

University of Wollongong

Research Online

Faculty of Science, Medicine and Health -
Papers: part A

Faculty of Science, Medicine and Health

1-1-2014

Mangrove expansion and salt marsh decline at mangrove poleward limits

Neil Saintilan

Office of Environment and Heritage (OEH), Neil.Saintilan@environment.nsw.gov.au

Nicholas Wilson

Forest Institute of South Vietnam, rstylosa@gmail.com

Kerrylee Rogers

University of Wollongong, kerrylee@uow.edu.au

Anusha Rajkaran

Rhodes University

Ken W. Krauss

US Geological Survey, kraussk@usgs.gov

Follow this and additional works at: <https://ro.uow.edu.au/smhpapers>



Part of the [Medicine and Health Sciences Commons](#), and the [Social and Behavioral Sciences Commons](#)

Recommended Citation

Saintilan, Neil; Wilson, Nicholas; Rogers, Kerrylee; Rajkaran, Anusha; and Krauss, Ken W., "Mangrove expansion and salt marsh decline at mangrove poleward limits" (2014). *Faculty of Science, Medicine and Health - Papers: part A*. 1314.

<https://ro.uow.edu.au/smhpapers/1314>

Research Online is the open access institutional repository for the University of Wollongong. For further information contact the UOW Library: research-pubs@uow.edu.au

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

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

Saintilan, N., Wilson, N., Rogers, K., Rajkaran, A. & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, 20 (1), 147-157.

Mangrove expansion and salt marsh decline at mangrove poleward limits

N. Saintilan^{1*}, N.C. Wilson², K. Rogers³, A. Rajkaran⁴, and K.W. Krauss⁵

^{1*} Corresponding author:

Neil Saintilan, Office of Environment and Heritage, NSW Department of Premier and

Cabinet

PO Box A290, Sydney South NSW 1232, Australia

Email: neil.saintilan@environment.nsw.gov.au

² Nicholas C. Wilson: Forest Institute of South Vietnam, 1 Pham Van Hai Street, Tan Binh District, Ho Chi Minh City, Vietnam

Email: rstylosa@gmail.com

³ Kerrylee Rogers, School of Earth and Environmental Science, University of Wollongong, Northfields Ave, Wollongong 2522, Australia

Email: Kerrylee@uow.edu.au

⁴ Anusha Rajkaran, Department of Botany, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa

Email: A.Rajkaran@ru.ac.za

⁵ Ken W. Krauss, US Geological Survey, National Wetlands Research Center
Lafayette, LA, 70506 USA

Email: kraussk@usgs.gov

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 CO₂ (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) and Nearmap (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., CO₂, 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) 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 (2.24mmy^{-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 19th 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 CO₂ (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 CO₂ 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 ± 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).

ACKNOWLEDGEMENTS

The authors thank Edwin Gerardo, and Dr J. Manuel Charcape Ravelo, National University of Piura, for their comments and photographs of mangroves in Peru. Robert J. Williams is thanked for comments on an earlier version of this manuscript. The use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank the UNEP World Conservation Monitoring Centre (WCMC) for access to mangrove and salt marsh distribution data, and Professor Guangchun Lei of Beijing Forestry University for his observations and photographs of mangrove encroachment into salt marsh in Guangdong Province, China.

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, 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).

REFERENCES

- Adams JB, Colloty BM, Bate, GC (2004) The distribution and state of mangroves along the coast of Transkei, Eastern Cape Province, South Africa. *Wetlands Ecology and Management*, **12**, 531-541.
- Alleman LK, Hester MW (2011) Refinement of the fundamental niche of black mangrove (*Avicennia germinans*) seedlings in Louisiana: Applications for restoration. *Wetlands Ecology and Management*, **19**, 47-60.
- Alongi DM (2008) Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, **76**, 1-13.
- Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390-407.
- Bedin T (2001) The progression of a mangrove forest over a newly formed delta in the Umhlatuze Estuary, South Africa. *South African Journal of Botany* **67**, 433-438.
- Berry EW (1916) *The Lower Eocene Floras of Southeastern North America*. Professional Paper 91, U.S. Geological Survey, Washington, DC, USA.
- Berry EW (1924) *The Middle and Upper Eocene Floras of Southeastern North America*. Professional Paper 92, U.S. Geological Survey, Washington, DC, USA.
- Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW (2013) Historical reconstruction of mangrove expansion in the Gulf of Mexico: Linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science*, **119**, 7-16.
- Bischof BC (1995) Aerial photographic analysis of coastal and estuarine mangrove system dynamics of the Everglades National Park, Florida, in response to hurricanes:

Implications of the continuing sea level rise. MS Thesis, University of Miami, Coral Gables, Florida, USA.

