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## Mangrove expansion and salt marsh decline at mangrove poleward limits

### Abstract

Mangroves are species of halophytic intertidal trees and shrubs derived from tropical genera and are likely delimited in latitudinal range by varying sensitivity to cold. There is now sufficient evidence that mangrove species have proliferated at or near their poleward limits on at least five continents over the past half century, at the expense of salt marsh. *Avicennia* is the most cold-tolerant genus worldwide, and is the subject of most of the observed changes. *Avicennia germinans* has extended in range along the USA Atlantic coast and expanded into salt marsh as a consequence of lower frost frequency and intensity in the southern USA. The genus has also expanded into salt marsh at its southern limit in Peru, and on the Pacific coast of Mexico. Mangroves of several species have expanded in extent and replaced salt marsh where protected within mangrove reserves in Guangdong Province, China. In south-eastern Australia, the expansion of *Avicennia marina* into salt marshes is now well documented, and *Rhizophora stylosa* has extended its range southward, while showing strong population growth within estuaries along its southern limits in northern New South Wales. *Avicennia marina* has extended its range southwards in South Africa. The changes are consistent with the poleward extension of temperature thresholds coincident with sea-level rise, although the specific mechanism of range extension might be complicated by limitations on dispersal or other factors. The shift from salt marsh to mangrove dominance on subtropical and temperate shorelines has important implications for ecological structure, function, and global change adaptation.

### Keywords

decline, poleward, limits, salt, mangrove, marsh, expansion

### Disciplines

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## **Mangrove expansion and salt marsh decline at mangrove poleward limits**

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## ABSTRACT

Mangroves are species of halophytic intertidal trees and shrubs derived from tropical genera and are likely delimited in latitudinal range by varying sensitivity to cold. There is now sufficient evidence that mangrove species have proliferated at or near their poleward limits on at least five continents over the past half century, at the expense of salt marsh. *Avicennia* is the most cold-tolerant genus worldwide, and is the subject of most of the observed changes. *Avicennia germinans* has extended in range along the US Atlantic coast and expanded into salt marsh as a consequence of lower frost frequency and intensity in the southern USA. The genus has also expanded into salt marsh at its southern limit in Peru, and on the Pacific coast of Mexico. Mangroves of several species have expanded in extent and replaced salt marsh in the largest protected coastal wetland in China, the Zhanjiang Mangrove National Nature Reserve. In south-eastern Australia, the expansion of *Avicennia marina* into salt marshes is now well documented, and *Rhizophora stylosa* has extended its range southward, while showing strong population growth within estuaries along its southern limits in northern New South Wales. *Avicennia marina* has extended its range southwards in South Africa. The changes are consistent with the pole-ward extension of temperature thresholds co-incident with sea-level rise, although the specific mechanism of range extension might be complicated by limitations on dispersal or other factors. The shift from salt marsh to mangrove dominance on subtropical and temperate shorelines has important implications for ecological structure, function, and global change adaptation.

**KEYWORDS:** Climate change, temperature, mangrove, salt marsh, range expansion, USA, Australia, South Africa, South America

## **INTRODUCTION**

The increase in global average surface temperature of 0.74°C (1906-2005) (Solomon *et al.*, 2007) has already caused shifts in the structure and distribution of ecological communities at a variety of scales (Walther *et al.*, 2002; Parmesan and Yohe 2003). Arctic shrubs have advanced northward in response to decreases in intensity of freezing (Sturm *et al.*, 2001), and an advance in range has been demonstrated for butterfly species (up to 200 km) (Parmesan *et al.*, 1999) as well as birds (an average of 20 km for 12 bird species in Britain) (Thomas & Lennon, 1999). Minimum temperatures globally are increasing at twice the rate of maximum temperatures (Walther *et al.*, 2002). In temperate climates, increasing temperature and decreasing intensity and frequency of frost are likely to cause transitions in the distribution of temperature sensitive higher plants (Bakkenes *et al.*, 2002; Loarie *et al.*, 2008), which in many instances provide structural habitat and organic carbon to organisms and ecosystems.

In many ways, mangroves are ideal species for monitoring the impacts of global climate change on vegetated habitats. Mangroves are sensitive to several global environmental conditions undergoing change, including enhanced atmospheric CO<sub>2</sub> (McKee & Rooth, 2008), sea level (Woodroffe, 1990; McKee *et al.*, 2007), temperature (Alongi, 2008), and rainfall (Semeniuk, 2013). All mangrove species are hydrochorous and thus often have some potential for dispersal to new localities by sea currents and drift (see Friess *et al.*, 2012; Van der Stocken *et al.*, 2013). Mangroves are conspicuous and can be identified from aerial

photography at a scale represented in easily accessible geographic applications such as Google Earth ([www.google.com/earth/index.html](http://www.google.com/earth/index.html)) and Nearmap ([www.nearmap.com](http://www.nearmap.com)), displaying an emergent canopy above salt marsh in temperate and subtropical intertidal environments, although on-ground verification may be required when grading to freshwater woody vegetation. They are an important habitat for estuarine, nearshore and terrestrial biota (Nagelkerken *et al.*, 2008), and play a critical role in coastal environments in stabilising shorelines (Gedan *et al.*, 2011), and sequestering atmospheric carbon (Chmura *et al.*, 2003; Donato *et al.* 2011).

