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Rainfall and its possible hysteresis effect on the proportional cover of tropical tidal-wetland mangroves and saltmarsh–saltpans

Norman C. Duke[A,E], *Colin Field*[B], *Jock R. Mackenzie*[A], *Jan-Olaf Meynecke*[C] *and Apanie L. Wood*[D]

[A]James Cook University, TropWATER – Centre for Tropical Water and Aquatic Ecosystem Research, Mangrove Hub, Townsville, Qld 4811, Australia.

[B]University of Technology, Sydney, NSW 2007, Australia.

[C]Griffith Centre for Coastal Management and Australian Rivers Institute, Griffith University, Gold Coast, Qld 4222, Australia.

[D]MangroveWatch Ltd, PO Box 1250, Elanora, Qld 4221, Australia.

[E]Corresponding author. Email: norman.duke@jcu.edu.au

Abstract. Mangrove–saltmarsh tidal wetlands are highly dynamic ecosystems, responding and adapting to climate and physical conditions at all spatial and temporal scales. Knowledge of the large-scale ecosystem processes involved and how they might be influenced by climate variables is highly relevant today. For tidal-wetland sites well within the latitudinal range of the mostly tropical mangrove communities, we confirm that average annual rainfall influences vegetative cover, as well as species composition and biomass of tidal wetlands. On the basis of 205 largely unmodified, tropical and subtropical estuaries of northern Australia, a sigmoidal relationship, with a centroid inflection point ~1368 mm, was derived between rainfall and the relative amounts of high-biomass mangroves and low-biomass saltmarsh–saltpan vegetation. The presence and probability of observed combinations of these community types were quantified using the wetland cover index, which is the ratio of total mangrove area to that of mangroves plus intertidal saltmarsh and saltpans. Accordingly, periodic changes in rainfall trends are likely manifest as either encroachment or dieback of mangroves along the ecotones separating them from tidal saltmarsh–saltpans. Presented is a new conceptual framework and model that describes how such ecosystem-scale processes take place in tropical and subtropical tidal wetlands.

Summary. A revised look at tidal wetlands in remote northern Australia has uncovered a startling new understanding of their responses to changing climate. Mangrove and saltmarsh–saltpan communities appear to act as one combined ecological niche. As rainfall conditions vary, one seems to expand while the other contracts, with no net change in total area. Despite all the pressures on tidal wetlands, it seems that moisture and salinity are the dominant and predictable determinants of relative cover for these globally recognised habitats of tropic and subtropic regions.

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Ecotone shift in tropical tidal wetlands

Additional keywords climate change, ecosystem state change, ecotone shift, tidal saltmarsh, wetland cover index.

Introduction

Mangroves and saltmarsh tidal wetlands occur widely within climate and physical conditions that vary at broad spatial and temporal scales (Duke *et al.* 1998; Saintilan 2004; Feller *et al.* 2010). The presence of mangrove forests today, after more than 50 million years (Duke 2017), is testament to their capabilities for longer-term survival and adaptive success. However, these inherent capabilities do not necessarily ensure their continued survival in the face of growing and cumulative direct human influences such as pollutants and physical damage, coupled with rapid changes in climate, sea-level rise and other detrimental pressures (Duke 2014; Spalding *et al.* 2014; Harris *et al.* 2018). Recent events, such as the widespread mass dieback of mangroves in Australia's Gulf of Carpentaria (Duke *et al.* 2017), provide a cogent indication of the limits and vulnerabilities of these otherwise robust and durable ecosystems. At this time, there is great relevance in explaining the role of large-scale processes that are likely to bring change and may, or may not, be linked to global climate change (IPCC 2014). Where the extent and character of tidal-wetland vegetation are constrained by climatic factors (cs. Duke *et al.* 1998), the resulting changes might subsequently affect function as well as the many ecosystem services derived from these habitats, such as their carbon-storage potential (Duke *et al.* 2007; Wilkie 2007; Ward *et al.* 2016).

Several physical and climate drivers are recognised for their ability to limit and influence processes within coastal–estuarine wetland habitats (Duke *et al.* 1998). These specifically include rising sea levels leading to upland encroachment (Jiang *et al.* 2015; Lovelock *et al.* 2015), increases in temperature, driving species shifts to higher latitudes (Osland *et al.* 2013; Saintilan *et al.* 2014), and variations in rainfall, affecting vegetation cover within the tidal-zone habitat (Eslami-Andargoli *et al.* 2013; Osland *et al.* 2014, 2016). Although these studies and others have made substantive contributions, fundamental gaps remain in our understanding of how tidal-wetland ecosystems respond to change, and how particular drivers specifically influence ecosystem processes. Furthermore, both ecological knowledge and the underlying physical data appear lacking. In a recent review of mangrove cover from around the world, Friess and Webb (2014) reported that the fundamental parameter of spatial extent was deficient, leaving year-to-year quantification of longer-term trends fraught at best (also see Jennerjahn *et al.* 2016; Rogers *et al.* 2016). This situation appears compounded further by a limited appreciation of how landscape-scale ecological processes might be affected as specific climate variables change.