Breen CM, Hill BJ (1966) A mass mortality of mangroves in the Kosi estuary. *Transactions of the Royal Society of South Africa*, **41**, 285-301.

Burns BR, Ogden J (1985) The demography of the temperate mangrove [*Avicennia marina* (Forsk.) Vierh.] at its southern limit in New Zealand. *Australian Journal of Ecology*, **10**, 125-133.

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, **17**, 1111.

Clarke PJ, Allaway W (1993) The regeneration niche of the grey mangrove *Avicennia marina* – effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia* **93**, 548-556.

Clarke PJ, Myerscough PJ (1993) The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: The effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology* **18**, 307-315.

Clarke PJ, Kerrigan RA, Wetphal CJ (2001) Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? *Journal of Ecology* **89**, 648-659.

Clüsener M, Breckle SW (1987) Reasons for the limitation of mangrove along the west coast of northern Peru. *Vegetatio*, **68**, 173-177.

Comeaux RS, Allison MA, Bianchi TS (2012) Mangrove expansion in the Gulf of Mexico with climate change: Implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, **96**, 81-95.

- de Lange WP, de Lange PJ (1994) An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. *Journal of Coastal Research*, **10**, 539-548.
- Dodd R., Afzal Rafii Z (2002) Evolutionary genetics of mangroves: continental drift to recent climate change. *Trees*, **16**, 80-86.
- Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4**, 293-297.
- Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, **7**, 27-47.
- Durango-Cordero JS, Satyanarayana B, Zhang J, Wang J, Chen M, Fanghong X, Chan JCW, Kangying L, Bogaert J, Koedam N, Dahdouh-Guebas F (2013) Vegetation structure at Zhangjiang Mangrove National Nature Reserve (ZMMNR), P.R. China: a comparison between original and non-original trees using ground-truthing, remote sensing and GIS techniques. www.vliz.be/imisdocs/publications/232700.pdf
- Eamus D, Palmer AR (2008) Is climate change a possible explanation for woody thickening in arid and semi-arid regions? *International Journal of Ecology* **2007**, 5.
- Egler FE (1952) Southeast saline Everglades vegetation, Florida, and its management. *Vegetatio*, **3**, 213-265.
- Ellison AM, Farnsworth EJ, Merkt RE (1999) Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, **8**, 95-115.
- Eslami-Andargoli L, Dale P, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, **85**, 292-298.

- Everitt JH, Judd FW, Escobar DE, Davis MR (1996) Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas gulf coast. *Journal of Coastal Research*, **12**, 64-69.
- Field CD (1995) Impact of expected climate change on mangroves. *Hydrobiologia*, **295**, 75-81.
- Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews*, **87**, 346-366.
- Gedan K, Kirwan M, Wolanski E, Barbier E, Silliman B (2011) The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Climatic Change*, **106**, 7-29.
- Gee CT (2001) The mangrove palm *Nypa* in the geologic past of the New World. *Wetlands Ecology and Management*, **9**, 181-194.
- Gilman EL, Ellison J, Duke NC, Field CD (2008) Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany*, **89**, 237-250.
- Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T, Duke NC (2011a). Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, *20*(1), 154-159.
- Giri C, Long J, Tieszen L (2011b) Mapping and monitoring Louisiana's mangroves in the aftermath of the 2010 Gulf of Mexico oil spill. *Journal of Coastal Research*, **27**, 1059-1064.
- Graham A (1995) Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. *Biotopeica*, **27**, 20-27.