Temperature has long been considered the primary limit to the latitudinal range of mangroves. Walsh (1974) postulated that this pole-ward threshold corresponded to a mean monthly atmospheric temperature of 20°C for the coldest month. Duke *et al.* (1998) more accurately identified the winter position of the 20°C isotherm for sea surface temperature (SST) as corresponding to the latitudinal limit in both hemispheres (Figure 1), although SST and air temperature at the latitudinal limit of individual species and genera may vary between continents (Quisthoudt *et al.*, 2012). While mean temperatures provide a correlative explanation for mangrove distribution, quantifying minimum temperature requirements (and measures of extreme winter events) provide an even better mechanistic approach for quantifying thresholds (Osland *et al.*, 2013). That mangroves will shift their distribution after meeting minimum temperature thresholds in response to changing climate is well attested by the fossil record. Mangrove species distribution has changed in concert with small changes in temperature since the early Holocene. For example, a slight cooling following the mid-Holocene highstand (6000 years BP) is associated with the less common occurrence of Rhizophoraceae in northern NSW (Hashimoto *et al.*, 2006), and the loss of *Avicennia marina* from the Poverty Bay-East Cape region of New Zealand (Mildenhall, 1994).

However, caution should be exercised in interpreting changes in distribution and latitudinal limits solely to temperature. The effects of temperature upon mangroves are mediated by interactions with other aspects of global change (e.g., CO<sub>2</sub>, precipitation, sea level rise, nutrients). Geomorphic changes in response to rising, and then stabilising sea-level exerted the strongest control on mangrove extent over the Holocene (e.g. Grindrod *et al.* 1999; Hashimoto *et al.*, 2006). Both fluctuating sea levels and temperature regimes have vastly influenced mangrove distributions globally since much older geological time frames than the Holocene (Sherrod and McMillan, 1985; Ellison *et al.*, 1999). Contemporary distributions are shaped by suitable intertidal habitat, and the capacity of floating propagules to access these locations. Impediments to colonization therefore include unfavourable ocean currents, closed estuary entrances, or on arid and hard-rock coastlines, an absence of estuaries with depositional environments suitable for mangrove establishment (Saintilan *et al.* 2009). Such impediments have slowed the filling of potential niche as defined by temperature thresholds for many species (Quisthoudt *et al.*, 2012).

SUGGEST INSERT Figure 1

Several publications have postulated that mangroves will migrate to higher latitudes, replacing salt marsh as an outcome of global warming (Woodroffe & Grindrod, 1991; Field, 1995; Gilman *et al.*, 2008). However, assessments of changes in mangrove extent at pole-ward limits are restricted to a few site specific studies. In this paper, we use published historic records of occurrence and distribution limits, contemporary published surveys, and our own observations to provide a global synthesis of evidence for proliferation and extension of mangroves at pole-ward limits. Mangroves are absent from Europe and the Mediterranean

Sea but co-exist with salt marsh in temperate settings in Asia, Africa, Australia/New Zealand, North America and South America.

## **METHODS**

We present a synthesis of literature from four continents detailing changes in the distribution of mangroves. In some cases we provide additional analyses using remote sensing, field survey and local expert observations. We used Google Earth Pro ([www.google.com/earth/index.html](http://www.google.com/earth/index.html)) to confirm occurrence within estuaries and poleward extent in each of the focus regions using the most recent available imagery. These images included photography of Cedar Keys, Florida (imagery dated 19 January 2012), Virilla estuary, Peru (imagery dated 19 January 2010, DigitalGlobe), and Piura estuary, Peru (imagery dated 10 February 2011, DigitalGlobe). We also used Google Earth Pro's polygon area function to estimate the extent of mangroves where these had expanded from the time of previously published estimates, including an update of the estimates in Stevens et al (2006) for the US Gulf Coast, and the area of mangroves in Piura, Peru. We interpreted mangrove and salt marsh using techniques defined in Wilton and Saintilan (2000). Our identification of mangroves in Vichayal, Peru using Google Earth Pro was confirmed by photographs provided by Edwin Gerardo and Manuel Ravelo.

## **RESULTS and DISCUSSION**

### **Northern Hemisphere**

#### North America



Mangroves occupied intertidal locations in the southeastern USA at least as far back as the early Eocene Epoch (~45 Million years BP), but those fossil deposits were associated with a vastly different coastline boundary driven by a warmer climate and higher sea level (Berry, 1916; Berry, 1924; Westgate and Gee, 1990). Mangrove forests from the Eocene Epoch likely occurred at densities similar to those seen in modern-day Neotropical mangrove forests, just much farther north (Sherrod and McMillan 1985; Gee, 2001). The first fossil evidence of *Avicennia* in the Caribbean appeared in the late Miocene Epoch (~10 Million years BP), and by the mid-Pliocene Epoch (~3.5 Million years BP) multiple mangrove genera were evident (Graham, 1995). A prominent lack of mangrove fossil evidence along the northern Gulf just preceding the Pleistocene Epoch (~11,700 years BP) until 3000-4000 years BP (from Holocene peat deposits in south Florida) suggests an eradication event for mangroves along the northern Gulf of Mexico, perhaps related to colder temperatures when mangroves were aligned in distribution closer to the equator (Sherrod and McMillan, 1985).

