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REMOTE SENSING (P BUNTING, SECTION EDITOR)

Mangrove Response to Environmental Changes Predicted Under Varying Climates: Case Studies from Australia

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Abstract Over the past few decades, many of the world's mangrove forests have experienced significant change, which can be attributed to human activities and also natural causes. However, a component may also be due to factors that are commonly associated with anthropogenic climate change including higher air temperatures, variations in rainfall, increases in storm frequencies and intensities, and rising sea levels. The expected responses of mangrove to these drivers include changes in extent (latitudinal, seaward and landward), growth rates and productivity, and species composition. This paper reviews such responses and then, using examples from Australia, illustrates how these might appear within and be detected using single-date or time-series of remote sensing data acquired in different modes (e.g., aerial photography, optical and radar). In doing so, it informs countries and organisations of the potential impacts of climate change on mangrove forests and how these may be monitored using remote sensing data.

Keyword Mangrove · Estuary · Monitoring · Remote sensing · Climate change · Sea-level rise

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Introduction

For natural and modified mangrove ecosystems, attributing a particular event or process to climate change has proved difficult given the uncertainties as to what constitutes change from a *normal* climate pattern. However, the potential impacts of a changing climate on mangroves can be suggested by observing what has occurred in response to specific and historic climate-related phenomena including extremes of temperatures and precipitation, warming and drying trends, damaging storms and cyclones, flooding, storm surges, ocean acidification and CO_2 fertilisation [1••, 2]. This paper therefore reviews current evidence of the impacts of climate-related phenomena on the extent, structure, biomass, species composition and functioning of mangroves at a global level.

The effects of climate change are most evident where mangroves have remained relatively undisturbed from human activities. However, finding such areas is difficult as mangroves have already been cleared from over 200,000 km^2 of coastline [3] through resource use, industrialization, urbanisation and aquaculture. Many have also been affected by pollution and upstream land use [4]. The most likely areas for identifying the impact of climate change, therefore, are protected areas (e.g., national parks). Within these, human impacts are minimal and mangrove response is likely to be a function of natural events and processes, including climate-related phenomena, and multifaceted interactions between sea level, precipitation, hydrology, sediment dynamics and rate of accumulation, storm events and land position/subsidence [5–7]. Australia is particularly well suited for studying climate impacts as mangrove forests are extensive and undisturbed from human activities due to vast areas that are uninhabited and legislative protection in reserves. This paper therefore reports on case studies from the north and east of the continent where changes in mangroves have been observed within single-date or time-series of optical and/or radar remote sensing data, which represent those associated with climate-related event or process.

There are numerous papers to suggest mangroves are affected by climate change, including sea level fluctuation [8, 9••, 10], rainfall [5, 11], air temperature [12, 13] and cyclonic/storm activity [14, 15]. However, many of these deal with the future (potential) rather than the actual impacts [5, 16–19]. In addition, there is often confusion when delimiting individual causes due to complex climatic and environmental interactions such as the relationship between water level and rainfall [20•]. The intention of this study therefore is to provide examples of how contemporary climate-related impacts may manifest themselves within the remote sensing data whilst not claiming that these are the result of human-induced climatic change nor that the responses identified in Australia can be directly extrapolated across the tropics.

Drivers of Change

During the period 1880 to 2010, the globally averaged combined land and ocean temperature warmed by 0.85 (0.65–1.06) °C [2] and, by the end of the twenty-first century, is likely to increase by a further 3.2–5.4 °C [2, 21]. The rate of warming of the ocean is, however, significantly less than over land due to the high specific heat capacity of water and increased evaporation [21]. Global Sea Surface Temperature (SST) increased by 0.76 °C±0.19 °C between 1850 and 2005 and the average rate of warming over the last 50 years was 0.13 °C±0.03 °C per decade; double that for the previous century [2]. This change in SST has influenced ocean stratification and circulation and led to a reduction in sea ice at higher latitudes.

Global precipitation over the terrestrial land surface has increased by approximately 2 % since 1900, with an uneven spatial distribution [22]. During the 20th century, precipitation increased by 0.5–1 % every 10 years over the majority of the mid and high latitude regions of the northern hemisphere. The subtropical northern hemisphere noted a decrease in rainfall of 0.3 % per decade whilst tropical regions only experienced an increase of 0.2–0.3 % per decade [23]. Whilst difficult to obtain averages over large oceanic regions, direct measurements and models have inferred that precipitation is increasing over the majority of the tropical oceans. For example, [24] predicted an increase in global precipitation of approximately 25 % by 2050, with an uneven regional distribution. Precipitation will directly influence river discharge and indirectly result in changes to salinity.

In recent years, models and theories have been used to indicate likely future trends in the frequency and intensity of storms and cyclones. Some predict increased frequencies and intensities of cyclones with an associated increase in the mean and peak rainfall intensity [24–26]. The predictions are based upon cyclonic histories and predicted changes in, for example, atmospheric and ocean temperatures. For instance, in the North Atlantic, an increase in the intensity of tropical cyclones has been observed since 1970; with this coinciding with increased SSTs. Therefore, future predictions assume that as SSTs increase, there may be more frequent and intense cyclones in some regional ocean basins with greater precipitation, wind speeds and therefore wave heights. However, the datasets are incomplete and often contain conflicting results, which compromises the identification of long-term cyclonic patterns and future predictions. In particular, it is the lack of complete cyclone records before regular satellite observations in 1970 that prevents accurate long-term predictions [27, 28]. Cyclone tracks are also expected to shift in a poleward direction, particularly in the southern hemisphere [2].

