhar 1984; Ball 1988). The absence of *Aegiceras corniculatum* from more southerly estuaries is not surprising given the dominance of ICOLLs in southern NSW (Haines 2006) with intermittently open entrances, and differences in dispersal and establishment properties of *Aegiceras* and *Avicennia* (Smith III 1987; Clarke and Allaway 1993).

Avicennia marina var. *australasica* occupies the intertidal zone of temperate southeastern Australia and New Zealand; other varieties (var. *marina* and var. *eucalyptifolia*) are distributed along tropical coastlines (Duke 1991). This variety is particularly noted for intertidal expansion over the past century (Saintilan and Williams 1999) and cold tolerance (Stuart et al. 2007). The close proximity of the Great Dividing Range to the coast of southeastern Australia and the ensuing coastal escarpment has afforded some protection from cold fronts that move across the continent from the Southern Ocean. Consequently, frosts as they are regionally known (viz. freezes), are not severe and are relatively short in duration. The absence of *Avicennia marina* from Tasmania implies cold limitation; however, success of experimental plantings in Tasmania adds some credibility to the noted cold tolerance of this variety (noted in Woodroffe and Grindrod 1991). Consequently, there is significant evidence of a dispersal barrier, namely currents through Bass Strait, limiting establishment of mangrove on northern shorelines of Tasmania. Both mangrove and saltmarsh are virtually absent from the rocky

coastline of the Great Australian Bight, with saltmarsh restricted to salt spray affected bluffs on cliffs and rocky shorelines (Saintilan and Rogers 2013). The tide-dominated estuaries near Adelaide, South Australia, do afford some protection from wave-energy from the Southern Ocean, and dense *Avicennia marina* occupy the intertidal zone between mid-tidal levels and spring high tide level, merging with saltmarsh dominated by succulents and saltbush (Gostin et al. 1984). These mangroves are expanding in the hypersaline conditions of these inverse estuaries (Burton 1982; Nunes and Lennon 1986). Similarly, mangrove and saltmarsh occupy low-energy shorelines of embayments along the southern coastline of Victoria. Corner Inlet, Victoria supports mangrove at the highest latitude of both the northern and southern hemispheres. While being shorter in stature than their tropical counterparts, their height is taller than the 0.5–0.8 m reported by Bridgewater and Cresswell (1999), with heights now ranging to 3 m (*unpublished data.*).

Multiple drivers were initially proposed for the observed intertidal expansion of mangrove in southeastern Australia in the twentieth century. These included precipitation in the latter part of the twentieth century, recovery of areas previously used for agricultural purposes, altered tidal regimes associated with engineering works within estuaries or sea-level rise, increased sedimentation and associated nutrients following catchment clearing, and subsidence of intertidal surfaces (Saintilan and Williams 1999). Nutrient addition has been precluded from facilitating mangrove establishment based on field experimentation, with carbohydrates in cotyledons purported to sustain mangrove in their first year (Saintilan 2003). Rates of mangrove expansion as related to relative sea-level rise, which included both sea-level rise at the nearest tide gauge and subsidence of the saltmarsh surface, have been established (Rogers et al. 2006). Expansion has also been correlated with increasing rainfall (Eslami-Andargoli et al. 2009). Regional rainfall and relative sea-level variation both correlate with broader climatic perturbations associated with ENSO, which confounds analyses aimed at distinguishing the influence of rainfall and sea-level rise on mangrove expansion (Rogers et al. 2014). This has been further validated by a nation-wide analysis of sea level trends and variability that demonstrated a strong influence of ENSO on sea level (White et al. 2014). Groundwater may also be a significant control on mangrove distribution with evidence that mangrove use groundwater as an alternative water source (Lovelock et al. 2017), mangrove distribution is influenced by fresh groundwater seepage (Semeniuk 1983), and mangrove and saltmarsh surface elevations decrease when groundwater is depleted (Rogers and Saintilan 2009).

Only one species of mangrove occupies the temperate intertidal zone of Western Australia. *Avicennia marina* var. *marina* (Duke 1991) is restricted to the intertidal zone of the Abrolhos Islands and Leschenault Inlet, and are regarded to be

outliers from distributions during the Holocene (Woodroffe and Grindrod 1991). Dispersal of mangrove from these outlier populations may be limited by geomorphic constraints on the availability of suitable habitat along the wave dominated coastline of Western Australia. There are few estuaries between Shark Bay (25.98°S, 113.78°E) and Hutt Lagoon (28.16°S, 114.25°E); and these estuaries have relatively steep slopes, and little suitable habitat for mangrove establishment. Mangroves occur in all estuaries between Hutt Lagoon and Tobys Inlet (33.64°S, 115.16°E) (Geosciences Australia 2011); but like southeastern Australia, estuaries of southwestern Australia undergo intermittent closure, and may restrict mangrove establishment in estuaries south of Bunbury (33.33°S, 115.64°E).