At the northern limits of present-day mangrove extent in the Gulf of Mexico, population extent has in the recent past been periodically reduced by frost (McMillan & Sherrod, 1986), with heavy frost in 1983 and 1989 leading to 95-98% loss amongst several of the northernmost populations (Lonard & Judd, 1991; Everitt *et al.*, 1996; Montague & Odum, 1997). This observation prompted Snedaker (1995) to suggest that periodic heavy frost would limit northern expansion for some time. Ecotypic differences in cold tolerance among natural mangrove populations in the Gulf do have the potential to buffer this impact somewhat. This is especially true for populations of *Avicennia germinans* (McMillan, 1971); those populations growing along the Texas coast were especially tolerant to freezing among others surveyed in the wider Caribbean region (Markley *et al.*, 1982). However, in more than 20 years since the 1989 freeze event, winters have been sufficiently mild to allow rapid

expansion of mangroves at their northern limits into salt marsh, documented in Texas (Comeaux *et al.*, 2012; Bianchi *et al.*, 2013), Louisiana (Perry & Mendelssohn, 2009; Alleman & Hester, 2011; Pickens & Hester, 2011) and Florida (Stevens *et al.*, 2006).

*Avicennia germinans* coverage increased from 57 ha in 1986 to 1182 ha in 2006 in Louisiana, but fluctuated from a maximum documented coverage of approximately 2180 ha in 1983 before the freeze of that same year (Giri *et al.*, 2011b). By another account, *A. germinans* increased in abundance by nearly fivefold between 2002 and 2009 within the Louisiana deltaic plain (Michot *et al.*, 2010). Populations of *A. germinans* seem to be regulated strongly by air temperatures of -6.7 to -8.9°C or less (Lonard and Judd, 1991; Stevens *et al.*, 2006; Osland *et al.*, 2013). This threshold is more restrictive for other Neotropical mangrove species (Lugo and Zucca, 1977; Krauss *et al.*, 2008). For instance, there was no reported survival of transplanted *Rhizophora mangle* seedlings after the 1983 freeze in Texas (Sherrod *et al.*, 1986), and embolism is a common consequence of temperatures slightly below 0°C in the same species (Fig. 2, A and B). Likewise, *Laguncularia racemosa* trees are highly susceptible to repetitive freeze-induced dieback events (Fig. 2, C), although re-sprouting from the base is a common response in both *L. racemosa* and *A. germinans*.

#### SUGGEST INSERT FIG 2

Indeed, after extensive losses during the 1983 freeze, mangroves have extended in many Gulf study sites since 1984 (Giri *et al.*, 2011) although have not reached pre-1983 extent (Giri, unpublished data). Mangrove trees have been documented visually in Louisiana as early as 1938 (Penfound and Hathaway, 1938) and in Texas as early as 1853 (cited in Sherrod and McMillan 1981). Using an historical time-series of aerial photography extending back to

1956, Perry and Mendelssohn (2009) were able to demonstrate that mangroves first occupied their Louisiana site in 1995. Along with a reduced incidence of freeze-induced mortality, recent expansion of mangroves in Louisiana has been assisted by widespread dieback of *S. alterniflora* resulting from drought; *Avicennia germinans* was unaffected by drought and proliferated (McKee *et al.*, 2004). Environmentally mediated competition between *S. alterniflora* and mangroves also occurs along latitudinal gradients in Florida (Kangas and Lugo, 1990) and was probably of importance during post-Pleistocene recolonization of mangroves toward northern latitudes. A recent analysis applied to the northern Gulf suggests that short-statured *A. germinans* vegetation has an overall lower requirement for water use in early growing season assessments than *S. alterniflora* (Krauss *et al.*, 2013). This may help to explain the differential survival of *A. germinans* over *S. alterniflora* during drought, and suggests an interaction between climate variability in both temperature and rainfall (Krauss *et al.*, 2013).

Much of what we are now documenting in the Southern USA is the northern boundary of the post-Pleistocene recolonization (*sensu* Sherrod and McMillan, 1985). Currently, mangroves (primarily *A. germinans*) have also extended north on the Florida Atlantic coast at least as far as St Augustine, occupying back-barrier intertidal flats as scattered clusters of individuals (29° 57'59" N), and have expanded within this estuary since the early 1990's. In fact, *A. germinans* has expanded into salt marsh at several other sites on the Atlantic coast, including the Indian River lagoon (Harris and Cropper, 1992). To the south, *Rhizophora mangle* has expanded landward more than a kilometre into previously *Cladium* and *Eleocharis* marshlands in the Everglades (Ross *et al.* 2000), possibly in response to higher sea-levels, changing water levels, and shifting fire regimes (Smith *et al.*, 2013). Similar landward expansion has been noted on the Pacific coast of Mexico at Magdalena Bay, Baja California.

Here, a 20% increase in mangrove extent through landward encroachment into sparse halophytic shrubland was attributed to sea-level rise, and was particularly pronounced during *El Nino* seasons (Lopez-Medellin *et al.*, 2011).

On the Gulf Coast of Florida, mangroves increased coverage in the Ten Thousand Islands National Wildlife Refuge by 35% since 1927, principally at the expense of salt marsh (Krauss *et al.*, 2011). Over a similar time period, oscillations between marsh and mangrove area have been documented in other Gulf coastal areas of Florida (Egler, 1952; Bischof, 1995; Smith *et al.*, 2013); sometimes to the detriment of marsh and sometimes to the detriment of mangroves. In the absence of any discernable change in mean number of freeze days over the period, encroachment of mangroves onto marsh was attributed primarily to the increase in sea level over the period ( $2.24\text{mmy}^{-1}$  at the Key West station: Krauss *et al.*, 2011). After comparing mangrove extent at three sites in Cedar Keys between 1995 and 1999, Stevens *et al.* (2006) predicted that all three sites would develop complete mangrove cover within 25-30 years, if not impacted by frost. Our assessment of the same sites using 2012 aerial photography (Google Earth imagery, 19 January 2012) suggests that this outcome has been realized in less than half the predicted time.