In the present assessment, we focused first on temperature and then rainfall as the two dominant climate drivers. Both are known to influence the relative cover of mangrove and the extent of saltmarsh tidal wetland, as defined in the following two groupings:

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(1) *Temperature-influenced changes* to areas of mangrove *v.* saltmarsh vegetation in the vicinity of higher-latitude limits of mangrove. These studies include mangrove expansion linked to periods of greater warmth (Gilman *et al.* 2008; Osland *et al.* 2013, 2014, 2016; Saintilan *et al.* 2014) and the alternate scenario, i.e. mangrove dieback or retreat linked to severe frosts and cooling (Kao *et al.* 2004; Ross *et al.* 2009; Feller *et al.* 2010; Saintilan *et al.* 2014).

(2) *Rainfall-influenced changes* to mangrove *v.* saltmarsh vegetation within the latitudinal limits of mangroves, where mangrove expansion was linked primarily to wetter conditions (Duke *et al.* 2003; Gilman *et al.* 2008; Eslami-Andargoli *et al.* 2013; Duke 2014). The alternate scenario is that mangrove loss or retreat is linked to drought and decreased precipitation (Duke *et al.* 2003; Gilman *et al.* 2008; Duke 2014; Duke *et al.* 2017). A further subgroup concerns rainfall-dominated saltmarsh dieback at sites beyond the higher latitudinal limits of mangrove occurrences. In these cases, there may have been links to drought, decreasing rainfall and sea-level changes (McKee *et al.* 2004; Silliman *et al.* 2005).

Each of these instances featured direct links between temperature and/or rainfall, and ~~the~~ ecological responses of tidal wetland vegetation as physical conditions changed. Although such responses are likely to be confounded at higher-latitude limits of mangroves, it seems reasonable to assume for locations well within the latitudinal range of mangroves, that temperature might be less influential. The observed variability in the vegetative extent among the low-latitude sites appears consistent with the greater importance of rainfall in influencing both the biodiversity and biomass of mangrove vegetation (Duke *et al.* 1998), as well as the percentage cover.

Finding a definitive relationship between vegetation cover and climate variables, particularly between rainfall and observed tidal-wetland vegetation states, has proven elusive. This is despite observations made more than half a century ago by an eminent field botanist, Fosberg (1961), who reported that ‘vegetation-free zones’ of coastal tidal wetlands of northern Australia and Central America were more expansive in locations with drier climates. Fosberg (1961) went on to propose a direct relationship between the vegetation cover of tidal wetlands and rainfall (exemplified in Fig. 1). Several studies since have considered this proposal (Bucher and Saenger 1994; Danaher 1995; Digby *et al.* 1999; Mount and Bricher 2008; Gilman *et al.* 2008; Eslami-Andargoli *et al.* 2013).

Eslami-Andargoli *et al.* (2013) analysed changes in the areal extent of mangrove and saltmarsh within Moreton Bay in Queensland, Australia, and found that mangrove expansion into saltmarsh–saltpan areas was linked to rainfall. Importantly, this was indicative also of how these two habitats could be influenced by each other. However, the strength of the relationship was considered weak, because rainfall explained less than 51% of the variance. They concluded that although additional factors such as localised sea-level variability may have influenced the relationship, it was more likely that there were serious confounding effects from surrounding anthropogenic influences, especially where these differed greatly between estuaries. More recently, a non-linear relationship between mangrove vegetation cover and rainfall was reported by Osland *et al.* (2014, 2016) for tidal wetlands of the Gulf of Mexico, USA. Although these studies appear to have direct relevance to our inquiry, it is likely that their results were confounded by the influence of low temperature because mangrove sites were mostly at, or close to, their upper-latitudinal (= low-temperature) limit.

Bucher and Saenger (1994) used data from both temperate and tropical locations in Australia and described similar relationships of wetlands with rainfall and temperature. Wetland cover was expressed as a proportion of the sum of estuarine areas by both intertidal and subtidal habitats (mangroves, saltmarsh–clay pan, seagrass, lower intertidal flats and open water; Bucher and Saenger 1994). The inclusion of, arguably, independent subtidal habitats in the index, coupled with likely inherent-scale errors in their spatial quantification (cs. the inclusion of below-water seagrass habitat) undermined the reliability of Bucher and Saenger's index. Bucher and Saenger (1994) reported linear trends in mangrove and saltmarsh cover with rainfall, but made no comment on a possible co-relationship between the vegetation types. Here, we present an extended assessment of how wetland cover relates to temperature and rainfall, using a specifically targeted index, the wetlands cover index (WCI). Fig. 2 illustrates how the choice of index affects estimates of vegetation cover.

This study aimed to identify the likely key ecosystem processes involved in governing wetland cover, and how these might influence the temporal change at individual locations. The following three hypotheses were tested: (1) linear or non-linear relationships exist between vegetative cover of tidal wetlands and rainfall; (2) dynamic relationships in the biomass and dominant vegetation states of tropical tidal wetlands correlate with longer-term trends in rainfall; and (3) the ecotone between dominant vegetative components shifts in corresponding retreat or expansion of mangroves depending on longer-term rainfall.