In Northern Australia, saltwater intrusion and mangrove expansion have been associated with drier than average monsoonal conditions, low-intensity cyclonic events and above-average ocean water levels (Knighton et al. 1991; Mulrennan and Woodroffe 1998; Winn et al. 2006), and demonstrate the overarching influence of climatic perturbations on local climate variables. Remote sensing of mangrove shorelines in the Gulf of Carpentaria indicated that *Avicennia marina* was expanding in a seaward direction where sedimentary conditions were favourable, and was accompanied by seaward expansion of *Rhizophora stylosa* into *Avicennia marina* forests (Asbridge et al. 2016). The cause of the resulting increase in mangrove width along the coast was correlated with increasing rainfall, flooding and sea-level rise in the region, with the combined effect being the development of mudflats and increasing inundation. Recent widespread dieback in Northern Australia may indicate that mangrove have an upper temperature threshold (Duke et al. 2017). The effect of high temperatures on photosynthetic carbon assimilation has been established for Australian mangroves (Clough et al. 1982; Andrews et al. 1984; Ball 1988); however, this dieback occurred at a time of high temperatures, lower sea levels and a rainfall deficit (Lucas et al., in press). Consequently, thermal stress has been suggested as one of a suite of possible causes (Duke et al. 2017). Interestingly, the recent dieback appears to have set-back the pattern of mangrove expansion that was evident in the decade prior (Lucas et al. 2018). The effect of thermal stress on mangrove is likely limited to tropical and arid coastlines, and is projected to have little effect on mangrove survival on temperate mangrove of southeastern Australia.

Elevated atmospheric CO₂ concentrations may enhance plant growth and water use efficiency, with C3 plants including mangrove and many saltmarsh species, increasing growth rates in response to CO₂ enrichment. In contrast, plants using the C4 photosynthetic pathway, which includes some saltmarsh species, are typically less responsive to CO₂ (McKee et al. 2012). Ecophysiological studies focussed on Australian mangrove species have considered the effect of

CO₂, salinity and humidity on the performance of two mangrove species (*Rhizophora stylosa* and *R. apiculata*), demonstrating negative feedbacks between growth and carbon dioxide concentrations that are facilitated by improved water use efficiency (Ball et al. 1997). These feedbacks were improved under enhanced humidity conditions, but not under conditions when salinity limited growth, indicating that elevated CO₂ may not alter the salt tolerance of species, but could influence competition of species along salinity and aridity gradients. For species occurring near the latitudinal limit in southeastern Australia (*Avicennia marina* and *Aegiceras corniculatum*), stomatal conductance and photosynthetic capacity decreased under conditions of ambient atmospheric carbon dioxide concentration, increasing salinity and decreasing humidity (Ball et al. 1997). As mangroves are C3 plants and may respond favourably to elevated CO₂, it can be inferred that declines in photosynthetic capacity occurring due to salinity changes with sea-level rise or humidity changes with altered air temperatures may be ameliorated by enhanced growth under conditions of elevated CO₂. The linkages between elevated atmospheric CO₂, enhanced mangrove growth and mangrove expansion and saltwater intrusion in Australia have been inferred, but are yet to be clearly distinguished (Williamson et al. 2011; Saintilan and Rogers 2015).

Mainland USA

The intertidal zone of the northern Gulf of Mexico (i.e. mainland USA) primarily supports saltmarsh, on the east coast largely dominated by *Spartina alterniflora* as a lower marsh dominant, with other marsh species increasing in dominance along the western Gulf of Mexico (Texas) including *Batis maritima*, *Sporobolus virginicus* and *Sesuvium portulacastrum* (Jones et al. 2016). Only three true mangrove species occur along the shores of the US mainland: *Avicennia germinans*, *Rhizophora mangle* and *Laguncularia racemosa*, and their historic distribution has fluctuated along the shorelines of the southern US states (Fig. 3b). In the Eocene (approximately 45 Ma), mangrove pollen records indicate mangrove distribution as far north as the state of Tennessee, but certainly mangroves commonly occurred in the states of Alabama, Mississippi, Louisiana and Texas corresponding to warmer climates and higher sea levels (Sherrod and McMillan 1985). The pollen record became more obscure after the Eocene, but re-emerges in the mid-Holocene (~3500 y BP). As Caribbean mangroves at this time were limited only to equatorial regions this suggests eradication of mangroves from progressively colder temperatures before and into the Pleistocene (Sherrod and McMillan 1985). A post-Pleistocene recolonisation period initiated as the climate warmed. Accordingly, *Avicennia* was back in Texas by 1853 (Sherrod and McMillan 1985), whilst herbarium specimens of *avicennia americana* (syn. *A. germinans*) were collected in

1812 from Louisiana (McKee and Vervaeke 2018). Since this time, the recent historical northern limit for mangrove in eastern North America is believed to be near 30°N (Savage 1972), approximating a region near St Augustine, Florida (29.90°N, 81.31°W). The northern distribution of each mangrove species has been documented for the eastern coastline of Florida (Williams et al. 2014), with *A. germinans* having the most northerly distribution in 2013. The most northerly individual for each species was located between 26 and 67 km farther north than a prior assessment in 2007. Extreme freezes during the 1980s have been documented as a significant contributor to declines in mangroves throughout the northern Gulf of Mexico (McMillan 1986; Watson 1986; Montague and Wiegert 1990; Montague and Odum 1997), which are now recovering.