- Grindrod J, Moss P, Kaars SVD (1999) Late Quaternary cycles of mangrove development and decline on the north Australian continental shelf. *Journal of Quaternary Science*, **14**, 465-470.
- Guo H, Zhang Y, Lan Z, Pennings SC (in press) Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. *Global Change Biology*
- Harris LD, Cropper WP, Jr. (1992) Between the devil and the deep blue sea: implications of climate change for Florida's fauna. In: *Global Warming and Biological Diversity* (eds. R.L. Peters and T.E. Lovejoy). Yale University Press, New Haven, CT.
- Hashimoto TR, Saintilan N, Haberle SG (2006) Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research*, **44**, 63-76.
- Hoekstra JM, Molnar JL, Jennings M, Revenga C, Spalding MD, Boucher TM, Robertson JC, Heibel TJ, Ellison K (2010) *The Atlas of Global Conservation: Changes, Challenges, and Opportunities to Make a Difference* (ed. Molnar JL). Berkeley: University of California Press.
- Hennessy K, Page C, McInnes K, Jones R, Bathols J, Collins D, Jones D (2004) Climate change in New South Wales, Part 1: past climate variability and projected changes in average climate. In: (ed. C.R.F.T.N.G. Office). CSIRO Atmospheric Research, Aspendale, Victoria.
- Hoppe-Speer S, Adams J, Rajkaran A (submitted). Mangrove expansion rate and population structure of a planted forest.
- Howe AJ, Rodríguez JF, Saco PM (2009) Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. *Estuarine, Coastal and Shelf Science*, **84**, 75-83.

- Kangas PC, Lugo AE (1990) The distribution of mangroves and saltmarshes in Florida. *Tropical Ecology*, **31**, 32-39.
- Krauss KW, Lovelock CE, McKee KL, López-Hoffman L, Ewe SML, Sousa WP (2008) Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany*, **89**, 105-127.
- Krauss KW, From AS, Doyle TW, Doyle TJ, Barry MJ (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Inlands region of Florida, USA. *Journal of Coastal Conservation*, **15**, 629-638.
- Krauss KW, McKee KL, Hester MW (2013) Water use characteristics of black mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern geographical limit. *Ecohydrology* (in press).
- Lee T-M, Yeh H-C (2009) Applying remote sensing techniques to monitor shifting wetland vegetation: A cases tudy of Danshui River estuary mangrove communities, Taiwan. *Ecological Engineering*, **35**, 487-496.
- Leempoel K, Bourgeois C, Zhang J, Wang J, Chen M, Satyaranayana B, Bogaert J, Dahdouh-Geubas F (2013). Spatial heterogeneity in mangroves assessed by GeoEye-1 satellite data: a case-study in Zhanjiang Mangrove National Nature Reserve (ZMNNR), China. *Biogeosciences Discussions* **10**, 2591-2615.
- Li MS, Lee SY (1997) Mangroves of China: a brief review. *Forest Ecology and Management*, **96**, 241-259.
- Li Y, Zheng D, Liao B, Zheng S, Wang Y (1998) Preliminary report on introduction of several superior mangroves. *Forest Research* **11**, 652-655.
- Loarie SR, Carter BE, Hayhoe K, McMahon S, Moe R, Knight CA, Ackerly DD (2008) Climate change and the future of California's endemic flora. *PLoS ONE*, **3**, e2502.

- Lonard RI, Judd FW (1991) Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the Lower Rio Grande Valley, Texas. *The Southwestern Naturalist*, **36**, 213-217.
- Long SP, Mason CF (1983) *Saltmarsh Ecology*. Blackie, 160pp
- Lovelock CE, Feller IC, Ellis J, Schwarz AM, Hancock N, Nichols P, Sorrell B (2007) Mangrove growth in New Zealand estuaries: The role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, **153**, 633-641.
- Macnae W (1963) Mangroves swamps in South Africa. *Journal of Ecology*, **51**, 1-25.
- Markley JL, McMillan C, Thompson GA Jr (1982) Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany*, **60**, 2704-2715.
- McKee KL, Rooth JE (2008) Where temperate meets tropical: multi-factorial effects of elevated CO₂, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology*, **14**, 971-984.
- McKee KL, Mendelsohn IA, Materne M (2004) Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, **13**, 65-73.
- McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16**, 545-556.
- McKee KL, Rogers K, Saintilan N (2012) Responses of Salt Marsh and Mangrove Wetlands to changes in Atmospheric CO₂, Climate and Sea-Level. In *Global Change and the Function and Distribution of Wetlands*. (ed. by BA Middleton), pp 63-96, Springer