Methods

Study system

A key feature of tidal wetlands is their distinctive zonation and uniform vegetation assemblages (Snedaker 1982; Bunt 1996; Duke *et al.* 1998; Tomlinson 2016). These zones are defined by a small number of notable ecotones. The two primary ecotones follow either the sea-edge contour at lower elevations (~mean sea level), or upper-elevation limits for mangroves that generally mark the landward margin (~highest astronomical tide level). Above the upper ecotone occurs upland, supra-tidal plants and habitat. Between these two ecotones, there are other distinct zones described by their often-uniform assemblages of species-specific vegetation units. The most prominent of these is the ecotone between low-biomass vegetation consisting of herbaceous microphyte-dominated flats of tidal saltmarsh and saltpans (Adam 1995; Johns 2010; Sainty *et al.* 2012) and the high-biomass macrophyte-dominated shrub and tree vegetation of mangroves (Duke 1992; Spalding *et al.* 1997; Tomlinson 2016). An important deduction is that these zones must alter and shift as the constraining

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factors change, such as sea level, inundation frequency, moisture stress, salinity, temperature and exposure, along with other direct human influences such as added nutrients.

Spatial data and the study area

Data on estuarine habitats for tropical northern Australian estuaries within Western Australia, Northern Territory and Queensland were sourced from the OzCoasts database (Australian Government Geosciences Australia 2017). OzCoasts is maintained by the Australian Government Geoscience Australia and includes data collated by Bucher and Saenger (1994). These data were supplemented, for northern Queensland, with survey results from the Cape York Peninsula Land Use Strategy project (Danaher 1995). Collectively, these data included 770 estuaries reported for the Australian region. These data provided classifications of the relative condition of each estuary as pristine, largely unmodified, modified or extensively modified. The analysis in the present study was restricted to 205 pristine or largely unmodified estuaries in tropical Australia, of a scale of 10–100 km^2 (Table1). Estuaries <10 km^2 were excluded to minimise mapping error. Ozcoasts mapping data followed the National Intertidal–Subtidal Benthic (NISB) Habitat Classification Scheme (Mount and Bricher 2008), which is more accurate in larger systems owing to better resolution of available aerial photography and lessened scale-dependent mapping errors. Estuaries >100 km^2 were removed to minimise the impact of within-estuary heterogeneity of rainfall. Measures were taken at any spatial scale, but they represented significant portions of any estuarine system, having most upper-tidal levels represented.

The sites sampled (situated between 11 and 23°S) had maximum temperatures between 30 and 36°C and minimum temperatures between 18 and 24°C, on the basis of the 20–30-year averages. Accordingly, changes in temperature were not considered to have a major defining influence on the sites considered.

Rainfall data

Rainfall data were sourced from the Australian Government Bureau of Meteorology (weather stations, and maps showed isohyets of rainfall zones (Australian Government Bureau of Meteorology, 2017). Rainfall was quantified as the average annual rainfall (AAR) received by each estuary and catchment over the previous 20–30 years. For estuaries >100 km^2, the AAR data available from the Australian Bureau of Meteorology was generated not only on a time-based statistic, but also on the result of an average of all rainfall data available over each catchment.

Wetland cover index and the notable vegetation ecotone

The dramatic and often stark height and biomass gradient between woody plant communities (tree/shrub) and saltmarsh-saltpan plants forms a clearly defined and identifiable ecotone boundary, or zone limit, within tidal wetlands. This ecotone marks a distinct limit of mangrove establishment along the tidal elevation profile defined by seedling desiccation and low soil water content (cs. Clarke and Myerscough 1993). The WCI was applied to broadly quantify the position of this natural ecotone, on the basis of the relative abundance of mangrove vegetation within the tidal wetland overall, and specifically, as the ratio 'mangrove area : total area of tidal wetland', where 'mangrove' equals mangrove-dominated, 'tidal wetland' equals mangrove plus tidal saltmarsh and saltpan, 'saltmarsh and saltpan' equals tidal saltmarsh plus high intertidal saltpans. The WCI provided a simple measure of the dynamic state of tidal-wetland vegetation cover for all 205 estuarine catchments (Table 1).

Data analysis

Two regressions were performed between the variables WCI and the AAR. The first regression was a linear least-square regression and the second was a non-linear regression fitting a logistic curve of the general form

$$y = \frac{1}{1 + e^{-bx-c}}$$

where y is the fitted value of continuous probability of mangrove presence in the range 0–1, b is the slope parameter, and c is the estimated centre of transition. The two models were then examined for statistical significance and compared using Akaike information criterion (AIC). The AIC is a measure of the relative quality of statistical models for a given set of data. The lower the value of the AIC number, the better the model. Models were fitted using R (ver. 3.3.3, xxx; 6 March 2017). The resulting logistic curve was evaluated by calculating the point of inflection and the maximum rate of change. The basic differential equation underlying the logistic curve was assumed to be as follows:

$$\frac{\mathrm{d}(\mathrm{WCI})}{\mathrm{d}(\mathrm{AAR})} = \alpha \mathrm{WCI}(1 - \mathrm{WCI})$$

where α is a positive constant. By taking the second differential, it can be shown from this equation that the point of inflection must occur when WCI is 0.5. The value of AAR at the point of inflection and maximum rate of change of WCI with AAR can be found using this equation and the derived logistic equation.

Results

There was a significant linear relationship between the WCI and AAR over 20–30 years (regression analysis: $F_{203} = 72.31$, $P < 0.001$, $R^2 = 0.259$; linear equation: WCI = 0.00048 × AAR – 0.16; see Fig. 3). The logistic regression of the WCI against the AAR over 20–30 years produced the following equation:

$$\mathrm{WCI} = \frac{1}{1 + e^{(0.00224\mathrm{AAR} - 3.013)}} \quad \text{(see Fig. 3)}$$

This equation gives the probability of the presence of mangrove. Both the coefficient of AAR and the intercept were significant at the <0.001 level. The linear regression had an AIC value of 1953 and the logistic regression yielded an AIC value of 243. Therefore, it can be concluded that the logistic regression yielded the superior model.