Sea level has been rising since the mid-1800s. During the twentieth century, global sea level rose by 0.17–0.21 m, which equates to approximately 1.5–2.0 mm per annum [29]. Between 1993 and 2010, the rates of sea level rise ranged from 2.8 to 3.6 mm per annum [2]. Satellite measurements during the early twenty-first century also imply the rate of increase has risen to 3.1 mm per annum. Future sea level projections suggest the rate is likely to increase further, although the exact magnitude is currently disputed. The disagreement occurs largely due to differences in the likely contributions of melting land-based ice and thermal expansion [2]. For instance, a number of sea level projections have not accounted for the ice sheet dynamics [26], the gravity-driven movement of which increases in accordance with a rise in temperature. Moreover, there are discrepancies regarding predicted global temperature increases, due to a range of different scenarios based on the level of possible emissions [30].

Representative concentration pathways (RCPs) are used for modelling greenhouse gas emission projections based on population size, economic activity, lifestyle, energy use, land use patterns, technology and climate patterns [30, 31]. The RCPs were developed under the collaboration of the Integrated Assessment Modelling Consortium, the World Climate Research Programme's Working Group on Coupled Modelling and the International Geosphere-Biosphere Programme's earth system modelling project [32]. RCP2.6 represents a scenario whereby the atmospheric temperature is 2 °C above pre-industrial levels; RCP8.5 relates to a state with very high greenhouse gas emissions and a ~9 °C rise in temperature above pre-industrial levels [33]. Under all emission scenarios, surface temperatures are projected to rise over the twenty-first century and it is very likely that extreme precipitation events will become more intense and frequent in many regions. In addition, it is predicted that 95 % of the ocean area will experience a rise in sea level, very likely at a faster rate than observed from 1971 to 2010, with this being 0.26 to 0.55 m for RCP2.6 and 0.45 to 0.82 m for RCP8.5. One of the most widely accepted predictions is a rise in sea level of 0.18–

0.59 m from 1990 to 2090 [26]. Approximately 70 % of the coastlines worldwide are expected to experience a sea level change within ±20 % of the global mean.

Manifestation of Changes in Mangroves

The primary changes in mangroves associated with variations in climate-related phenomena are highlighted in Fig. 1, together with the direction of change. In general, increases in temperature and precipitation have a positive impact on mangroves up to an upper threshold, whereas storm/cyclone damage has an adverse effect particularly in the short-term. The impact of rising sea levels is less obvious with these being dependent on the hinterland geomorphology, degree of development and sediment availability, as outlined in the following sections.

Fluctuating Sea Levels

Mangroves are one of the primary ecosystems to be impacted by sea level fluctuations [34] and changes in extent, species composition, structure and function are expected. Three widely accepted scenarios regarding the response of mangroves are given in Table 1 [44]. In the case of Scenario 2 (landward expansion), coastal development or terrain can be limiting [1••], with this leading to mass mortality or the confinement of mangroves to a narrow fringe [45]. The mangrove response is however, complex and will also be influenced by a combination of responses including the size and shape of estuaries, water circulation patterns, geology, topography, land use, local sediment composition and dynamics, freshwater and groundwater inputs, competition from terrestrial species, and propagule availability [46]. Climate conditions are also important, as increases in the frequency and intensity of rainfall and storms will exacerbate the effect of a rise in sea level by altering the salinity, sediment influx and nutrient concentration. Several studies observing a response to sea level rise are listed in Table 2.

Changes in surface elevation, including those associated with sediment accretion, are controlled by physical and biological processes [49]. Vertical gains are driven by the influx of groundwater, inorganic sedimentation and geological uplift together with organic deposition, root growth and algal mat growth. Losses are predominantly a consequence of physical sediment compaction, erosion, organic matter production-decomposition, subsidence and aridity. Natural disturbances (e.g., cyclones and tsunamis) may also increase the elevation through sediment influx or decrease this through mangrove mortality and peat collapse. Mangroves can survive a rise in sea level by actively accumulating sediment and adapting to the coastal environment [50]. However, where sediment