Controlled experiments indicate that freeze-induced embolism and its influence on hydraulic conductivity may alter distribution of mangrove at larger spatial scales, with interspecific differences mediated by xylem vessel architecture, and intraspecific differences mediated by genetic variability, trait evolution and/or phenotypic plasticity (Markley et al. 1982; Stuart et al. 2007; Madrid et al. 2014; Cook-Patton et al. 2015). Analyses of intraspecific variation along latitudinal gradients indicate that individuals near the range limit exhibit greater resilience to chilling than more equatorial populations (Cook-Patton et al. 2015). Vessel architecture also varies with soil salinity, and the combined influence of both temperature and salinity on vessel architecture, conductance capacity and carbon fixation potential may contribute to lower canopy heights where temperature and/or salinity approach tolerance thresholds (Madrid et al. 2014). Temperature thresholds on performance reportedly range between -2 and -8 °C for all three species (Osland et al. 2013; Cavanaugh et al. 2014; Osland et al. 2017), but there are important local-scale interactions embedded in this response related to saltmarsh species being replaced, and interactions between salinity and seedling age (Coldren and Proffitt 2017). *A. germinans* has been consistently found to be the most cold tolerant; however, comparative experiments with *A. marina* indicate significantly greater cold tolerance in the latter species, which does not occur in the USA (Stuart et al. 2007). There is reported variation in the tolerance of *Rhizophora* and *Laguncularia* that may relate to life stage of the plants (Markley et al. 1982; Cavanaugh et al. 2015; Cook-Patton et al. 2015). To this end, chilling tolerance has been found to vary with life stage. Greater cold tolerance of *A. germinans* at the dispersal stage, as opposed to stranded and seedling stages, may facilitate landward expansion of mangrove (Pickens and Hester 2011). Freeze damage is reportedly lowest for tall *A. germinans* and seedlings compared to short trees, whilst recovery following a freeze was highest for tall *A. germinans* (Osland et al. 2015).

Expansion of mangrove throughout mainland USA has generally been associated with the absence of extreme freezes

in Florida (Stevens et al. 2006; Krauss et al. 2011; Cavanaugh et al. 2014; Rodriguez et al. 2016), Louisiana (Patterson and Mendelssohn 1991; Perry and Mendelssohn 2009; Osland et al. 2017) and Texas (Comeaux et al. 2012; Bianchi et al. 2013; Armitage et al. 2015). However, factors contributing to expansion have been difficult to differentiate due to the overarching influence of recovery following freeze events. Analyses of contemporary mangrove distribution dynamics in southern Florida, where studies have identified no discernible change in the pattern of freeze events throughout the region (Duever et al. 1994), provide the opportunity to control for extreme freeze events and explore the influence of other factors on mangrove distribution dynamics. Landward expansion of mangrove at various sites in southern Florida has been related to drainage of freshwater wetlands, diversion of run-off, changes in localised rainfall, sea-level rise, and factors facilitating propagule dispersal such as construction of new waterways and mosquito ditching (Teas et al. 1976; Ball 1980; Krauss et al. 2011; Smith III et al. 2013); declines in landward ecosystems have also been associated with sea-level rise (Ross et al. 1994; Doyle et al. 2010). Analysis of fringing mangrove extent at Tampa Bay (27.76°N, 82.54°W) in the 1870s from historical navigation maps indicate almost complete replacement of saltmarsh by mangrove. This expansion of mangrove attests to environmental changes operating at least over a century, with sea-level rise and freshwater withdrawal implicated (Raabe et al. 2012). The distribution of peats and marls underlying expanding mangrove forests at Biscayne Bay (25.57°N, 80.23°W) imply that recent landward expansion does not represent recovery to a prior extent, at least in recent history (Ball 1980). Unfortunately evidence of prior mangrove distribution in the greater Everglades region of south Florida may have been disturbed with peats largely oxidised or burned (McCally 1999).

Analyses of saltmarsh loss have also been associated with mangrove expansion following decades of relatively mild winters in Texas; however, conversion of saltmarsh to tidal flats or open water attests to the influence of sea-level rise on both mangrove establishment and saltmarsh conversion (Armitage et al. 2015). A more comprehensive approach incorporating multiple controls of mangrove extent near the northern limit of Florida proposed that 95% of variation in mangrove extent over time was explained by temperature, precipitation, sea level and time (Cavanaugh et al. 2015). While sea level only marginally improved model efficacy, the interacting effect of intertidal geomorphology and sea-level rise was not adequately incorporated within the model, which could be simply achieved by incorporating elevation within the model, or more accurately achieved with a hydrodynamic model. Just as most sea-level rise models have historically excluded climatic variables, most climatic models exclude sea-level rise and natural dispersal barriers, limiting inference of both model types.

As mangrove extent is periodically set-back by freezes, many studies have correlated increasing mangrove extent with potential drivers, particularly temperature. By extrapolation they have also correlated rates of poleward expansion and threshold temperature tolerances based on current distribution. For example, Williams et al. (2014) report hypothetical rates of poleward expansion, which presumes that absence of extreme freeze events are the primary determinant of poleward mangrove expansion. Cavanaugh et al. (2014) identify temperature related ecological thresholds, specifically reduction in frequency of days colder than -4°C , which corresponds to historical estimates (Davis 1940). Similarly, Osland et al. (2013) propose a minimum temperature threshold of -8.9°C for mangrove presence/absence, and -7°C for mangrove dominance. These temperature threshold estimates presume that mangrove currently occupy their fundamental niche; an assumption that has been questioned by Giri and Long (2014) who propose that mangrove expansion is not poleward in direction, but constitutes recovery following freezing temperatures in 1983 and 1989. Mangrove expansion along the eastern coastline is reportedly occurring within the historical northernmost limit, in this case documented using ~ 35 years of satellite imagery and occurring at a higher latitude in Louisiana in 1980 (Giri and Long 2016). Mapping of mangrove dynamics in this region attests to the interacting affect of multiple drivers upon mangrove distribution, with freezes causing dieback, milder temperatures associated with recovery, and subsidence and erosion variably associated with mangrove expansion and contraction dynamics between 1983 and 2010 in Louisiana (Giri et al. 2011a). To this list of possible causes could be added the early hypothesis of Penfound and Hathaway (1938), who documented dense mangrove stands near the coast of up to 7.6 m height, that have higher elevation and soil salinities than adjoining saltmarsh, and would readily invade lower communities except for annual marsh fires (but see Smith III et al. 2013). However, absence of fires in the subsequent years would preclude this hypothesis. Further evidence from the historical record and additional data sources, such as high-resolution elevation data (e.g. LiDAR), is required to confirm controls on mangrove establishment where distribution fluctuates over confounding micro-topographies and micro-climates.