The point of inflection and the maximum rate of change of WCI with AAR were derived from the logistic equation, using Eqn 1 (see Methods). The point of inflection occurred at WCI = 0.5 and AAR = 1368 mm. The maximum rate of change of WCI with AAR was 5.5% of WCI for 100 mm of AAR. The range in which the probability shifts by more than 5% per 100 mm of rainfall was between an upper limit of probability of 0.65 and a lower limit of 0.39. It follows that in the range of 1086–1651 mm of AAR, the probability of the presence of mangroves shifts positively by 5% per 100 mm of rainfall.

Discussion

Tidal wetlands redefined

Tidal wetlands along tropical and subtropical coastlines worldwide form a distinct ecological niche between the mean sea level and the highest tide level. This upper tidal niche, regularly inundated and washed by tidal waters and estuarine flows, is occupied by two well recognised vegetation types of mangroves and tidal saltmarsh with saltpans. Plants of these unique vegetation types share specialised physiological, morphological and anatomical traits for coping with salt and regular inundation by river and sea waters. This is in deference to their often quite different ancestral lineages and genetic make-up (Tomlinson 2016; Duke 2017). Such inherent differences explain in part why the various species of mangrove and saltmarsh plants respond differently to overall environmental drivers such as rainfall. Where rainfall conditions differ, these broad vegetation types appear to adjust their relative cover, while occupying the same combined area. Accordingly, estuarine sites with a higher rainfall had greater proportions of mangroves and, correspondingly, smaller areas of tidal saltmarsh and saltpan (see Fig. 1). In locations where rainfall levels were relatively low, the opposite was observed, with a reduced proportion of mangroves and a greater extent of saltmarsh and saltpan. Although it remains to be fully appreciated, the most plausible explanation is a dynamic process where changes in prevailing rainfall conditions lead to adjustments and changes in the respective amounts of dominant vegetation types. Accordingly, it is proposed that the relative extent of tidal-wetland plants is influenced by moisture availability, affecting the presence and growth of taller, high-biomass plants that capture light and out-compete their shorter co-inhabitants in circumstances when rainfall levels are sufficiently high.

Our current assessment re-examined the overall relationship between mangrove and saltmarsh vegetation, and AAR, as observed by Fosberg (1961). We found that the relationship was best described by a sigmoidal curve rather than a linear one. This sigmoidal relationship gave a measure of the probability of the presence of mangroves as a function of AAR. In so doing, the relationship has been usefully described and quantified as a model defined by proposed shifts in the ecotone between mangrove and tidal saltmarsh–saltpan vegetation. The model specifically depicts a range of AAR between 1086 mm and 1651 mm, where the probability of the presence of mangroves increases by 5% per 100 mm of AAR.

Geographic characterisation of the relationship with rainfall

The relationship between rainfall and WCI can be used also to identify areas at risk of change in the composition of tidal-wetland vegetation. In Fig. 4, zones of predicted WCI values are shown for northern Australia, as derived from the 30-year AAR map (1976–2005). The time period corresponds with the majority of OzCoasts estuarine-mapping data taken from imagery collected up to 2005. It should also be noted that upland areas are shaded well inland because tidal wetlands are influenced by rainfall throughout their larger catchment areas, as well as on the downstream tidal-wetland areas themselves (Smith and Duke 1987; Duke *et al*. 1998). This tidal-wetland risk map can be used in the following two ways (see Fig. 4): (1) to compare predicted vegetative states with observed values at specific sites; and (2) to show tidal-wetland areas that are likely to have specific vegetative states, along with the underlying risks and vulnerabilities associated with each. It was evident that observed vegetative states at specific sites broadly matched the predicted WCI zones.

Furthermore, on the basis of the relationship between the AAR and WCI (Fig. 4), notable changes may be expected along the tidal-wetland ecotone in response to changes in AAR. These effects are likely to manifest as an ecotone shift, with either mangrove expansion or mangrove loss being expected under the following scenarios: (1) increases of ~100 mm in AAR in zones with predicted WCI values between 40 and 80% (mapped as pink and green zones) might result in gains up to 10% in the WCI, equating to significant mangrove expansion; or (2) declines of ~100 mm in AAR in zones with predicted WCI values between 20 and 40% (mapped as pink and yellow zones) might result in losses up to 10% in the WCI, equating to severe mangrove dieback. The likelihood of such changes is expected to differ according to these zones where, for example, outside the zones (i.e. in regions receiving <500 mm or >2000 mm AAR) changes of 200–1000 mm in AAR would have a limited effect on the WCI, and the proportional extent of mangrove cover would, therefore, remain relatively constant. The position of an estuarine system within a zone exhibiting a predicted WCI value between 20 and 80% (mapped as yellow, pink and green in Fig. 4) is most pertinent for estuarine systems that have been subject to either long-term increases or long-term declines in the AAR over the past half century. In Fig. 4, the zone of pink shading with red-dashed line indicates those regions falling near the ‘inflection point’ in vegetative status, making them most at risk of significant impacts from relatively small changes in the AAR (±100 mm, see below). As such, the ‘inflection point line’ or zone identifies both areas most at risk, and the dividing line between mangrove-dominated and tidal saltmarsh–saltpan-dominated wetlands. It is of interest that this zone of relatively unstable conditions includes most coastal areas of northern Australia.