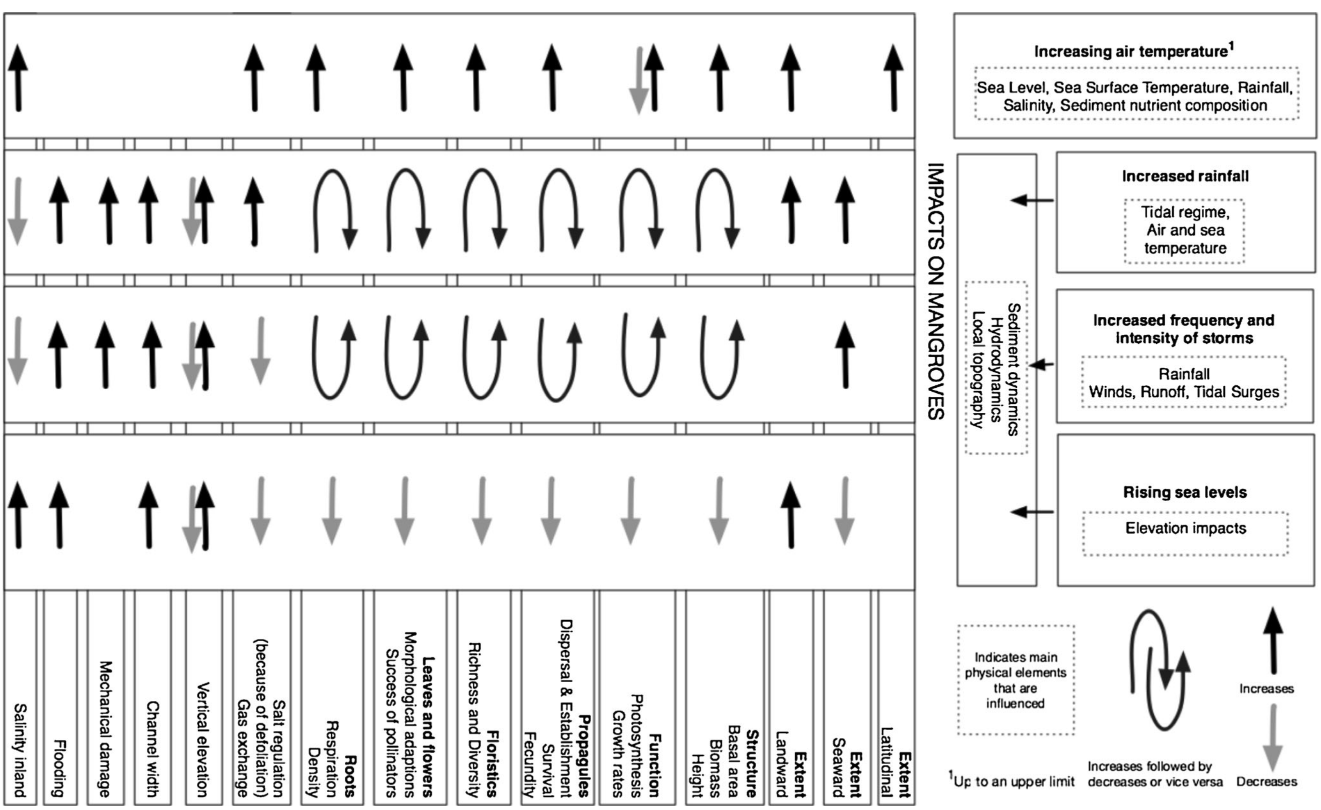

Fig. 1 Summary of the influence of an increase in atmospheric temperature (below the upper optimal threshold, which lies at approximately 29–30 °C), rainfall, storm/cyclonic activity and sea level on mangrove biogeography

Table 1 Response of mangroves to changes in sea level

Scenario	Change in sea level	Mangrove response	Reason	Reference
1	Increase	No change	Sediment accumulation by mangroves facilitates maintenance of extent	[8, 35–38]
2	Increase	Landward expansion	Mangroves seeking reduced inundation	[39]
3	Decrease	Steady state (with adaption), landward dieback and/or seaward expansion[a]	Mangroves adapting to account for changing inundation and sedimentation levels[a]	[40–43].

[a] Depends upon an adequate supply of sediment and propagules

accretion does not keep pace with increases in sea level, even if only temporary, the ecosystem can collapse [51, 52]. For example, in the Pacific islands where sea level is increasing by 2 mm per year and upper predictions are 5.9 mm year^{-1} by 2100 [26, 53], mangroves are estimated to experience a 12 % reduction in area because of comparatively slower sediment accretion [9••, 54•].

Landward migration associated with a rise in sea level is likely to change the species composition of the forest, because of the varying tolerances to the periods and frequencies of inundation and salinity. Using the SELVA-MANGRO model, [55] indicated that in the Gulf region of the USA, *Rhizophora mangle* can survive in sediments that are consistently inundated whereas *Laguncularia racemosa* and *Avicennia germinans* can only tolerate short periods of inundation followed by sediment exposure and drying. Salinity has a lower impact on species composition compared to the period and frequency of inundation [41, 56]. The sensitivity of mangrove species to sea level rise was investigated in Micronesia, and the response to inundation was primarily related to root morphology (i.e., horizontal or vertical root systems [54•]). For example, the root system of *A. germinans* consists of a large proximal mass of interwoven roots which remains close to the sediment surface because of intolerance of anaerobic conditions. From this mass, cable roots extend horizontally with anchoring roots growing downwards from these. By contrast, species such as *Rhizophora* have vertically orientated roots that extend above the surface and are taller than other species of similar size. As sea levels rise, anaerobic conditions will adversely affect species such as *Avicennia* whilst *Rhizophora* will survive because of the greater height of the aerial roots [57]. However, there is evidence for localized plasticity with regards to *Avicennia* pneumatophore extension. *Rhizophora* is also better positioned to survive increasing sea levels as rates of peat accumulation are higher (e.g., 5.3 mm/year) compared to other species such as *Bruguiera* and *Excoecaria* (2.6 mm/year) [58]. Therefore, a rise in sea level is expected to lead to a reduction in diversity due to the dominance of species with tall vertical root structures and high rates of peat accumulation. By contrast, species with horizontal root structures, small aerial roots and low rates of peat accumulation may become less common. Although the forest may survive sea level rise by becoming dominated by one or two species, the overall community resilience will be reduced, which places the system at risk from disturbances such as cyclonic activity. Changes in the physiochemical composition of the sediments that are linked to sea level rise are also likely to influence the species composition of mangroves [59•]. Other changes that might occur include alterations in leaf morphology and physiology [60], and area [16] and later flowering and reduced production of flowers [61], with these often being species specific and affecting plant function.