At small spatial scales, mangrove establishment is strongly influenced by factors that influence the salinity of surface and soil water, and the degree of soil saturation. For example, in greenhouse growth studies seedlings of *A. germinans* exhibited favourable growth response under low to moderate levels of stress or disturbance associated with salinity regimes (optimal at 24–48 ppt), sediment burial (optimal at 0–10 cm), and inundation depth (optimal at 15–30 cm) (Alleman and Hester 2011). In a field-based study measurements of basal increments indicated that growth correlated with hydroperiod-mediated phosphorus subsidies for all species (Krauss et al.

2006). The competitive growth response of stunted *A. germinans* is reflected in its higher water use efficiency and lower water demand at high salinities compared to *Spartina alterniflora* on at least one Louisiana site (Krauss et al. 2014). There is now increasing recognition of the role of biotic factors in mediating mangrove expansion, including propagule dispersal (Ball 1980), trapping of propagules by saltmarsh vegetation (Lewis and Dunstan 1975; Stevens et al. 2006; Peterson and Bell 2012), interspecific competition (Ball 1980; Patterson et al. 1993; McKee and Rooth 2008; Guo et al. 2013), and precocious reproduction (Dangremond and Feller 2016). More complex multifactorial effects between abiotic and biotic factors are also being recognised including CO₂, nitrogen enrichment, facilitation, and differential warming influences in the mediation of competition between *Spartina* and *A. germinans* (Farnsworth et al. 1996; McKee and Rooth 2008).

Mangrove establishment in expanding zones has been conceptualised by Ball (1980) who proposed that seedlings will colonise any area that is available, providing propagules can be transported to the location and basic requirements are met (e.g. soil moisture prevents propagule desiccation). As reserves in cotyledons temporarily sustain establishment and development, species composition of seedlings in expanding areas does not reflect physiological tolerance to edaphic conditions or the role of competition; these factors become critical as individuals mature and competition for in situ resources becomes important.

Synthesis of Contemporary Distribution Changes

Studies in both regions that correlate mangrove expansion with other variables attest to a large scale pattern of mangrove expansion. While this expansion is currently synchronous in both regions, differences emerge that reflect species evolution over longer-timescales and the interacting effect of region-specific processes. Time-series mapping from aerial or satellite imagery indicates that expansion is occurring in three directions: i) poleward or latitudinal expansion; ii) along estuaries (sometimes referred to as longitudinal expansion along eastern and western coastlines); and iii) across the intertidal zone.

Poleward Expansion Only limited evidence exists on the expansion of mangrove in the estuaries of southeastern Australia; *Rhizophora stylosa* and *Bruguiera gymnorhiza* may be expanding, *Aegiceras corniculatum* distribution is reportedly stable, while latitudinal expansion of *Avicennia marina* is limited by the geographic barrier of Bass Strait. Poleward expansion of mangrove has received considerably more attention in the mainland USA, particularly in the states of Florida, Texas and Louisiana. In this region, freezes are associated with climatic oscillations occurring in the North

Atlantic (North Atlantic Oscillation) and the Pacific (ENSO) (Downton and Miller 1993), operating over decadal time-scales and causing periodic physical damage. Variation in these atmospheric circulation patterns and the ensuing ecological effects on mangrove distribution are poorly described using remote sensing techniques that have a relatively short temporal range (typically less than 25 years of data collection), as they do not adequately capture mangrove response to the full variation in the intensity and frequency of freeze events. In addition, studies that establish correlations based on patchy mangrove distributions may be more accurately explained by processes operating at smaller spatial scales, such as micro-climatic variability, propagule dispersal and nutrient availability. Expansion of mangrove is currently occurring within the range of mangrove distribution of the early 1980s and likely represent recovery following dieback of mangrove, rather than northerly expansion beyond their historic range limits. When analysing temporal changes in species distribution it is important to distinguish between the range of environmental conditions in which a species establishes and survives, commonly identified as the fundamental niche, and the range of conditions in which a species currently occurs, defined as the realised niche. Based on the stochastic nature of freezes in North America, the current northern range of mangrove is likely to represent a realised niche, as distribution within the fundamental niche is periodically delimited by stochastic freeze events. Expansion of mangrove in mainland USA is now synchronous and occurring at all northern limits in Florida, Louisiana and Texas. This synchronicity in expansion relates to the large spatial extent of freeze damage to mangroves, and not to a single process operating consistently across mainland USA to facilitate mangrove establishment. Rather, recent mangrove expansion is likely related to processes operating over smaller spatial scales, such as hydroperiod, nutrient availability, competition, and propagule dispersal, enabling the realised niche to expand until mangrove occupy their fundamental niche. Relationships between the area of mangrove and time since freeze events are evident (Cavanaugh et al. 2014; Osland et al. 2017), but rarely recognise that processes contributing to mangrove establishment are also time dependent. Until mangrove has fully recovered and occupied their fundamental niche, identifying processes other than freezes controlling mangrove distribution over longer timescales (e.g. climate change effects on temperature and sea-level rise) will be masked by variability occurring over shorter timescales, and more specifically be influenced by episodic dieback and recovery following the freeze.