### Asia

There are insufficient historic data on the southeast Japanese coast to unequivocally argue for an extension in natural range of *Kandelia obovata* (syn. *K. candel*). The northern limit of *K. obovata* in Japan was reported by Wakushima *et al.* (1994) to be Kiire, Kagoshima Prefecture ( $31^{\circ} 30' \text{ N}$ ), although they note the long-term survival of a planted population in the estuary of the Aono river in the Shizuoka Prefecture at  $34^{\circ} 38' \text{ N}$ .

Determining changes in northern limits of mangroves in China and Taiwan is complicated by extensive clearance. A further complication in China is the introduction of mangroves north of their natural limits: *K. obovata* in Zheihang (Li and Lee, 1997); and *Sonneratia caseolaris* and *Bruguiera sexangula* in Guangdong (Li *et al.* 1998). One of the few locations where mangroves and salt marshes co-exist in near natural state on the Chinese mainland coast is in the Zhanjiang Mangrove National Nature Reserve on the Leizhou Peninsula of Guangdong Province (21° 34' N; 109° 45' E). The reserve is a Ramsar-listed wetland of international significance and supports nearly one third of China's mangroves. Regionally, mangroves have declined due to agricultural developments, and extensive dyking restricts landward encroachment (Leempoel *et al.*, 2013). However, within the reserve mangroves, dominated by *Avicennia marina*, *Aegiceras corniculatum* and *Kandelia obovata*, have expanded fourfold, including encroachment on salt marsh (Prof. Guangchun Lei, pers. comm.; Durango-Cordero *et al.*, 2013; Figure 3).

### **SUGGEST INSERT FIG 3**

The northernmost mangrove community in Taiwan is located in the Danshui River estuary (21° 09' N; 121° 26' E) and is the largest *Kandelia obovata* forest in the world (Lee and Yeh 2009). The mangrove and associated *Phragmites communis* salt marsh community has been protected in the Danshui Mangrove Reserve since in mid 1980's. Mangroves have doubled in extent since the establishment of the reserve, and in detailed satellite imagery analysis Lee and Yeh (2009) were able to demonstrate landward encroachment of mangrove on non-mangrove vegetation, presumably *Phragmites* salt marsh.

## **Southern Hemisphere**

### Australasia

The grey mangrove *Avicennia marina* extends south on the Australian mainland to the southernmost intertidal flats within Corner Inlet, Victoria (38° 54' 25" S), and has occupied this range since the earliest historic records from the 19<sup>th</sup> century. These are the southernmost mangroves in the world, and the Bass Strait provides an effective barrier to further dispersal to the north coast of Tasmania. *Avicennia marina* in southern Australia is exposed to more frequent but less extreme frosts than those encountered in the US Gulf Coast by *A. germinans*, and has developed a greater resistance to freeze-induced embolism (Stuart *et al.* 2007).

Mangrove expansion within estuaries is a near ubiquitous trend in southeastern Australia, (Saintilan & Williams, 1999), and New Zealand (Burns & Ogden, 1985; Morrissey *et al.*, 2003; Lovelock *et al.*, 2007; Stokes *et al.*, 2010), and has been occurring since the time of earliest aerial photographic records (1950's), and perhaps earlier (McLoughlin, 1988, 2000). Temperature increases across the region over the past century are likely to be one of a suite of regional environmental changes promoting mangrove growth and a corresponding loss of salt marsh, including sea-level rise (Rogers *et al.*, 2006), increases in sedimentation following catchment development (emphasized in New Zealand studies: Lovelock *et al.*, 2007; Swales *et al.* 2009; Morrissey *et al.* 2010) and, in Queensland, higher rainfall (Eslami-Andargoli *et al.*, 2009). Mangroves in New Zealand have expanded across 29 locations by an average of 165% since the 1940's. There is less obvious salt marsh decline than in Australia (Morrissey *et al.* 2010), possibly due to higher sedimentation rates and elevation gain (Stokes *et al.* 2010), although some landward encroachment has been noted (Burns and Ogden 1985). A median estimate of 30% of salt marsh has been lost to mangrove encroachment across SE

Australia (Saintilan and Williams 2000; Straw and Saintilan 2006), with some evidence that rates of loss are lower towards the southern limit in Victoria (5-10%) (Rogers *et al.*, 2005), although this may be due to competitive resilience of large saltbushes of the genus *Tecticornia*, as much as colder conditions slowing mangrove expansion in the south.