Changes in Precipitation

Gradual changes in the frequency and intensity of precipitation are likely to have a minimal and lesser effect on mangroves in the short-term compared to extreme events such as drought or flooding. In the long-term, however, changes in precipitation patterns will influence mangrove distributions, species diversity, structure, growth and productivity as a function of physiological tolerance [5, 62••, 63]. Mangroves may also be more affected by precipitation changes in regions where human activities have modified the tidal exchange system and freshwater inflow [19]. In Australia, it is likely that arid coastal regions, such as near Townsville, North

Table 2 Studies observing a response of mangroves to rising sea levels

Location	Observed response	Cause	References
South Florida, USA	Mangroves extended inland by 1.5 km since 1940s	Sea level and combined effects of temperature and rainfall	[47]
Pacific coast of Mexico, Magdalena Bay, Baja California	Mangrove expansion into saltmarsh	Linkages with El Nino phases	[48]
Hungry Bay, Bermuda	Mangrove retreat on the seaward margin	Sea level rise greater than the rate of peat accumulation coupled with increased erosion	[41]

Queensland, will observe mangrove expansion into the saltmarsh in response to even small increases in precipitation due to a reduction in sediment salinity.

Mangroves thrive where the annual mean precipitation is approximately 1500–3000 mm and evenly distributed throughout the year; they also benefit from heavy runoff and seepage from catchments and the resulting sedimentation [64]. In these environments, mangroves are often tall (up to 40 m) and diverse [17, 65, 66]. A trend towards these conditions is therefore likely to lead to increased productivity of mangroves, changes in diversity, structure and extent (Table 3).

The impacts of changing rainfall patterns on mangrove extent have been observed in several studies. In southeast Queensland, a positive relationship between rainfall and the area encroached by mangroves was reported using a 32-year time-series of rainfall data and aerial photography (1972 to 2004) [5]. From 1943 to 1991 the area of saltmarsh in the Hinchinbrook Channel, Queensland, Australia, reduced by 78 % due to the expansion of mangrove forests; this coincided with significant increases in annual precipitation [73]. Similarly, Buckney [74] noted substantial mangrove expansion in the Hunter Estuary, New South Wales, Australia, during the wettest years, and loss of vigor and a lack of further expansion during dry years (e.g., during the 1982 El Nino drought).

Lower salinity, associated with an increase in precipitation, has also been associated with greater species richness and diversity [64, 75], with notable differences on the wetter east coast compared to the drier west coast of Australia (18 species compared to 4 respectively at 20° latitude) and towards the equator. With increases in salinity, only species tolerant of these conditions may survive. Species with a wide tolerance for salinity include *Avicennia marina*, which is partly responsible for its wide geographical distribution [76, 77]. By contrast, *Sonneratia alba* has a restricted range as the trees can only tolerate a salinity slightly lower than normal seawater (i.e., along estuaries). In general, *Rhizophora*, *Bruguiera* and *Aegiceras* species cannot tolerate hypersaline sediments [78–80]; however, there can be variations in tolerance within the genera. For instance, *Rhizophora apiculata* and *Rhizophora stylosa* can grow next to each other in some locations but only *R. apiculata* can grow in areas of reduced salinity and *R. stylosa* is often found on coral terraces with high salinities [81]. However, it is important to be aware that *A. marina* also has a wide tolerance to inundation and temperature, allowing for a wide spatial distribution both at a global and local scale. This broad tolerance threshold confounds identification of primary drivers of change in its distribution.

As the intensity and frequency of precipitation increases, there can be negative implications for mangroves due to persistent inundation and the influx of sediments of different types. For example, significant sedimentation following intense rainfall and flooding in American Samoa covered the aerial knee roots of *Bruguiera* species and the associated reduction in gas exchange led to mass mortality in 16-m-tall stands [82•]. [83, 84] also noted that complete burial of *Avicennia* pneumatophores and *Bruguiera* knee roots caused mortality of these species. The height of the roots does not directly correspond to greater tolerance to sedimentation, as the number of lenticels declines with distance from the sediment surface [85]. However, there is evidence that, for some species (e.g., *Xylocarpus mekangensis*), greater aerial extension as a result of adaptation to higher levels of inundation does increase their ability to cope with burial [86]. Hence, given the expected increase in rainfall and sedimentation in some regions, forests dominated by *Avicennia* and *Bruguiera* may not survive and other species such as *X. mekangensis* are likely to dominate. Even so, higher rainfall can deliver a greater supply of fluvial sediment that is rich in organic matter and detritus and hence increases mangrove productivity and diversity up until a maximum threshold [62••, 63]. The sediment accumulation and input of groundwater (causing subsurface swelling) also maintains high vertical surface elevations, which can act as a buffer against increases in sea level. In this way, forest margins remain stable and mangroves can proliferate [87, 88]. Increased rainfall may however increase erosion within the mangrove forest and result in an overall reduction in productivity and growth [89].