- McLoughlin L (1988) Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cover River, Sydney, 1780's-1880's. *Wetlands (Australia)*, **7**, 13-24.
- McLoughlin L (2000) Estuarine wetlands distribution along the Parramatta River, Sydney, 1788-1940: Implications for planning and conservation. *Cunninghamia*, **6**, 579-610.
- McMillan C (1971) Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. *Ecology*, **52**, 927-930.
- McMillan C, Sherrod CL (1986) The chilling tolerance of black mangrove, *Avicennia germinans*, from the Gulf of Mexico coast of Texas, Louisiana and Florida. *Contributions in Marine Science*, **29**, 9-16.
- Michot TC, Day RH, Wells CJ (2010) Increase in black mangrove abundance in coastal Louisiana. Louisiana Natural Resources News, Newsletter of the Louisiana Association of Professional Biologists, January 2010, 4-5.
- Mildenhall DC (1994) Early to Mid Holocene pollen samples containing mangrove pollen from Sponge Bay, East Coast, North Island, New Zealand. *Journal of the Royal Society of New Zealand*, **24**, 219-230.
- Montague CL, Odum HT (1997) The intertidal marshes of Florida's Gulf Coast. *Ecology and Management of Tidal Marshes: A Model from the Gulf of Mexico* (ed. by C.L. Coultas and Y. Hsieh), pp. 1-9. St Lucie Press, Delroy Beach, Florida, USA.
- Morrisey DJ, Skilleter GA, Ellis JI, Burns BR, Kemp CE, Burt K (2003) Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. *Estuarine, Coastal and Shelf Science*, **56**, 581-592.
- Morrisey DJ, Swales A, Dittman S, Morrison MA, Lovelock CE, Beard CM (2010) The ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review*, **48**, 43-160.

- Nagelkerken I, Blaber SJM, Bouillon S, et al. (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany*, **89**, 155-185.
- NOAA 2013. Sea surface temperature (SST) contour charts. Prepared by National Oceanic and Atmospheric Administration (NOAA) satellites and Information. Accessed on 6 July 2013 at http://www.ospo.noaa.gov/data/sst/contour/global_small.c.gif
- Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes versus mangrove forests in the southeastern U.S. *Global Change Biology*, **19**, 1482-1494.
- Parmesan C, Ryrholm N, Stefanescu C., et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Patterson CS, Mendelsohn IA (1991) A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. *Wetlands* **11**,139-161.
- Patterson CS, Mendelsohn IA, Swenson EM (1993) Growth and survival of *Avicennia germinans* seedlings in a mangal/salt marsh community in Louisiana, U.S.A. *Journal of Coastal Research* **9**, 801-810.
- Patterson CS, McKee KL, Mendelsohn IA (1997) Effects of tidal inundation and predation on *Avicennia germinans* seedling establishment and survival in a sub-tropical mangal/salt marsh community. *Mangroves and Salt Marshes* **1**, 103-111.
- Penfound WT, Hathaway ES (1938) Plant communities in the marshlands of southeastern Louisiana. *Ecological Monographs*, **8**, 1-56.
- Perry C, Mendelsohn I (2009) Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands*, **29**, 396-406.

- Pickens C, Hester M (2011) Temperature tolerance of early life history stages of black mangrove *Avicennia germinans*: implications for range expansion. *Estuaries and Coasts*, **34**, 824-830.
- Polley HW, Mayeux HS, Johnson HB, Tischler CR (1997) Viewpoint: atmospheric CO₂, soil water and shrub/grass ratios on rangelands. *Journal of Range Management* **50**, 278-284.
- Quisthoudt K, Schmitz N, Randin C, Dahdouh-Guebas F, Robert ER, Koedam N (2012) Temperature variation among mangrove latitudinal range limits worldwide. *Trees*, **26**, 1919-1931.
- Quisthoudt K, Adams J, Rajkaran A, Dahdouh-Geubas F, Koedam N, Randin CF (2013) Disentangling the effects of global climate and regional land-use on the current and future distribution of mangroves in South Africa. *Biodiversity Conservation* in press DOI 10.1007/s10531-013-0478-4
- Rogers K, Saintilan N, Heijnis H (2005) Mangrove encroachment of salt marsh in Western Port Bay, Victoria: The role of sedimentation, subsidence and sea level rise. *Estuaries*, **28**, 551-559.
- Rogers K, Wilton KM, Saintilan N (2006) Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science*, **66**, 559-569.
- Ross MS, Meeder JF, Sah JP, Ruiz PL, Telesnicki GL (2000) The southeast saline Everglades revisited: 50 years of coastal vegetation change. *Journal of Vegetation Science* **11**, 101-112.
- Saintilan N (2009) Biogeography of Australian saltmarsh plants. *Austral Ecology*, **34**, 929-937.

- Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in South-East Australia. *Global Ecology and Biogeography*, **8**, 117-124.
- Saintilan N, Rogers K, McKee K (2009) Saltmarsh-Mangrove interactions in Australasia and the Americas. Chapter 31 in Perillo GME, Wolanski E, Cahoon DR, Brinson MM (eds.) *Coastal Wetlands; an integrated ecosystems approach*. Elsevier pp. 855-883.
- Semeniuk V (2013) Predicted response of coastal wetlands to climate changes: a Western Australian model. *Hydrobiologia*, **708**, 23-43.
- Schaeffer-Novelli Y, Cintron-Molero G, Adaime RR, de Camargo TM (1990) Variability of mangrove ecosystems along the Brazilian Coast. *Estuaries*, **13**, 204-218.
- Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**, 517-544.
- Semeniuk V (1983) Mangrove distribution in Northwestern Australia in relationship to regional and local freshwater seepage. *Vegetatio*, **53**, 11-31.
- Sherrod CL, McMillan C (1981) Black mangrove, *Avicennia germinans*, in Texas: Past and present distribution. *Contributions in Marine Science*, **24**, 115-131.
- Sherrod CL, McMillan C (1985) The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science*, **28**, 129-140.
- Sherrod CL, Hockaday DL, McMillan C (1986) Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas. *Contributions in Marine Science*, **29**, 27-36.
- Siegle E, Asp NE (2007) Wave refraction and longshore transport patterns along the southern Santa Catarina coast. *Brazilian Journal of Oceanography*, **55**, 109-120.

- Smith TJ III, Foster AM, Tiling-Range G, Jones JW (2013) Dynamics of mangrove-marsh ecotones in subtropical coastal wetlands: Fire, sea-level rise, and water levels. *Fire Ecology*, **9**, 66-77.
- Snedaker S (1995) Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. *Hydrobiologia*, **295**, 43-49.
- Soares MLG, Estrada GCD, Fernandez V, Tognella MMP (2012) Southern limit of the Western South Atlantic mangroves: Assessment of the potential effects of global warming from a biogeographical perspective. *Estuarine, Coastal and Shelf Science*, **101**, 44-53.
- Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.) (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Sousa WP, Kennedy PG, Mitchell BJ, Ordonez BM (2007) Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? *Ecological Monographs* **77**, 53-76.
- Spalding M. (2012). *World atlas of mangroves*. Routledge.
- Steinke TD (1986) Mangroves of the East London area. *The Naturalist* **30**, 50-53
- Steinke TD (1999) Mangroves in South African estuaries. *Estuaries of South Africa* (ed. by B.R. Allanson and D. Baird), pp. 119-140. Cambridge University Press, Cambridge, United Kingdom.
- Steinke TD, Ward CJ (2003) Use of plastic drift cards as indicators of possible dispersal of propagules of the mangrove *Avicennia marina* by ocean currents. *Africal Journal of Marine Science*, **25**, 169-176

- Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, **14**, 435-444
- Stokes DJ, Healy TR, Cooke PJ (2010) Expansion dynamics of monospecific, temperate mangroves and sedimentation in two embayments of a barrier-enclosed lagoon, Tauranga Harbour, New Zealand. *Journal of Coastal Research*, 113-122.
- Straw P, Saintilan N (2006) Loss of shorebird habitat as a result of mangrove incursion due to sea-level rise and urbanization. *Waterbirds Around the World*, 717-720.
- Stuart SA, Choat B, Martin KC, Holbrook NM, Ball MC (2007) The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist* **173**, 576-583.
- Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546-.
- Swales A, Bentley SJ, Lovelock C, Bell RG (2007) Sediment processes and mangrove-habitat expansion on a rapidly prograding muddy coast, New Zealand. In *Coastal Sediments '07. Proceedings of the Sixth International Conference on Coastal Engineering and Science of Coastal Sediment processes, New Orleans, May 2007*. Reston, Virginia, USA: American Society of Civil Engineers, 1441-1454.
- Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213-213.
- Tutiempo (2012) *Climate East London*. Available at:
http://www.tutiempo.net/en/Climate/East_London/688580.htm (accessed 7 November 2012)
- Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* **90**, 2931-2942.