Further deductions from the relationship

Because the spatial evidence presented portrays a range of wetland-cover (WCI) states correlated with rainfall, it is reasonable to assume that these states could have been achieved only if past vegetative states had responded to ambient rainfall conditions. And, as rainfall conditions changed, the corollary is that vegetative states need to have responded for the correlation to hold. Therefore, it can be deduced from these spatial data that changes between mangrove-dominated and saltmarsh–saltpan-dominated vegetative states appear to exist and function in a state of hysteresis. There is good reason to believe that vegetative condition depends on the on-going condition of climate factors, in particular rainfall. A range of possible states and intermediate conditions are portrayed in the conceptual model (Fig. 5). Trends towards alternate extreme states depend on both spatial and temporal aspects of climate and levels of precipitation. In accordance with such circumstances, the model schematic describes a range of condition states defined by the WCI, where there might be expansion or contraction of mangroves in regions within their natural latitudinal range. The model depicts the extreme range of hypothetical states, with trends between possibly increasing wet- or dry-condition states. To fully understand how these habitat responses in vegetation cover take place, case studies of historical change are needed to exemplify how temporal changes in vegetation cover match past changes in climate.

Overall conclusions

Our findings affirmed Fosberg's (1961) assertion of a significant and meaningful relationship between vegetative cover of tidal wetlands and rainfall of tropical and subtropical areas. In addition, the relationship describes the strong likelihood of a functionally dynamic ecosystem alternating between high- and low-biomass states determined by longer-term trends in rainfall and climate. This observation is likely to have wider implications when considering associated and dependent biota, as well as the overall productive capacity of these habitats and their delivery of ecosystem services. The model developed helps explain how the relative cover of mangrove and saltmarsh vegetation of tidal-wetland systems are demonstrably predictable, provided local, direct human pressures are minimal.

Changes are also likely manifest as longer term, decadal-scale shifts in vegetation ecotones between high-biomass and low-biomass tidal-wetland communities. In each case, the relationship identified provides a means to extrapolate levels of longer-term rainfall from current observations of extent of tidal-wetland plant assemblages. Although case studies of change to specific estuarine systems are needed (cs. Nicholls *at al*. 1997), it will be important to consider whether the model described in the present treatment can help explain each instance of loss or gain within tidal-wetland plant assemblages. Future mapping of tidal-wetland areas must at least include concurrent measures of both mangrove and tidal saltmarsh–saltpan communities, as well as the clear attribution of the dates of source imagery.

We identified a marked ecotone at the interface between distinctly high- and low-biomass vegetation types. This dynamic interface is likely to manifest further as the location for encroachment–expansion or dieback–contraction to match corresponding increases or decreases in longer term rainfall. Future case studies are needed to record how, where and when mangrove vegetation might change as rainfall conditions change. They are also needed for an evaluation of the role of moisture stress to help explain each significant instance of loss or gain within tidal-wetland assemblages.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

<edb>Adam, P. (1995). Saltmarsh. The State of the Marine Environment report for Australia: technical annex 1. The marine environment. (Eds L. P. Zann and P. Kailola.) pp. 97–105. Department of the Environment, Sport and Territories, Canberra (Ocean Rescue 2000), ACT, Australia.</edb>

<jrn>Allan, R. J., Beck, K., and Mitchell, W. M. (1990). Sea level and rainfall correlations in Australia: tropical links. *Journal of Climate* **3**, 838–846. doi:10.1175/1520-0442(1990)003<0838:SLARCI>2.0.CO;2 </jrn>

<jrn>Asbridge, E., Lucas, R., Ticehurst, C., and Bunting, P. (2016). Mangrove response to environmental change in Australia's Gulf of Carpentaria. *Ecology and Evolution* **6**(11), 3523–3539. doi:10.1002/ece3.2140 </jrn>

<eref>Australian Government Bureau of Meteorology (2018). BOM website. Accessed between 2013–2018. http://www.bom.gov.au.</eref>

<eref>Australian Government Geosciences Australia (2018). OzCoasts website. Accessed between 2013-2018. http://ozcoasts.org.au.</eref>

<jrn>Bucher, D., and Saenger, P. (1994). A classification of tropical and subtropical Australian estuaries. *Aquatic Conservation* **4**, 1–19. doi:10.1002/aqc.3270040102 </jrn>

<jrn>Bunt, J. S. (1996). Mangrove zonation: an examination of data from seventeen riverine estuaries in tropical Australia. *Annals of Botany* **78**, 333–341. doi:10.1006/anbo.1996.0128 </jrn>

<jrn>Clarke, P. J., and Myerscough, P. J. (1993). The intertidal distribution of the grey mangrove (*Avicennia marina*) in south-eastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology* **18**, 307–315. doi:10.1111/j.1442-9993.1993.tb00458.x </jrn>

<other>Danaher, K. F. (1995). Marine vegetation of Cape York Peninsula. Technical report number NR06: marine plant (seagrass/mangrove) distribution. CYPLUS – Cape York Land Use Strategy, Office of the Co-ordinator General of Queensland, Brisbane, Department of the Environment, Sport and Territories, Canberra, ACT, Australia, *and* Queensland Department of Primary Industries, Brisbane, Qld, Australia.</other>