Increases in the frequency and intensity of precipitation can result in prolonged flood events. A number of studies concerning sustained flooding in mangrove forests have

Table 3 Implications of increased rainfall for mangroves

Process change	Reason	Consequences	References
Seaward expansion	Increased sediments and formation of new mudflats or wetlands	Mangrove forests extend their range[a]	[5]
Increased productivity	Increase in nutrient rich sediment via runoff; optimal growth conditions. Reduced tissue salt concentrations	Mangroves grow faster and taller	[62••, 63, 67, 68••]
Inland intrusion	Increased rainfall results in a reduction in the area of hypersaline flats allowing for mangrove expansion	Saltmarsh species are replaced by mangrove species	[65, 69]
Increased diversity	Increased survival of seedlings for species that are sensitive to lower salinities	Mangrove species tolerant of lower salinities proliferate	[62••, 65]

[a] Controlled by other factors such as tidal regime, sedimentation, topography and nutrient concentration [70, 71], which affect the availability of propagules and establishment success, flooding stress and competition from terrestrial species [72]

focused on the capacity for leaf gas exchange [90, 91]. The studies identified that long-term inundation by floodwaters does not affect gas exchange for *A. germinans*, *L. racemosa* and *R. mangle*, yet frequent short-term flooding reduces respiration and maximum assimilation. In addition, flooding also reduced the leaf water potential and stomatal conductance for *Bruguiera gymnorrhiza* and *A. marina* in accordance with duration of inundation [92]. The results suggest flooding can have a negative impact upon metabolic processes that will ultimately reduce productivity.

A reduction in precipitation can also lead to an increase in the incidence of droughts, particularly in subtropical and temperate regions. In these situations, the lack of sediment moisture combined with increased evaporation (as a result of increased temperatures) and salinity may result in the long-term replacement of tall forests by trees that are small in stature (1–2 m) and with a reduced basal area [93]. This suggests a shift in mangrove energetic priority towards roots and/or leaves which require moisture to a greater extent. Extreme aridity can also negatively influence the photosynthetic capacity of mangroves [94]. If climate change predictions are realised, mangroves in some regions could soon be experiencing widespread mortality and losses to productivity due to significant reductions in photosynthesis and metabolism. This has already been observed in environments of increasing aridity in Puerto Rico [95] and Western Australia [96]. However, there is evidence that subtropical mangrove forests in areas predicted to experience increased drought conditions may be able to remain productive and diverse if they are under the influence of large monsoonal river systems that drain wet-season basins [97]. Such environments include the Flinders River estuary in the eastern Gulf of Carpentaria, northern Australia.

Under drought or dry conditions, there is a limited capability of mangroves to regenerate or colonise, although this varies with species. For example, in terms of propagule establishment, those of *A. germinans* and *L. racemosa* are sensitive to desiccation, with the majority experiencing mortality within 2–4 days of exposure to dry sediment. By contrast, *R. mangle* propagules often survive several weeks without water [98]. However, no propagules can establish on dry sediment; the roots may begin to grow but they will die due to desiccation. Recently established seedlings will also experience mortality as only mangroves with a developed root system will be able to survive [99].

Increased Cyclonic/Storm Activity

Cyclonic/storm activity is expected to increase in frequency but also intensity, with both having impacts on the extent, structure and functioning of mangroves. A common outcome is mass mortality of mangroves, which can be the result of direct mechanical destruction (e.g., windthrow) or indirect damage (e.g., prevention of gas exchange in the aerenchyma of the pneumatophores; [100•]). As examples, mass mortality was observed following the passing of a cyclone over the Kosi estuary of South Africa in January, 1966, which led to enhanced rainfall, significant erosion and transport of sediments and a 6 m storm surge [101]. Flooding from Cyclone Domoina, Natal, South Africa, in January 1984 resulted in extensive erosion of the two main river channels, with retreat and widening of 100 m and 300 m respectively occurring in some locations. The river depth also increased by 10–14 m. The period of submersion was influential on the dieback of mangroves, with the smaller (<1 m) trees dying after a number of days to weeks whereas the taller (up to 3.5 m) trees remained alive for longer but experienced mortality following inundation of up to 4 months [102].

An increase in the frequency and/or intensity of cyclonic events has the capacity to change sediment elevation over vast intertidal regions for a prolonged period of time due to erosion and deposition and subsurface processes [103]. This can lead to a complete loss of mangrove forests as propagules cannot establish and the system may then be converted into mudflats. Sediment collapse is expected to differ within the mangrove ecosystem. For instance, basin forests often experience sediment collapse for a longer period of time compared to fringe forests. The difference in collapse rate is likely to be due to the sediment structure and the subsequent response rate to mass mangrove mortality [104]. The impacts of long-term changes in sediment dynamics on propagule establishment were noted following Hurricane Mitch, which impacted Mangrove Bight, Guanaja, Central America, in 1998. After the storm, there was no mangrove recovery for nearly 3 years. The lack of propagule establishment and root growth resulted in decomposition of below-ground organic matter (peat) due to mangrove mortality and an absence of inorganic sediment deposition, which led to sediment collapse. A reduction in sediment elevation was predicted to continue for 10 years, assuming there was no inorganic sediment input or root growth, thereby resulting in ecosystem collapse [104, 105].