Along Estuaries Expansion of mangrove along estuaries, based on written, cartographic and pictorial materials from the Sydney region, indicates that mangrove was likely absent from the upper Parramatta River from the time of European occupation in 1788, expanding until the 1940s when aerial

photography indicates mangrove extent began to be delimited by increasing urbanisation and industrialisation (McLoughlin 2000). Similar expansion of mangrove along the Hawkesbury River has been observed in response to increasing siltation up until the 1940s–60s when extensive mangrove areas were converted to other land uses (Recher et al. 1993). From this time mangrove proliferation has largely occurred across the intertidal zone (Saintilan and Williams 1999). The New South Wales (NSW) Government has mapped the upstream tidal and mangrove limit in estuaries along NSW in an effort to establish a benchmark against which subsequent changes can be monitored (DNR 2006). This pattern of mangrove expansion along the wave-dominated estuaries of southeastern Australia may be hydrologically similar to mangrove expansion associated with saltwater intrusion in the tide-dominated rivers of Northern Australia (Knighton et al. 1991; Mulrennan and Woodroffe 1998; Winn et al. 2006). Estuarine expansion of mangrove in the mainland USA is masked by mangrove recovery dynamics following prior freeze events, and the north-south orientation of estuaries behind shore parallel barrier deposits and their connection to form the intra-coastal waterway along the Atlantic coastline of Florida.

Across the Intertidal Where the influence of frost or freezes is reduced, studies of mangrove expansion across the intertidal zone in both regions have been linked to a range of factors. Topographic control on expansion is evident in southeastern Australia (Rogers 2004) and southern Florida, attesting to an influence of hydroperiod on mangrove distribution. Post-freeze mangrove recovery exhibits a similar topographic pattern in some locations, reflecting a local scale niche defined by accommodation space or hydroperiod (see for example Armitage et al. 2015; Osland et al. 2017). Irrespective of the driver of change, the underlying affect on an individual mangrove is typically hypothesised to be either a decrease in soil salinity and/or anaerobic conditions associated with enhanced hydroperiod. Laboratory and field experiments support both hypotheses (Krauss et al. 2006; Alleman and Hester 2011). In Florida, factors operating at larger spatial scales that influence hydroperiod are typically implicated, such as sea-level rise; however, other site-specific factors operating at smaller spatial scales may also influence rates of mangrove expansion, including drainage of wetlands, forest fires and morphology of the intertidal zone. The large spatial scale at which expansion is occurring in southeastern Australia has also focussed attention upon climatic-related drivers such as rainfall and sea-level rise, with local factors proposed to mediate these drivers. Disentangling the coincident nature of drivers of mangrove distribution is difficult in both regions. Consequently studies that correlate mangrove distribution changes with possible drivers will fail to clearly identify a driver of current mangrove distribution changes. Field, laboratory or greenhouse based analyses at smaller spatial scales will provide essential

information about the response of mangrove to various drivers. Analyses of this type are currently focussed on temperature thresholds in mainland USA (McMillan and Sherrod 1986; Pickens and Hester 2011), and tolerance to salinity and dispersal properties in southeastern Australia (Clarke and Myerscough 1991; Clarke 1993; Clarke and Allaway 1993).

Projections

Projections of mangrove distribution at a range of spatial scales have been prompted by management needs and a desire to improve ecosystem outcomes under a changing climate. Focussing primarily upon applying climate change projections at the landscape scale, these projections often apply scenarios of sea-level rise and temperature increase to project mangrove distribution or persistence. At the local or individual-scale, mangrove models focus on resource, regulator, and hydroperiod gradients under a range of disturbances (e.g. hurricanes, lightning strikes) to predict stand development and identify sensitive drivers (e.g. nutrient concentrations) for further experimental tests (see for example Berger et al. 2008; Twilley and Rivera-Monroy 2009).

Australia

As there is little evidence of thermal control on mangrove extent in southeastern Australia, projections in this region have focused on changes occurring across the intertidal zone associated with sea-level rise. The exact response of mangrove and saltmarsh to sea-level rise is dependent upon local topography, sediment sources, rates of sediment supply, and the rate of sea-level rise (Woodroffe 1990). As rates of sediment supply and subsequent vertical accretion are proportional to accommodation space or hydroperiod, empirical data indicate that sedimentation is always higher in mangrove compared to adjacent saltmarsh in southeastern Australia (Rogers et al. 2006), translating to greater gain in surface elevation and improved capacity to adjust to sea-level rise. Analyses of carbon addition as mangrove encroaches upon saltmarsh demonstrates the greater capacity of mangrove to add organic material to the substrates (Kelleway et al. 2016). The enhanced capacity of mangrove to accumulate organic and mineral sediments as the sea rises has been conceptualised to have negative consequences for saltmarsh (Vanderzee 1988; Saintilan and Rogers 2013; Kelleway et al. 2016). This may be further assisted by enhanced assimilation of atmospheric CO₂ that improves growth and access to below-ground water resources (Saintilan and Rogers 2015).