<bok>Digby, M. J., Saenger, P., Whelan, M. B., McConchie, D., Eyre, B., Holmes, N., and Bucher, D. (1999). ‘A physical classification of Australian estuaries.’ (Land and Water Resources Research and Development Corporation: Canberra, ACT, Australia.)</bok>

<edb>Duke, N. C. (1992). Mangrove floristics and biogeography. In ‘Tropical Mangrove Ecosystems’. (Eds A. I. Robertson and D. M. Alongi.) pp. 63–100. (American Geophysical Union: Washington, DC, USA.)</edb>

<jrn>Duke, N. C. (2001). Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. *Wetlands Ecology and Management* **9**, 257–269. doi:10.1023/A:1011121109886 </jrn>

<bok>Duke, N. C. (2006). ‘Australia’s Mangroves. The Authoritative Guide to Australia’s Mangrove Plants.’ (University of Queensland and Norman C Duke: Brisbane, Qld, Australia.)</bok>

<edb>Duke, N. C. (2014). Mangrove coast. In ‘Encyclopedia of Marine Geosciences’. (Eds J. Harff, M. Meschede, S. Petersen, and J. Thiede.) pp. 412–422. (Springer: Dordrecht, Netherlands.)</edb>

<edb>Duke, N. C. (2017). Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities and common evolutionary processes. In ‘Mangrove Ecosystems: a Global Biogeographic Perspective. Structure, Function and Services, Vol. 2’. (Eds V. H. Rivera-Monroy, S. Y. Lee, E. Kristensen, and R. R. Twilley.) pp. 17–53. (Springer.) doi:10.1007/978-3-319-62206-4_2</edb>

<jrn>Duke, N. C., Ball, M. C., and Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* **7**(1), 27–47. doi:10.2307/2997695</jrn>

<bok>Duke, N. C., Lawn, P., Roelfsema, C. M., Phinn, S., Zahmel, K. N., Pedersen, D., Harris, C., Steggles, N., and Tack, C. (2003). Assessing historical change in coastal environments. Port Curtis, Fitzroy River Estuary and Moreton Bay regions. Historical Coastlines Project, Marine Botany Group, Centre for Marine Studies, The University of Queensland, Brisbane, Qld, Australia.</bok>

<jrn>Duke, N. C., Meynecke, J.-O., Dittmann, S., Ellison, A. M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K. C., Field, C. D., Koedam, N., Lee, S. Y., Marchand, C., Nordhaus, I., and Dahdouh-Guebas, F. (2007). A world without mangroves? *Science* **317**, 41–42. doi:10.1126/science.317.5834.41b </jrn>

<jrn>Duke, N. C., Kovacs, J. M., Griffiths, A. D., Preece, L., Hill, D. J. E., van Oosterzee, P., Mackenzie, J., Morning, H. S., and Burrows, D. (2017). Large-scale dieback of mangroves in Australia’s Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. *Marine and Freshwater Research* **68**(10), 1816–1829. doi:10.1071/MF16322</jrn>

<jrn>Eslami-Andargoli, L., Dale, P., and Sipe, N. (2013). Does spatial scale affect the pattern of mangrove change under different rainfall regimes? An example in southeast Queensland, Australia. *Austral Ecology* **38**, 208–218. doi:10.1111/j.1442-9993.2012.02393.x </jrn>

<jrn>Feller, I. C., Lovelock, C. E., Berger, U., McKee, K. L., Joye, S. B., and Ball, M. C. (2010). Biocomplexity in mangrove ecosystems. *Annual Review of Marine Science* **2**, 395–417. doi:10.1146/annurev.marine.010908.163809 </jrn>

<jrn>Fosberg, F. R. (1961). Vegetation-free zone on dry mangrove coasts. *US Geological Survey Professional Paper* **424-D**, 216–218.</jrn>

<jrn>Friess, D. A., and Webb, E. L. (2014). Variability in mangrove change estimates and implications for the assessment of ecosystem service provision. *Global Ecology and Biogeography* **23**(7), 715–725. doi:10.1111/geb.12140 </jrn>

<jrn>Gilman, E. L., Ellison, J., Duke, N. C., and Field, C. (2008). Threats to mangroves from climate change and adaptation options: a review. *Aquatic Botany* **89**, 237–250. doi:10.1016/j.aquabot.2007.12.009 </jrn>

<jrn>Harris, R. M. B., Beaumont, L. J., Vance, T., Tozer, C., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M., Keatley, M. R., Woodward, C. A., Williamson, G., Duke, N. C., and Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* **8**, 579–587. doi:10.1038/s41558-018-0187-9 </jrn>

<eref>IPCC (2014). Climate change. Synthesis report. Summary for policymakers. Intergovernmental Panel on Climate Change (IPCC), WMO & UNEP, Paris, France. Available at http://www.ipcc.ch/report/ar5/syr/ [Verified xx XXX xxxx].</eref>

<bok>Jennerjahn, T. C., Gilman, E., Krauss, K. W., Lacerda, L. D., Nordhaus, I., and Wolanski, E. (2016). Chapter 7: mangrove ecosystems and climate change. In ‘Mangrove Ecosystems’.</bok>

<jrn>Jiang, J., DeAngelis, D. L., Teh, S.-Y., Krauss, K. W., Wang, H., Li, H., Smith, T. J. III, and Koh, H.-L. (2015). Defining the next generation modeling of coastal ecotone dynamics in response to global change. *Ecological Modelling* **326**, 168–176 doi:10.1016/j.ecolmodel.2015.04.013.</jrn>