Defoliation through storm activity results in reduced primary productivity and reproduction as the mangrove immediately initiates a compensatory response whereby resources are allocated into the production of new leaves instead of the development of propagules [106]. This has a number of short-term advantages such as increased photosynthesis, regained ability to regulate salt and increased growth and fitness (Fig. 1). However, the reproductive output can be reduced considerably. For instance, an experiment in Hong Kong identified that following the defoliation of *Kandelia candel*, the number and size of propagules was significantly reduced for up to a year after the event suggesting limited availability of carbohydrates as resources were allocated to leaf growth [107]. Therefore, if cyclonic activity increases, mangroves may not be able to regenerate efficiently via propagule recruitment. If this is followed by subsequent disturbances such as flooding or droughts, the ability of the forest to recover will be further limited.

The recovery response of mangroves after a cyclone or storm varies between species. Following Cyclone Kathy impacting the Gulf of Carpentaria in March, 1984, *Rhizophora* species showed limited recovery, particularly amongst trees that had lost the outer branches (which often possess buds with the capacity to form new leaves). By contrast, *Avicennia* species were less susceptible to mechanical damage, demonstrating rapid recovery with substantial leaf regrowth [108]. *R. stylosa*, *Ceriops tagal* and *Bruguiera exaristata* exhibited significant mechanical damage due to windthrow, crown destruction and bole fracture and reorientation following Cyclone Tracey in December 1974 in Shoal Bay, Beagle Gulf, north Australia [109]. The sensitivity of *Rhizophora* to mechanical damage may explain the lack of this species in the Sunderbans of south Asia, which is impacted by 30–40 typhoons each year [110].

The difference in recovery rates between species following a storm event may be due to the presence of reserve or secondary meristematic tissues, which allows some species to coppice or grow trunk sprouts. New growth via coppicing can occur from the remains of the stump or the root collar [111]. *Rhizophora* and *Ceriops* species do not have reserve or secondary meristematic tissues and therefore do not recover efficiently. The lack of recovery of *R. mangle* was also noted following direct destruction in Florida, when compared to the relatively quick regeneration of *A. germinans* and *L. racemosa*. The rapid recovery of *A. germinans* was partially due to the development of trunk sprouts on the majority of trees, regardless of their orientation (upright or leaning) and the degree of leaf and branch defoliation [112].

Increasing Temperature

Mangroves are mainly distributed in tropical and subtropical regions, due to the limitations set by cool temperatures and frost conditions. However, there are exceptions at the farthest limits of the distribution range, including in Japan, the USA, South Africa, New Zealand and Australia [3]. Air temperature is the primary controlling factor for their distribution as it determines key physiological processes (e.g., photosynthesis, respiration and reproduction) [7]. The latitudinal limit of mangrove extent coincides with the winter position of the 20 °C SST isotherm [113], which occurs unevenly in the northern and southern hemisphere and between the east and west coastlines of continents. The greatest latitudinal extent is along easterly coastlines due to an influx of warmer waters originating from equatorial regions. Along western coastlines, there is often cooler water approaching the equator due to upwelling, resulting in a smaller area of mangrove [114]. Coastal currents have also been identified to potentially influence mangrove distribution, by moving in a northerly direction in the southern hemisphere, limiting the southward dispersal of propagules [115]. Therefore, with predicted increases in temperature over the coming decades [2, 21], mangroves are more likely to extend their latitudinal range in the north and along eastern continental margins (Fig. 1) [10, 116, 117].

Mangrove latitudinal expansion is limited by extreme low temperature events, with these being more frequent in temperate zones [59•, 118]. Frosts are particularly damaging and, even if endured for only a couple of hours, can result in mortality and a reduction in structural complexity (height, density, leaf area and size) [119]. For example, extreme frost events in the Gulf of Mexico and along the Atlantic coasts of Florida and Carolina have been primarily responsible for the cessation or reversal of the northward expansion of mangroves (Table 4). Fluctuations in atmospheric temperature by more than 10 °C can also damage mangroves [124]. However, in Australia, *A. marina* exhibits significant tolerance to cold temperatures, as demonstrated by having the highest latitudinal extent of all mangroves in [68••, 125]. This is in comparison to *A. germinans* in the USA where sudden and extreme frosts prevent expansion.

The tolerance of mangroves to low temperatures varies between species. For example, along the Texas coast, *A. germinans* was observed to be more tolerant of freezing compared to other species in the broader Caribbean region [119, 126, 127]. Similarly, in western Taiwan, *K. candel* has a more northerly distribution compared to *A. marina* because of its greater tolerance to lower temperatures although *A. marina* is more likely to expand northwards as the air and sea temperature warms [128•]. In general, increasing temperatures up to a threshold are likely to increase the productivity and species richness of mangroves, particularly where seasonal fluctuation is minimal [129], and species closer to the equator are likely to have a greater tolerance compared to those towards higher latitudes [128•]. Increasing temperatures also enhance, for many mangrove areas, flower production (e.g., number of events), the reproductive success of mangroves (i.e., the number of flowers in proportion to the total number of immature buds), flowering periods, the length and the frequency of fruiting and propagule dispersal periods, and maturation intensity [17, 130–135]. Pollinators for different species and hence flowering are also affected. These factors combined will ultimately influence the species composition of mangrove forests [136]. However, not all mangrove species or forests will respond in the same way. In the future, if atmospheric temperature continues to rise, there will be an adverse effect on mangroves, with high leaf stress and water loss, for example, reducing rates of growth and changing species distributions [137–139].