Landscape-scale projections of mangrove-saltmarsh distribution based on empirical data that incorporate feedbacks between hydroperiod, mineral and organic matter additions, and sea-level rise have been developed using readily available models such as the ‘sea level affecting marshes model’

(Akumu et al. 2011; Traill et al. 2011; Runting et al. 2016; Mogensen and Rogers 2018) or empirically driven numerical models (Oliver et al. 2012; Rogers et al. 2012, 2013; Mogensen and Rogers 2018). Both modelling approaches extrapolate elevation and distance dependent relationships between surface elevation gain and sea-level rise. In all cases, these models emphasise the capacity of mangrove and saltmarsh to adjust to low-to-moderate rates of sea-level rise, particularly when landward barriers (e.g. infrastructure, steep topography, levees) to expansion across adjacent low-lying land are absent; this capacity appears to be exhausted under high rates of sea-level rise that approach or exceed 9 mm/y. With the exception of Rogers et al. (2013) which incorporated levee management in scenarios, model scenarios have focussed on sea-level rise alone. A three model comparison of Oliver et al. (2012), SLAMM and an adjusted version of Temmerman et al. (2003) demonstrated the influence that model selection and parameterisation has on projections (Mogensen and Rogers 2018). Few studies of the effect of sea-level rise have been undertaken at larger spatial scales; as modelling approaches that more accurately capture feedbacks between inundation and elevation adjustment are difficult to develop and apply at larger spatial scales, in all instances a relatively simple bath-fill approach was used to project an upper threshold of inundation (DCC 2009; Boon et al. 2011).

Mainland USA

Along much of the northern Gulf of Mexico where mangrove and saltmarsh occur sympatrically, mangrove is positioned at higher elevations along creek banks where hydroperiod is reduced, and *Spartina alterniflora* is positioned at lower elevations with elevated hydroperiods either where bank gradients provide suitable accommodation space or in the interior of the marsh (Patterson et al. 1997, Fig. 4b). Higher sulphide concentrations associated with lower elevations in *Spartina* were hypothesised to limit *Avicennia* propagule establishment (Patterson and Mendelssohn 1991), and subsequent seedling and propagule plantation experiments confirmed reduced seedling growth rates (Patterson et al. 1993) and greater propagule herbivory and decay at lower elevations (Patterson et al. 1997). Loss-on-ignition measurements from soil collected under adjacent marsh and mangrove sites in Texas indicate greater organic matter contributions and carbon components within the soil volume at the generally lower elevations occupied by *Spartina* than higher elevations occupied by mangrove (Comeaux et al. 2012). Despite slight elevation differences between mangrove and *Spartina*, vertical accretion and surface elevation change measures to date are trend-free overall (Perry and Mendelssohn 2009; McKee and Vervaeke 2018). As mangrove are still recovering or developing after prior freezes, soil carbon may not yet be saturated in freeze affected

areas (Henry and Twilley 2013; Yando et al. 2016). However, this relationship is not consistent with mangrove carbon storage reportedly higher along a gradient of mangrove encroachment in Florida (Doughty et al. 2016). The pattern of carbon saturation beneath mangrove and saltmarsh is evidently site dependent and may be offset by rates of mineral sediment supply. This complexity and the overarching influence of freezes on mangrove distribution in mainland USA have resulted in projections focussing on the effects of increasing temperature on mangrove distribution.

Temperature thresholds that cause severe dieback of mangrove, derived using correlative techniques (Osland et al. 2013; Cavanaugh et al. 2014), have provided a means for extrapolation of mangrove distribution using various temperature scenarios. Osland et al. (2013) used a climate envelope approach to project mangrove forest presence and relative abundance within 352 coastal grid cells that covered a coastline of 172,024 km² based on future climate scenarios at 2070–2100, projecting broad-scale mangrove expansion and saltmarsh decline. Guo et al. (2013), recognising that other factors will improve climate envelope approaches specifically examined biotic interactions between *A. germinans* and saltmarsh vegetation along the Texas coast, accounting for latitudinal gradient, elevational gradient and life history stages of mangrove. They demonstrated that the response of mangrove is variable depending upon each of these factors. In doing so, they demonstrate that biotic interactions are an important component of mangrove-saltmarsh dynamics. Ignoring the overarching influence of hydroperiod and its interaction with topography, Stevens et al. (2006) extrapolated rates of mangrove expansion after a freeze event to propose complete coverage of mangrove seedlings at Cedar Key within 25–30 years since their analysis. Similarly, a study calling for analysis to look beyond sea-level rise excluded inundation parameters and individual species tolerance to both temperature and aridity to project areas of high vulnerability to changes in mangrove-saltmarsh dynamics for the mainland USA and globally on the basis of aridity gradients, winter air temperature gradients, and a combination of both factors (Osland et al. 2016).