- Van der Stocken T, DeRyck DJR, Balke T, Bouma TJ, Dahdouh-Guebas F, Koedam N
(2013) The role of wind in hydrochorous mangrove propagule dispersal.
Biogeosciences, **10**, 895-925.
- Valiela E, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major
tropical environments. *Bioscience* **51**, 807-815.
- Vannucci M (2001) Chapter 3, Indo-West Pacific, p.126 in de Lacerda, ed., *Mangrove
Ecosystems: Function and Management*, Springer
- Wakushima S, Kuraishi S, Sakurai N (1994) Soil salinity and pH in Japanese mangrove
forests and growth of cultivated mangrove plants in different soil conditions. *Journal
of Plant Research*, **107**, 39-46.
- Walsh GE (1974) Mangroves: a review. *Ecology of Halophytes* (ed. by R.J. Reimold and
W.H. Queen), pp. 51-174. Academic Press, London.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-
Guldberg O, Bairlein, F. (2002) Ecological responses to recent climate change.
Nature, **416**, 389-395.
- Ward CJ, Steinke TD (1982) A note on the distribution and approximate areas of mangroves
in South Africa. *South African Journal of Botany*, **3**, 51-53.
- Wells AG (1983) Distribution of mangroves species in Australia. *Biology and Ecology of
Mangroves* (ed. by HJ Teas), pp. 57-76. Dr W. Junk, The Hague, Netherlands.
- West RJ, Thorogood C, Walford T, Williams RJ (1985) Mangrove distribution in New South
Wales. *Wetlands(Australia)*, **4**, 2-6.
- Westgate JW, Gee CT (1990) Paleoecology of a middle Eocene mangrove biota (vertebrates,
plants, and invertebrates) from southwest Texas. *Palaeogeography,
Palaeoclimatology, Palaeoecology*, **78**, 163-177.

- Williamson GJ, Boggs GS, Bowman DMS, (2010). Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. *Regional Environmental Change*.
<http://dx.doi.org/10.1007/s10113-010-0109-5>.
- Willner W, Di Pietro R, Bergmeier E (2009). Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography*, **32**, 1011-1018.
- Wilson NC (2009) The distribution, growth, reproduction and population genetics of a mangrove species, *Rhizophora stylosa* Griff. near its southern limits in New South Wales, Australia. PhD Thesis, Australian Catholic University, North Sydney.
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquatic Botany*, **101**, 8-17.
- Wilton K, Saintilan N (2000). *Protocols for Mangrove and Saltmarsh Habitat Mapping*. Estuaries Branch, NSW Department of Land and Water Conservation, Sydney.
- Woodroffe CD (1990) *The impact of sea-level rise on mangrove shorelines*. Turpin, Letchworth, ROYAUME-UNI.
- Woodroffe CD, Grindrod J (1991) Mangrove biogeography: the role of quaternary environmental and sea-level change. *Journal of Biogeography*, **18**, 479-492.
- Wright CI, Lindsay P, Cooper JAG (1997) The effect of sedimentary processes on the ecology of the mangrove-fringed Kosi estuary/lake system, South Africa. *Mangroves and Salt Marshes*, **1**, 79-94.