Availability of Suitable Environments

The ability of mangroves to respond to climate-related phenomena depends upon a number of factors including the

Table 4 Impacts of frosts preventing northward expansion

Region	Extreme frost event	Impacts on mangroves	Reference
Southern Texas	Regular	Mortality, particularly of *R. mangle*	[120]
Northern Gulf of Mexico	1983 and 1989	95–98 % loss of cover	[121]
Georgia and Florida	1977, 1981 and 1989	Mass mortality following previous expansion in the 1970s	[59•, 122]
Louisiana	1983	Mass mortality	[123]

availability of suitable environments for colonisation. In New South Wales, Australia, landward expansion of mangroves has been reported, resulting in the replacement of saltmarshes [10]. The availability of saltmarshes in Texas [140, 141], Florida [130] and Louisiana [119, 142, 143] also allowed mangroves to expand during mild winters with a reduced frost intensity and frequency [10]. The recent latitudinal expansion of mangroves in Louisiana has been further aided by mass dieback of the dominant saltmarsh *Spartina alterniflora* as a consequence of drought. With *A. germinans* tolerating periods of drought, the species has been able to proliferate and extend inland [144] and latitudinally [49].

Case Studies

Latitudinal Expansion, South and East Coast of Australia

Increases in atmospheric temperature are linked to latitudinal increases in the extent of mangroves. By 2030 the temperature in Australia is expected to rise by 0.7–0.9 °C in coastal regions and 1–1.2 °C inland. By extrapolation, annual atmospheric warming by 2050 is expected to range from 1.2 to 2.2 °C and, by 2070 predicted to further increase by 1.8–3.4 °C. With Australia set to experience increased warming, the incidence of frost will also decrease, particularly as increases in cloud cover are anticipated [2, 145].

Since the 1950s, increasing temperatures, sea level rise, sedimentation and increased rainfall are considered responsible for the expansion of mangroves along estuaries in southeast Australia [5, 9••, 68••, 146, 147]. Mangrove expansion in southeast Australia has been observed within time-series of aerial photography, with approximately 30 % of the saltmarsh area replaced [68••, 148]. However, this proportion decreases with increasing latitude [87]. Particular species are also demonstrating the ability to expand their latitudinal range. For instance, *B. gymnorrhiza* has recently been identified in three southern New South Wales (NSW) estuaries: the Sandon, Moonee Creek and Wooli Wooli River [149]. Surveys have also identified *R. stylosa* colonisation in 16 estuaries, with a strong trend towards population growth in southerly NSW [117]. A hotspot in NSW highlighted for *R. stylosa* expansion is the 100 km southerly extension from Corindi estuary to South West Rocks Creek, with this corresponding with a rise in atmospheric temperatures [2]. For instance the mangrove extension to South West Rocks Creek coincided with a 0.2 ° C increase in mean minimum temperatures and a 1.3 ° C increase in the mean maximum temperature over the period 2000–2004 [149]. It is important to note that although southerly expansion can occur in stages, this is rarely observed. Instead it is often random, due to the variability in sediment dynamics and sea level between sites.

Storm Damage, Hinchinbrook Island, Queensland, Australia

Tropical cyclones in Australia are expected to increase in intensity and shift southwards [2, 28, 150]. Although the majority of studies agree there will be an increase in intensity, the predicted percentage increase shows considerable variation. For instance, [151] predict a 56 % increase in cyclone intensity by 2050, whereas [28] predict a 60 and 140 % increase for 2030 and 2070 respectively. However, the frequency of future cyclonic events in Australia remains under dispute with some studies suggesting the frequency will remain constant [150, 151] and others suggesting a significant decrease [28], particularly in Western Australia (44 % decline by 2070). There is also evidence that the duration of tropical cyclones will change with a decrease in Western Australia and an increase along the east coast [28, 150]. However, it is important to note that thus far, there is no convincing evidence to suggest that tropical cyclones and mid latitude storms have changed [24].

The impact of increased storm activity on mangroves [14] is illustrated by the damage imposed by Tropical Cyclone Yasi, which hit the northeast coast of Australia on 3rd February, 2011. The cyclone was approximately 700 km in diameter when it crossed the Queensland coast, producing gusts of up to 290 km h^{-1} and wave heights greater than 7 m. Rainfall was also intensive, with the cyclone also leading to the northeast coast of Australia having the second wettest summer on record. Most of the damage to mangroves occurred within the 200 km^2 area of Hinchinbrook Island (18° 13′ 46° S, 146° 13′ 58°E) [17, 152]. Here, 17.2 % of the mangrove area was damaged, with the northwest and northeast corners of the island at the most seaward fringe being most affected. However, there was significant mangrove destruction on the island in the Hinchinbrook Channel. The extent of damage was observed both through time-series comparison of Landsat sensor and also ALOS-2 PALSAR-2 radar data acquired over the area in the post-storm period (Fig. 2). Of note was an average reduction of 0.43 (±0.14, based on 30 regions of interest) in the Landsat-derived Normalized Difference Vegetation Index (NDVI) within damaged areas between the pre- and post-cyclone observations. The reduced NDVI corresponds to an increase in the L-band HH backscattering coefficient as a consequence of fallen trunks. The damage observed was a consequence of the high wind but also strong waves and a high sea level due to a storm surge that modified the sediment dynamics. The majority of the forest suffered direct destruction including broken trunks (boles), uprooting through windthrow and defoliation (Fig. 3).