Mangrove floristic diversity declines with increasing latitude on the east and west coasts of the Australian continent. On the west coast, patterns in mangrove diversity at a regional scale are strongly influenced by aridity, confounding the assessment of temperature effects on mangrove species range expansion (Semeniuk, 1983; Wells, 1983). The humid subtropical-temperate east coast presents an ideal setting to explore changes in mangrove diversity, with a cline in temperature extending across more than 150 estuaries, linked by the south-flowing East Australia Current south of the Great Barrier Reef. Species of the tropical family Rhizophoraceae (*Rhizophora stylosa* and *Bruguiera gymnorhiza*) were common in northern NSW during the early to mid Holocene, when temperatures and sea levels were likely to have been higher than present (Hashimoto *et al.*, 2006), although were rare in the earliest contemporary surveys (Wells, 1983; West *et al.*, 1985) with *R. stylosa* recorded in seven estuaries in northern NSW. Both *R. stylosa* and *B. gymnorhiza* appear to have expanded their range in recent decades. *B. gymnorhiza* has recently colonized at least three southerly estuaries, the Sandon and Wooli Wooli Rivers and Moonee Creek (Wilson 2009). *R. stylosa* has now been recorded within 16 estuaries (Wilson 2009), and has shown strong population growth within a number of NSW estuaries (Wilson and Saintilan, 2012). Although it is highly probable that *R. stylosa* was missed in at least two estuaries in earlier surveys in NSW, the colonization of others is clearly very recent, based on demographics. The 100 km southward extension of *R. stylosa* from the Corindi estuary to South West Rocks Creek (30° 53' 16" S), corresponds to the southward shift in temperature zones in the region over the past few

decades (Hennessy *et al.*, 2004). However, colonization of estuaries between these latitudes is sporadic rather than incremental, and leaf phenology does not suggest a temperature cline limiting growth (Wilson and Saintilan, 2012).

### South Africa

The earliest comprehensive survey of South African mangroves now dates back 50 years, and represents aerial photographic and field surveys over a 14 year period to 1962 (Macnae 1963). South of Port St Johns, Macnae (1963) reported stands of mangroves at the estuaries of the Mtata (29° 11'E, 31° 57'S) and Mngazana Rivers (29° 25'E, 31° 42'S), 'isolated clumps' of mangroves at the estuaries of the Mbashe (29° 25'E, 31° 42'S) and Nxaxo (28° 31'E, 32° 35'S) Rivers, and 'occasional trees' southward. Macnae (1963) reported temperature thresholds on the basis of his observations of distribution as being 19°C mean air temperature or where the mean of the coldest monthly air temperature does not drop below 13°C. This placed the Mbashe and Nxaxo estuaries at the southern limit (19.1°C mean, 11.9°C mean coldest monthly), with Buffalo River in East London outside of the range (17.7°C mean, 10.2 C mean coldest monthly).

Mean temperature at the Buffalo River for the period 1973-2011 rose from 17.7°C to 18.7°C, and the mean coldest temperature rose from 10.2°C to 14.4°C (Tutiemp, 2012), a shift extending the possible range of mangrove in South Africa to East London based on the untested thresholds of Macnae (1963). Some dispersal challenges on the Transkei coast include the proportionately high number of temporarily open/closed estuaries (17 of the 76 estuaries are permanently open), and although the Agulhas current flows south 2-3 km offshore, a counter-current develops between the Agulhas and the shoreline creating a predominantly northward drift (Macnae 1963). In spite of these challenges, and widespread



clearing of mangroves, in the 20 years to 1982 mangroves formed extensive stands in the estuaries of the Kobonqaba (28° 30' E, 32° 36' S, to the south of the Nxaxo), Nqabara (28° 47' E, 32° 30' S), Xora (29° 05' E, 32° 05' S), and Bulungula (29° 00' E, 32° 08' S ) Rivers (Ward and Steinke 1982). It is unlikely these were missed by Macnae; mangroves cover a larger area on the Xora estuary (16 ha) than the Mbashe (12.5 ha) and Nxaxo (14 ha), and line the lower shore of the estuary. In 1969 mangroves were observed for the first time in the Kwelera River (32° 54' S, 28° 04' E), still the southernmost known natural stand. Natural seeding in the Kwelera River is strongly suggested by the results of a drift card dispersal experiment, in which one of the cards dropped offshore of the Nxaxo River was retrieved within 100 metres of the Kwelera mangrove stand (Steinke and Ward 2003).

Mangrove area has increased by approximately 40% in South African estuaries since the 1970s, with most of the gains in the Umhlatuze estuary (increase from 197 ha to 489: Bedin 2001; Ward and Steinke 1982) and the Mtata (increase from 34 to 42 ha 1982-1999: Adams *et al.* 2004). Small declines were observed in more than half of estuaries sampled by Adams *et al.* (2004), and mangroves have been lost entirely from many estuaries (Quisthoudt *et al.*, 2013). This may be related to limited available habitat for colonization (Wright *et al.*, 1997) and in some cases the removal of mangroves manually (the Mnyameni: Adams *et al.*, 2004) but is principally attributed to prolonged inundation following long-term closure of the estuary mouths on temporarily open/closed estuaries (eg. the Bulungula, Mzimgvuba, Kosi and Kobonquaba rivers: Breen & Hill, 1966; Adams *et al.*, 2004).

However, mangroves appear to have established naturally in the Kei River (28°21'42" E, 32°40'00"S,) to the north of the Kwelera, and the Gqunube River (28° 02'E, 32° 56'S) to the

south, with the Kobonquaba River a possible source (Steinke 1986; Steinke and Ward 2003). It is uncertain whether the Gqunube River mangroves were naturally dispersed or planted.