<bok>Johns, L. (2010). ‘Field Guide to Common Saltmarsh Plants of Queensland.’ (Queensland Department of Employment, Economic Development and Innovation: Brisbane, Qld, Australia.)</bok>

<jrn>Kao, W. Y., Shih, C. N., and Tsai, T. T. (2004). Sensitivity to chilling temperatures and distribution differ in the mangrove species *Kandelia candel* and *Avicennia marina*. *Tree Physiology* **24**(7), 859–864. doi:10.1093/treephys/24.7.859 </jrn>

<jrn>Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., Rogers, K., Saunders, M. L., Sidik, F., Swales, A., Saintilan, N., Thuyen, L. X., and Triet, T. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**, 559–563. doi:10.1038/nature15538</jrn>

<jrn>McKee, K., Mendelssohn, I. A., and Materne, M. D. (2004). Acute saltmarsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? *Global Ecology and Biogeography* **13**, 65–73. doi:10.1111/j.1466-882X.2004.00075.x </jrn>

<bok>Mount, R. E., and Bricher, P. J. (2008). Estuarine, Coastal and Marine (ECM) National Habitat Mapping Project, project report, version 1, February 2008. Spatial Science Group, School of Geography and

Environmental Studies, University of Tasmania. Report to the Department of Climate Change and the National Land and Water Resources Audit, Canberra, ACT, Australia.</bok>

<jrn>Nicholls, N., Drosdowsky, W., and Lavery, B. (1997). Australian rainfall variability and change. *Weather* **52**(3), 66–71. doi:10.1002/j.1477-8696.1997.tb06274.x </jrn>

<jrn>Osland, M. J., Enwright, N. M., Day, R. H., and Doyle, T. W. (2013). Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology* **19**, 1482–1494 . doi:10.1111/gcb.12126</jrn>

<jrn>Osland, M. J., Enwright, N. M., and Stagg, C. L. (2014). Freshwater availability and coastal wetland foundation species: ecological transitions along a rainfall gradient. *Ecology* **95**, 2789–2802 . doi:10.1890/13-1269.1</jrn>

<jrn>Osland, M. J., Enwright, N. M., Day, R. H., Gabler, C. A., Stagg, C. L., and Grace, J. B. (2016). Beyond just sea-level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology* **22**, 1–11. doi:10.1111/gcb.13084 </jrn>

<jrn>Rogers, K., Boon, P., Branigan, S., Duke, N. C., Field, C. D., Fitzsimons, J., Kirkman, H., Mackenzie, J., and Saintilan, N. (2016). Can Australian legislation and policy protect mangrove and saltmarsh and their ecosystem services? *Marine Policy* **72**, 139–155. doi:10.1016/j.marpol.2016.06.025 </jrn>

<jrn>Ross, M. S., Ruiz, P. L., Sah, J. P., and Hanan, E. J. (2009). Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. *Global Change Biology* **15**(7), 1817–1832. doi:10.1111/j.1365-2486.2009.01900.x </jrn>

<jrn>Saintilan, N. (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine, Coastal and Shelf Science* **61**, 591–601. doi:10.1016/j.ecss.2004.07.002 </jrn>

<jrn>Saintilan, N., and Williams, R. J. (1999). Mangrove transgression into salt marsh environments in south-east Australia. *Global Ecology and Biogeography* **8**, 117–124. doi:10.1046/j.1365-2699.1999.00133.x </jrn>

<jrn>Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., and Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* **20**, 147–157. doi:10.1111/gcb.12341 </jrn>

<edb>Sainty, G., Hosking, J., Carr, G., and Adam, P. (Eds) (2012). 'Estuary Plants and What's Happening to Them in South-East Australia.' (Sainty Books: Sydney, NSW, Australia.)</edb>

<jrn>Silliman, B. R., Koppel, J. d., Bertness, M. D., Stanton, L. E., and Mendelssohn, I. A. (2005). Drought, snails, and large-scale die-off of southern US salt marshes. *Science* **310**, 1803–1806 . doi:10.1126/science.1118229</jrn>

<jrn>Smith, T. J. III, and Duke, N. C. (1987). Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. *Journal of Biogeography* **14**, 9–19. doi:10.2307/2844783 </jrn>

<edb>Snedaker, S. C. (1982). Chapter 1. Mangrove species zonation. Why? In ‘Contributions to the Ecology of Halophytes, Vol. 2’. (Eds D. N. Sen and K. S. Rajpurohit.) pp. 111–125. (Dr W. Junk: The Hague, Netherlands.)</edb>

<edb>Spalding, M. D., Blasco, F., and Field, C. D. (Eds) (1997). ‘World Mangrove Atlas.’ (International Society for Mangrove Ecosystems: Okinawa, Japan.)</edb>

<jrn>Spalding, M. D., McIvor, A. L., Beck, M. W., Koch, E. W., Möller, I., Reed, D. J., Rubinoff, P., Spencer, T., Tolhurst, T. J., Wamsley, T. V., van Wesenbeeck, B. K., Wolanski, E., and Woodroffe, C. D. (2014). Coastal ecosystems: a critical element of risk reduction. *Conservation Letters* 7(3), 293–301. doi:10.1111/conl.12074 </jrn>

<bok>Tomlinson, P. B. (2016). ‘The Botany of Mangroves’, 2nd edn. (Cambridge University Press: Cambridge.)</bok>