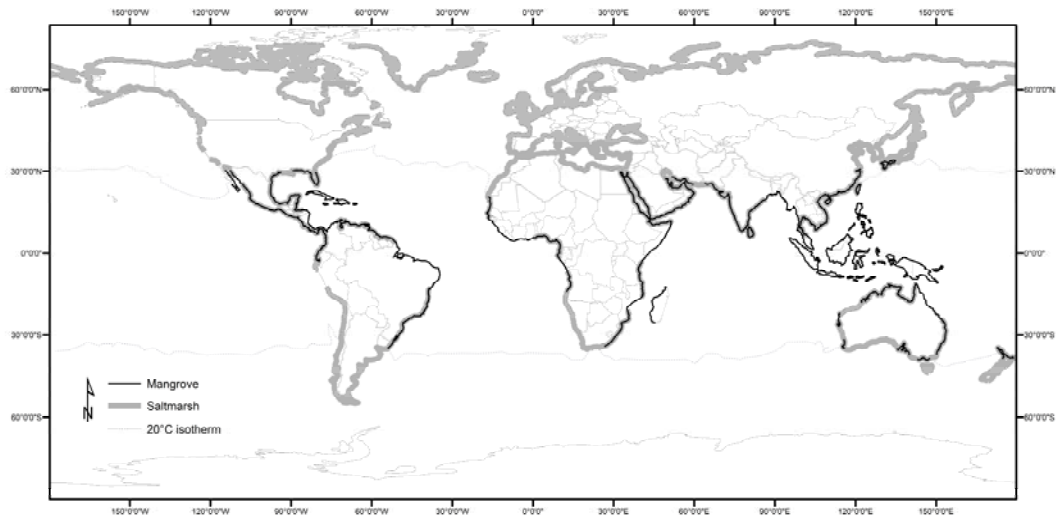


Fig. 1

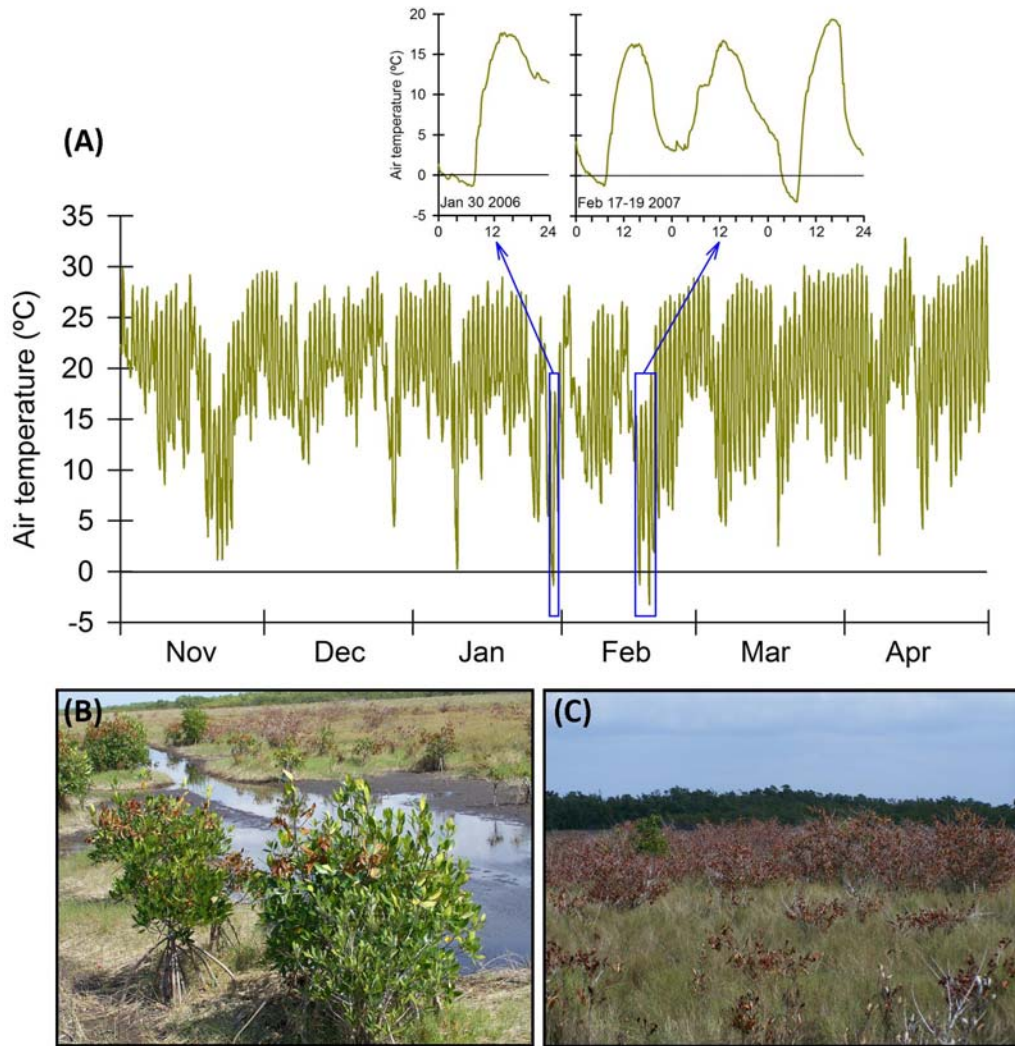


Fig. 2