*A. marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata* have also survived in the Nahoon estuary in East London after being transplanted from Durban Bay (Steinke, 1999), suggesting that climate was or is no longer a factor limiting their southern natural extent. Of these three species, it is only *A. marina* that has expanded substantially within the estuary, and now covers 1.6 ha of previously salt marsh flat, and is expanding at 0.1 ha per year (A. Rajkaran pers. obs. 2012; Hoppe-Speer *et al.* submitted). Quisthoudt *et al.* (2013) were able to successfully predict current distribution of *A. marina*, *B. gymnorrhiza* and *R. mucronata* based on current climate variables, with number of growing days above an 18°C threshold being the most important. On this basis, they predict latitudinal expansion of mangroves with continued climatic warming.

### South America

Mangroves grow south on the Atlantic coast to Santo Antonia Lagoon in the Municipality of Laguna (28° 28'S; 48° 50'W) (Soares *et al.*, 2012). This southern limit has not changed in the two decades since the survey of Schaeffer-Novelli (1990), although populations of the dominant species *Laguncularia racemosa* show evidence of recent recruitment (Soares *et al.*, 2012). At this site *L. racemosa* is stunted, a trait in common with species globally at their southern limit, although *Avicennia schaueriana* grows to 10 m, suggesting a vigour characteristic of a species well within its range (Soares *et al.*, 2012). Further southward expansion may be limited by a strong northerly current described by Siegle and Asp (2007) extending from Ararangua, an estuary 100 km south, to Laguna (Soares *et al.*, 2012).

The southern limit of mangrove communities on the South American west coast was considered by Clusener and Breckle (1987) to be the River Thumbes at 3° 35'S; beyond which were found only a few small individuals of *Rhizophora* near the village of Bocapan (at 3° 44'S), and a small stand of *Avicennia* at the mouth of the Piura River. Mangroves were successfully planted within this range in their experimental studies in 1984-85.

South of Cerro Illescas (6° 0' S) the cold Peruvian current precludes mangrove colonization (Clüsener & Breckle, 1987), and because of the aridity of the coast only three estuaries between Cerro Illescas and Bocapan provide intertidal conditions suitable for the development of mangrove, these being the Virrila estuary (5° 50'S); the Piura River (5° 30'S) and the Vichayal estuary (4° 53'S). The 'small stand' of *Avicennia* described by Clusener and Breckle (1987) at Piura is now very extensive, lining 9.5 km of shoreline and covering at least 38 ha in the north arm and 9 ha in the south arm of the estuary at San Pedro, the southernmost confirmed mangroves on the west coast (imagery dated 10 February 2011, DigitalGlobe, sourced from Google Earth Pro). The Vichayal estuary has a new stand of *Avicennia* at 4° 53'22.6" S; 81° 08' 56.4" W covering 1.87 ha (field photographs provided by Manuel Ravelo, imagery dated 19 January 2010, DigitalGlobe, sourced from Google Earth Pro). These are absent from aerial photographs taken in 1970 (Google Earth Pro) and reportedly established during the El Niño event in the first decade of this century (E. Gerardo pers. comm. 2012).

## CONCLUSIONS

Dispersal may be problematic in spite of the abundance of buoyant propagules produced by *Avicennia* spp. (Clarke *et al.*, 2001; Sousa *et al.*, 2007), and restricted gene flow in marginal populations (Dodd & Afzal Rafii, 2002) also suggests dispersal may be problematic in the expansion of range. In many places the latitudinal limit of mangroves appears to lag behind changes in temperature thresholds, as documented in New Zealand (de Lange & de Lange, 1994), east coast Australia (Wilson & Saintilan, 2012), South Africa (Steinke, 1999) and South America (Soares *et al.*, 2012). The difference between fundamental and realized niche is relatively large for *Avicennia* and *Rhizophora* on the basis of global comparisons (Quisthoudt *et al.*, 2012), and on some coastlines may reflect slow expansion from Pleistocene extents. Disequilibrium between tree species distribution and rapidly changing temperature regimes has been noted for terrestrial species also (Willner *et al.* 2009). It is likely that a more complex response than a steady stepping poleward will be the case for many mangrove species, especially those on relatively high wave energy coasts with few permanently open estuaries or where dispersal is subject to unfavourable currents. This infers that there is no simple function relating range extension and warming temperatures, something also implied by the global temperature and range analysis of Quisthoudt *et al.* (2012).

Parmesan and Yohe (2003) found poleward range shifts in 75-81% of 1045 species of higher plants and animals with quantitative records, with an average shift of 6.1 km per decade. Notwithstanding limited opportunities for dispersal and the difficulties of ‘threading the needle’ of estuarine entrances, an increase in range has been documented for the mangroves *A. germinans* in the USA and Peru, *A. marina* in South Africa and *R. stylosa* and *B. gymnorhiza* in eastern Australia; and expanding mangrove populations near poleward limits are obvious within estuaries in Australia, New Zealand, the Gulf and Atlantic coasts of the

USA, the Pacific and South Atlantic coasts of South America, and the Leizhou Peninsula of China, one of the few locations in southern China where large areas of mangrove and salt marsh are protected and have been retained. Poleward expansion in the coming decades will be most evident on open coasts where temperature currently exerts a strong control on contemporary distributions and available habitat exists. Osland *et al.* (2013) used contemporary mangrove forest distribution data and 30 year climate records from the Gulf and Atlantic US coasts to identify winter-climate based thresholds and develop mangrove species distribution and relative abundance models. Their models and analyses of the potential effect of alternative future winter climate scenarios show that, in southeastern USA and especially in Louisiana, Texas, and Florida, relatively small changes in winter climate can result in relatively dramatic mangrove range expansion at the expense of salt marsh. Applying a 2-4°C increase in annual mean minimum temperature would lead to a 95% reduction in salt marsh in Louisiana, 100% reduction in Texas and 60% reduction in Florida (Osland *et al.*, 2013).