<jrn>Ward, R. D., Friess, D. A., Day, R. H., and MacKenzie, R. A. (2016). Impacts of climate change on mangrove ecosystems: a region by region overview. *Ecosystem Health and Sustainability* 2(4), e01211. doi:10.1002/ehs2.1211 </jrn>

<edb>Wilkie, M. L. (Ed.) (2007). ‘The World’s Mangroves 1980–2005. A Thematic Study Prepared in the Framework of the Global Forest Resources Assessment 2005. FAO Forestry Paper.’ (Food and Agriculture Organization of the United Nations: Rome, Italy.)</edb>

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Table 1. Summary of available data for an estuarine site of minimal disturbance grouped according to average catchment rainfall, areas of key tidal-wetland vegetation types (mangrove, saltmarsh–saltpan) and estimates of wetland cover index (see text) for three Australian states

WA, Western Australia; NT, Northern Territory; Qld, Queensland. Source: Australian Government Geosciences Australia (2017)

Data feature	WA	NT	Qld	Total
Mangrove-species diversity*	19	32	45	46
Total in all of national database				
Estuarine systems in database	227	151	322	770
Area of mangrove (km^2)	1985	3289	3215	8560
Area of tidal saltmarsh–saltpan (km^2)	5137	4925	5253	15442
Wetland cover index (%)	27.9	40	38	35.7
Estuarine systems in study				
Pristine- and medium-area systems	35	76	94	205
Area of mangrove (km^2)	485	1255	1095	2834
Area of tidal saltmarsh–saltpan (km^2)	494	1425	1800	3720
Total tidal-wetland area (km^2)	979	2680	2895	6554
Mean annual rainfall (mm)	911	1339	1278	1248
Wetland cover index (%)	49.5	46.8	37.8	43.2

Fig. 1. Examples of tidal-wetland vegetation (mangrove plus tidal saltmarsh–saltpan, as high- and low-biomass states respectively), showing variations in percentage mangrove cover in relation to mean annual rainfall (Duke *et al.* 2003) for four sites in north-eastern Australia: (*a*) ~96% mangrove in Mutchero Inlet south of Cairns at ~3600 mm rainfall (17°14′01.75″S, 145°57′03.00″E); (*b*) ~75% mangrove in Cattle Creek near Ingham at ~1800

mm rainfall (18°52′40.91″S, 146°16′59.95″E); (*c*) ~47% mangrove in Alligator Creek south of Townsville at ~1032 mm rainfall (19°18′34.68″S, 146°55′56.27″E); and (*d*) ~28% mangrove on Balaclava Island off the mouth of the Fitzroy River, at ~700 mm rainfall (23°34′31.35″S, 150°56′00.07″E).

Fig. 2. Mangrove cover in relation to (*a*) rainfall and (*b*) Australian state or territory, as quantified by the wetland cover index (WCI, present study) and the BS index (Bucher and Saenger 1994). WCI expressed estuarine mangrove cover as a proportion of the sum of cover of intertidal habitats (mangroves, saltmarshes and saltpans). BS quantified mangrove cover as a proportion of intertidal as well as subtidal habitats (mangroves, saltmarsh/clay pan, seagrass, lower intertidal flats and open water). Indices were calculated from the dataset used by Bucher and Saenger (1994).

Fig. 3. The relationship between tidal-wetland vegetation cover and average annual rainfall in estuarine sites across northern tropical Australia. The 205 estuarine locations covered a range of climatic conditions from semi-arid to very wet conditions. Both linear and logistic regressions were significant. Based chiefly on the logistic curve, the pink-shaded selection of sites, bordered by yellow (more arid) and green (wetter) groupings, depict an inflection point (1000–1500 mm average annual rainfall) between saltmarsh–saltpan-dominated (low-biomass) systems and mangrove-dominated (high-biomass) systems.

Fig. 4. A map of northern Australia depicting areas at risk of change (cs. mangrove loss vs mangrove expansion) as a result of changes in longer-term trends in rainfall. Model parameters were based on the comparison of observed and predicted levels of dominance of tidal-wetland vegetation types before 2006, which were derived from area data sourced from the OzCoasts online database (Australian Government Geosciences Australia, 2017; see Table 1), and mean annual-rainfall data (Australian Government Bureau of Meteorology 2017; central inset). Coastal areas occupied by mangroves are shown with dark blue shading (modified from Duke 2006). Landward shaded zones show five levels of predicted vegetative dominance (see Methods and Fig. 3) for amounts of mean annual rainfall in respective coastal and estuarine catchment areas. The pink zone and red dashed line represent areas of greatest likelihood of change in vegetation cover, where annual rainfall had trended towards either wetter or drier conditions (see Fig. 3, 5). Individual site records in the OzCoasts database were plotted as coloured-circle symbols at respective coastal locations, each according to specific levels of WCI. The main legend (lower centre) describes the five mangrove-dominance groupings, rainfall conditions and summary parameters of predicted levels of risk.

Fig. 5. Proposed model of ecotone shift in mangrove tidal wetlands. The cycle has opposing extreme states in wet and dry climates respectively. Intermediate states are normal, with marked ecotones between mangrove and saltmarsh–saltpan vegetation types present. These observations describe the possible hysteresis pathway where the ecotone between mangroves and saltmarsh–saltpan shifts in predictable ways with longer-term trends in rainfall.