In southern Florida, where temperature control on mangrove survival does not dominate distribution dynamics, sea-level rise projections typically indicate landward expansion of mangrove. SLAMM has been used in this region to project changes in wetland vegetation classes indicating significant gains in tidal wetlands (mangrove and saltmarsh) at the expense of inland and coastal forest (Geselbracht et al. 2011; Sherwood and Greening 2014; Geselbracht et al. 2015). Comparisons of simple bath-fill approaches with SLAMM using elevation data of differing resolution demonstrate the usefulness of high resolution elevation models and improved vegetation distribution models (Zhu et al. 2015). At the regional scale, the sea level over proportional elevation

(SLOPE) model, which assumes the area of mangrove and saltmarsh is determined by the landform slope and vertical tidal forcing, was applied to the northern Gulf of Mexico (Doyle et al. 2010). They demonstrate significant spatial variation in the proportion of tidal freshwater forest lost and saltwater mangrove-saltmarsh gain based on current rates of relative sea-level rise of 18–20 cm and 10 cm acceleration in eustatic sea-level rise over the next century. With the purpose of identifying barriers to landward migration, bath-fill techniques were applied to LIDAR derived digital elevation models along the northern Gulf of Mexico (Enwright et al. 2016).

Synthesis of Projections

Due to the need to plan for sea-level rise and provide adaptation pathways for coastal wetlands, it is not surprising that projecting the response of mangrove and saltmarsh to sea-level rise has been the focus of research in both regions. All models are particularly sensitive to elevation and resolution/accuracy of input digital elevation models. Application of SLAMM has been the predominant approach applied at the local scale, while bath-fill approaches were applied at the regional scale. Few studies have considered the influence of data input, model selection and parameterisation on model outcomes (Rogers et al. 2012; Mogensen and Rogers 2018; Zhu et al. 2015); this is an area requiring further research in both regions so that site-specific variables can be adequately incorporated. Given the influence of freeze events on mangrove survival in the northern Gulf of Mexico, it is also not surprising that this has received considerable attention in this region; unfortunately, these studies have yet to integrate the overarching influence of sea level and the expression of sea level on coastal topography to accurately project increases in mangrove extent. Integration of multiple controls on mangrove distribution within models has begun to receive some attention (Guo et al. 2013), and future model improvements are anticipated.

Moving beyond Generalisations about Distribution Dynamics

The distribution of organisms is determined by a range of factors including: the geographical starting point for dispersal; the inherited ecological niche; dispersal limitations imposed by abiotic conditions; opportunities for niche evolution; and the time over which dispersal and evolution can occur (Wiens and Donoghue 2004), with anthropogenic activities augmenting these processes. Distribution patterns derive from the interaction of these factors, and their influence on establishment and long-term survival of individuals at different spatial and temporal scales. Unfortunately, mangrove scientists are often

lax in defining both the spatial and temporal scale of analysis; and this has been associated with contradictory interpretations due to correlations between variables that are not hierarchically comparable (Schaeffer-Novelli et al. 2000). In addition, few studies have analysed the broad range of factors controlling mangrove distribution (Friess et al. 2012). In an attempt to present a systematic treatise we have broadly identified a range of ecophysiological, geomorphological/geochemical, hydrological and meteorological/climatic processes influencing mangrove. While Fig. 1 presents these components as discrete units, it masks the complexity in these processes that intersect, combine, correlate, amplify and create feedbacks between and among each other. This complexity may be inherently limiting the capacity to move beyond generalisations regarding mangrove expansion.

Correlative techniques, commonly termed ‘ecological niche modelling’ or ‘species distribution modelling’ are becoming increasingly popular for ecologists and biogeographers (Peterson and Soberón 2012a, b), and dominate analyses of mangrove distribution. These techniques intend to establish relationships between mangrove distribution at various spatial and temporal scales with environmental variables, but are frequently used in ways whereby model outcomes do not correspond to what is known about species distribution in the real-world (Peterson and Soberón 2012a, b). Foundational to correlative studies is the assumption that the inherited ecological niche or fundamental niche is the primary control on distribution, that enough time has passed for the niche to be fully realised, and that this niche can be adequately defined using a few variables; that is, the niche they occupy is in dynamic equilibrium with correlative variables (Pearson and Dawson 2003). The paradox of these studies is that while they intend to describe mangrove distribution dynamics, they intrinsically ignore the spatial and temporal dynamics in mangrove ecosystems that allow mangrove to occupy a realised niche, as opposed to the fundamental niche. In addition, they fail to recognise the full range of factors that operate at similar spatial and temporal scales, and presume that factors operating at larger or smaller spatial scales are insignificant. In this regard, global scale analyses of mangrove expansion often ignore the local scale factors that can be so influential in rates of mangrove expansion and the proportional area of a wetland that mangrove occupies. While it is a well-known adage that ‘correlation does not imply causation’, emphasis of this concept is necessary, and further analysis is essential to confirm causation.

Climate change has necessitated the need for projections of mangrove and saltmarsh distribution under various climate change scenarios. However, the effect of assumptions from correlative studies are compounded when projecting mangrove distribution, particularly when the model is poorly parameterised and validated (Cowell and Thom 1994). Projecting species distribution changes under various climate

change scenarios entails acceptance that species distribution is non-equilibrium in nature and should therefore be undertaken cautiously. Correlations based on analyses of mangrove distribution over short temporal scales or small spatial scales, are particularly prone to being poorly parameterised, as the probability of missing important processes influencing mangrove distribution over longer timescales and larger spatial scales will be high. The validity of these models has also been questioned as they primarily focus on climatic variables, ignoring the many other variables influencing species distribution (Pearson and Dawson 2003).