The comprehensive replacement of salt marsh by mangrove (*cf.*, Osland *et al.*, 2013; Guo *et al.*, in press) is predicated on temperature as the key delimiting factor of mangrove range expansion. In addition to temperature, local patterns of mangrove expansion into salt marsh are likely to be influenced by interactions between hydroperiod, sedimentation, elevation and salinity, with nutrients playing a role in some settings (Patterson and Mendelssohn 1991; Patterson *et al.* 1997), all of which can be impacted locally by human agency, such as building walls and structures in estuaries, dredging, and development in the catchment. In coastal Louisiana, mangroves currently tend to dominate higher elevation settings such as the shorelines of tidal creeks, and exclusion from lower interior marshes has been attributed to higher predation, lower retention of propagules (Patterson *et al.* 1997), plant competition and

greater flooding stress (Patterson *et al.* 1993). By contrast, mangroves in eastern Australia show greater mortality in less frequently inundated higher salinity areas where propagules become desiccated (Clarke and Myerscough 1993; Clarke and Allaway 1993). That mangroves are invading salt marshes in contrasting settings along the northern Gulf of Mexico versus Australia would suggest that different mechanisms are at work, or that global changes are contributing to an increased capacity of mangroves to survive in previously marginal intertidal environments.

Mangrove expansion into salt marsh mirrors a global trend of woody shrub invasion of grassland (Knapp *et al.*, 2008; Williamson *et al.*, 2010), which has been attributed variously to altered fire and grazing intensity (Scholes and Archer, 1997; Van Auken, 2009), and elevated atmospheric CO<sub>2</sub> (Polley *et al.*, 1997; Eamus and Palmer, 2008). On most coastlines, there is little evidence that altered fire and grazing regimes are dominant drivers of vegetation change in intertidal settings. The proliferation of mangroves in previously salt marsh-dominated environments is likely to be driven by a suite environmental factors favouring mangrove and which are changing globally, including elevated sea-level, elevated atmospheric CO<sub>2</sub> and higher temperatures (Williamson *et al.*, 2010; McKee *et al.*, 2012). Landward encroachment of mangrove into salt marsh and salt pan has been attributed to sea-level rise in environments as disparate as Baja California (Lopez-Medellin *et al.*, 2011), the US Gulf Coast (Krauss *et al.*, 2011; Smith *et al.*, 2013), and east coast Australia, where Rogers *et al.* (2006) demonstrated a lower capacity of salt marsh to respond to sea-level rise through vertical accretion. Salt marsh floristic diversity increases in inverse correlation with mangrove diversity on the Australian east coast (Saintilan, 2009) and mangrove encroachment may place further pressure on an ecological community already listed as endangered in New South Wales.

The replacement of salt marsh by mangrove in temperate settings has important implications for ecosystem organization and function. Experimental studies in the Gulf of Mexico (Comeaux *et al.*, 2012) and temperate Australia (Rogers *et al.*, 2006) show improved mineral trapping leading to a higher rate of surface elevation gain in encroaching mangrove than surrounding salt marsh, suggesting mangrove has greater potential to respond to increasing sea levels, although some of these differences may relate to different topographic settings. Carbon sequestration may be enhanced in some settings as a result of mangrove encroachment (Howe *et al.*, 2009; Bianchi *et al.*, 2013) and reduced in others, if redox potential is enhanced by mangrove root formation (Comeaux *et al.*, 2012). The conversion of salt marsh to mangrove in the Gulf of Mexico alone could sequester  $129 \pm 45$  Tg C over 100 years (Bianchi *et al.*, 2013), more than 1% of 'Blue Carbon' estimates globally (Bianchi *et al.*, 2013; Hopkinson *et al.* 2012), and a proportion that may rise if the trend of tropical mangrove deforestation continues (Valiela *et al.*, 2001).

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## LIST OF FIGURES

Figure 1: Global mangrove and salt marsh distribution and the average 20°C sea-surface temperature isotherm. Sources: Spalding (2012), Hoekstra et al. (2010), and NOAA (2013).

Fig. 2: (A) Air temperatures (°C) for the Ten Thousand Islands region of Florida, USA from November 2006 through April 2007, with days having subzero temperatures highlighted (inset graphs). These subzero temperatures were responsible for (B) branch tip mortality from vasacular embolism in *Rhizophora mangle*, and (C) complete stem dieback in many *Laguncularia racemosa* trees growing in open environments. *Avicennia germinans* trees in the Ten Thousand Islands region were generally unaffected by this freeze. (Temperature data source: DBHYDRO Browser, South Florida Water Management District, [www.sfwmd.gov/dbhydro](http://www.sfwmd.gov/dbhydro), Station SGGWX, accessed 11 April 2013)

Fig 3: Colonization of *Spartina* by juvenile *Sonneratia apetela*, Leizhou Peninsula, China (photograph by Guangchun Lei, used with permission).