Manipulative experiments under field or laboratory conditions provide a means for validating observed spatial and temporal patterns established using correlative approaches, and afford additional evidence of causation. The outcomes of manipulative experiments can be fundamental to process based model development that can be used to project response to climate change variables (Dormann et al. 2012). However, they also incur their own challenges. First, they involve artificial manipulation of natural processes, which are inherently difficult to replicate. This is particularly pertinent under laboratory conditions where manipulation is largely limited to experiments on mangrove seedlings and juveniles, and unfeasible with adult mangrove. Second, experimental design in manipulative studies becomes increasingly difficult when manipulating processes operating over large spatial and temporal scales (Quinn and Keough 2002). Nevertheless, manipulative experiments provide important insights into the ecophysiological response of mangrove to environmental variables and should remain an important component of mangrove distribution research.

Our analysis of existing knowledge of the mangrove-saltmarsh distribution dynamics at a northern and southern hemisphere range limit of mangrove in Australia and mainland USA highlights the variation in processes influencing mangrove distribution within and between these regions. It also demonstrates the variation in processes that has occurred over geological, recent and contemporary timescales; establishing that there is little consistency in patterns of mangrove distribution between the regions. Planning for climate change requires some confidence in the ecological niche of mangrove and therefore necessitates acknowledgement of these differences. We therefore propose important considerations for biogeographical analyses that will assist with improving knowledge of mangrove distribution and enhance model confidence.

First, assumptions, caveats and limitations with correlative studies should be acknowledged and go beyond precursory acknowledgement that correlation does not mean causation. This requires recognition that both environmental controls on mangrove distribution, and mangrove distribution in itself, are spatially and temporally variable; sampling data are therefore incomplete, represent a 'snapshot' in space and time, and may be biased (Jarnevich et al. 2015). Establishment of

relationships that are more robust requires that predictor variables capture the bounds of the variability and the periodicity of variability. Not incorporating this variability will result in established relationships between the realised niche of mangrove distribution and environmental variables, and will have little value for projections of future distribution. In addition, the observed variability means that it is unreasonable to expect one correlative model to reproduce mangrove distribution for all species, at all spatial scales, and across all temporal scales.

Second, the same recognition is also required for manipulative studies, whether they occur in the field or under laboratory conditions in greenhouses. In this regard, experimental design is particularly important, and experimental design should account for spatial and temporal variability in environmental variables. This requires ecologists to extend the perceptual range of feasible experimental designs, as proposed by Wiens (1989). This can become particularly difficult under field conditions due to spatial heterogeneity, but nevertheless requires careful experimental design (Dutilleul 1993). Importantly, results of physiologically-based experiments should be interpreted in the context of the full range of possible drivers of mangrove distribution, including those factors that are poorly or impossible to replicate in manipulative experiments (Pearson and Dawson 2003).

Third, analyses that draw from a range of methods will provide greater confidence in model outcomes. Integration of correlation techniques with manipulative experimentation is increasingly advocated in biogeographic literature (Pearson and Dawson 2003; Guisan and Thuiller 2005; Guisan et al. 2006). Correlative studies can be used to formulate hypotheses regarding controls on mangrove distribution that can be subsequently applied as test variables in manipulative field and laboratory experiments, thereby establishing the physiological response of mangrove to the environmental variables observed to influence mangrove distribution. Alternatively, findings from manipulative experiments can be verified by observing similar patterns in nature, or not if the physiological response was misinterpreted.

Frameworks have been advocated that integrate layers of information influencing species distribution, including bioclimatic variables, dispersal, disturbance and resource factors that limit species to a realised niche (see for example Pearson and Dawson 2003; Hijmans and Graham 2006; Franklin 2010). Distribution or niche modelling, sometimes termed ecological niche modelling (ENM), species distribution modelling (SDM) or community distribution modelling (CDM), provide the means of modelling species distributions from distribution records. The availability of MaxEnt (Elith et al. 2011) or BIOMOD (Thuiller et al. 2009) tool sets, particularly within GIS and statistical applications, have improved the popularity of these approaches (Peterson and Soberón 2012a). Currently, there are few applications of these

approaches to modelling mangrove distribution (see for example Kramer-Schadt et al. 2013; Quisthoudt et al. 2013; Record et al. 2013), perhaps reflecting the need for model improvements. Distribution/niche modelling approaches are largely correlative in nature and aim to find associations between distribution data and abiotic predictors that are typically climatic, hydrological or geomorphological derivatives (Peterson and Soberón 2012a). There is considerable debate regarding the suitable application of distribution/niche modelling approaches, and many improvements have been proposed; users should refer to these suggestions prior to application (see for example Araújo and Guisan 2006; Jiménez-Valverde et al. 2008; Peterson and Soberón 2012a, b). Whilst distribution/niche modelling may provide a first approximation of abiotic controls on mangrove distribution when applied appropriately (Record et al. 2013), model outputs will be significantly improved by applying distribution/niche modelling techniques as a first pass assessment. Second and third-pass assessments that integrate the effect of biotic, mobility and temporal factors on mangrove distribution will significantly improve predictive capacity.

Given the need to plan for climate change, it is imperative that mangrove-saltmarsh distribution research moves beyond simple modelling approaches that assume equilibrium between realised and fundamental niches, and ignore spatial and temporal variability. Integration of modelling approaches from various disciplines interested in mangrove distribution is essential if robust conservation strategies are to be implemented that improve adaptation to climate change and maintenance of ecosystem services provided by coastal wetlands.

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