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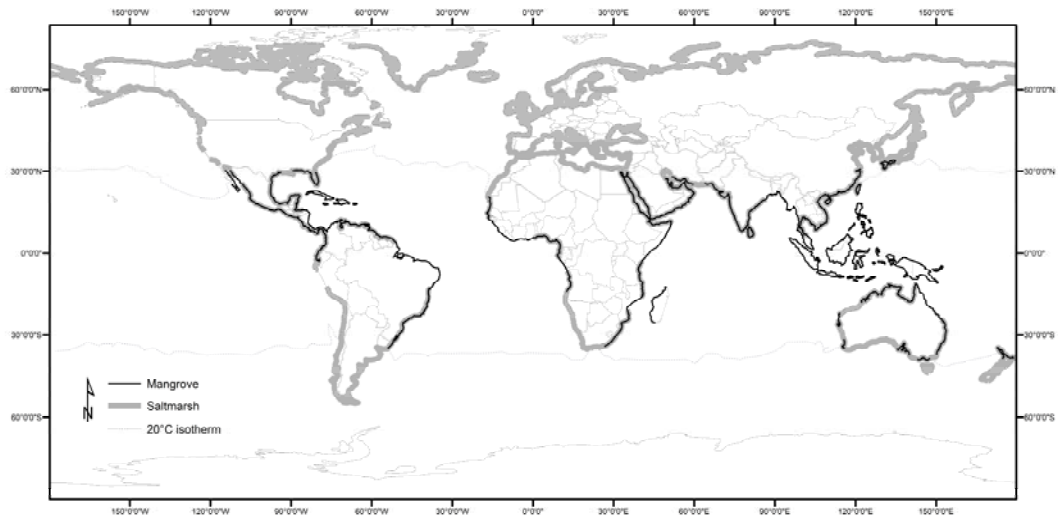


Fig. 1



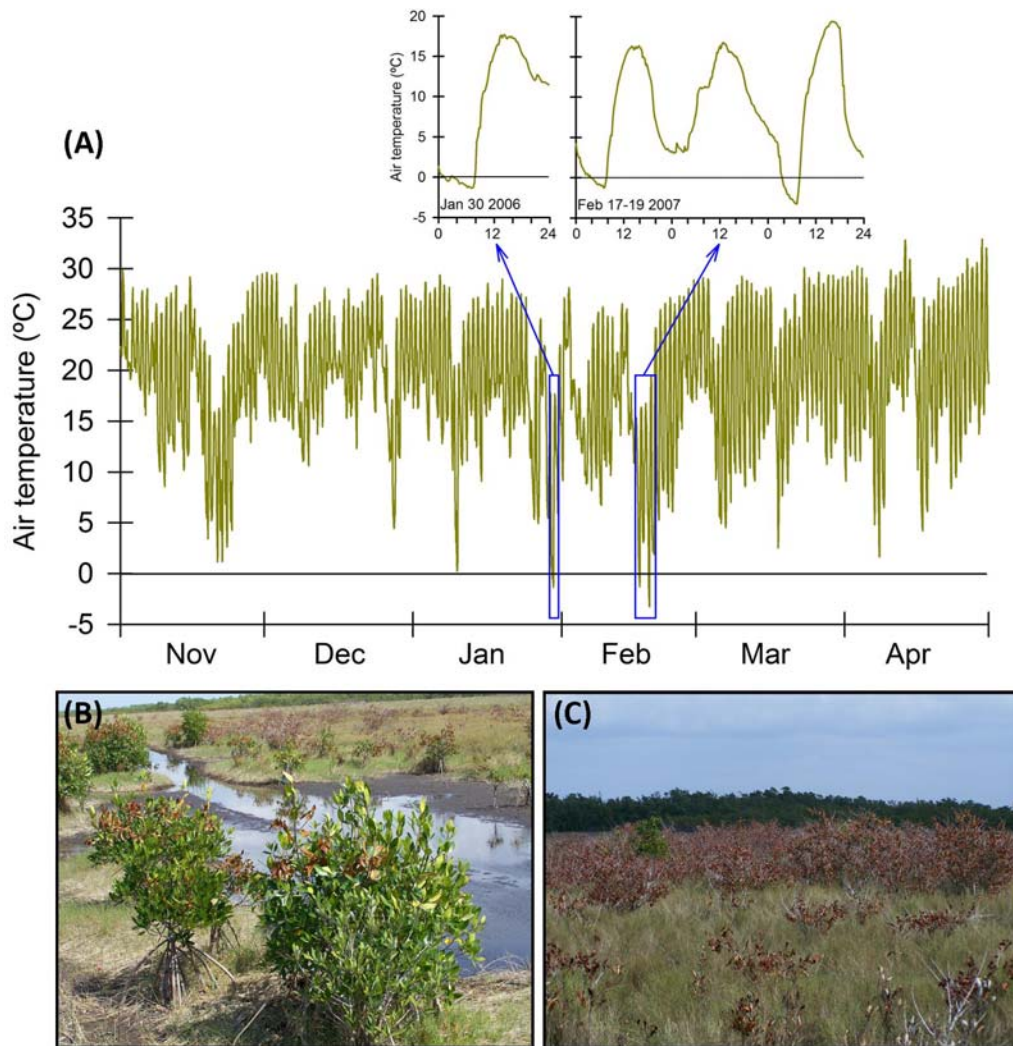


Fig. 2