In the years following the cyclone, significant regeneration of mangroves has occurred which is typical following such events and generally more rapid compared to areas experiencing changes in sediment dynamics, extensive tidal inundation and alterations to nutrient and gas exchange [100•, 153–155]. However, recovery is often interspecific and influenced by habitat characteristics [15]. Recovery will also depend on the success of propagule maturation, establishment and growth, which is directly influenced by the health of the forest and condition of the sediment. Recovery may however be limited by the combined effects of mangrove mortality, reduced fecundity, loss of elevation through erosion and the hostile sediment conditions and may be further delayed if the frequency and intensity of cyclonic events increases.

Major Flooding, Brisbane River, Queensland, Australia

Future rainfall projections for Australia vary considerably. The most accurate estimates of annual precipitation indicate negligible change in the far north by 2030, with reductions of 2–5 % elsewhere. There are likely to be small regional increases in rainfall in areas such as the central coast of New South Wales. Temporal variation is also expected by 2030 with a 5–10 % reduction during the winter and spring months and smaller decreases during the summer and autumn [156]. However, the incidence of extreme rainfall events is predicted to increase across Australia [157].

Where extreme rainfall occurs, which is often (but not limited to) storm events, the resulting discharge can have a significant impact on the mortality and dynamics of mangroves as illustrated by the Brisbane River in southeast Queensland. Prior to 1974, mangroves were sparse along the Brisbane River and mainly located at the mouth [158]; therefore, the impact of a major flood in 1974 on the mangrove forests was minimal. The increase in mangroves along the river post-1974 was attributed largely to the construction of the Wivenhoe Dam in the early 1980s, which reduced the number of flood events that impacted downstream regions and resulted in saltwater intrusion into the river. Gravel dredging in the Brisbane River also encouraged mangrove growth due to enhanced silt deposition along the river banks [159]. Prior to January 2011, there was 82.3 km of mangroves lining the banks of the Brisbane River, with a relatively low species richness dominated by *A. marina*, *Aegiceras corniculatum* and *Excoecaria agallocha* [160••].

From September to November 2010, there was extensive rainfall associated with a strong La Niña phase, which resulted in saturation of the catchment. In early January 2011, further prolonged heavy rainfall (600–1200 mm) occurred due to a combined low-pressure system and monsoonal troughs, which resulted in moderate to major flooding downstream of

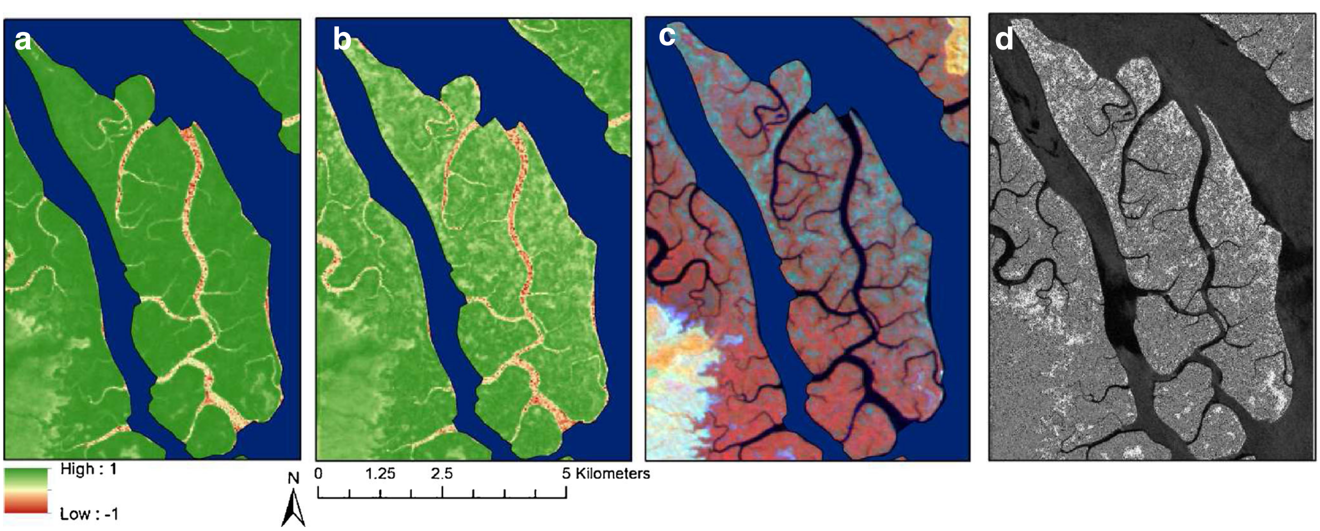

Fig. 2 **a** Landsat-5 Normalized Difference Vegetation Index (NDVI) for **a** 1st June, 2010 and **b** following Cyclone Yasi on the 4th June, 2011. The *bright green* areas in (**b**) indicate loss of foliage cover. **c** A colour composite of the Landsat Enhanced Thematic Mapper (ETM+) image (near infrared, shortwave infrared and red wavebands in RGB) highlighting loss of vegetation cover (in *grey*) and (**d**) an ALOS-2 PALSAR-2 image, (copyright: 2015 JAXA METI) from 12th November 2015 with bright areas reflecting the fallen tree trunks as seen in Fig. 3

Fig. 3 Windthrow of mangrove trees following Cyclone Yasi observed in Very High Resolution (VHR) satellite imagery (copyright: 2015 CNES/Astrium Digital Globe)

the confluence with the Bremer River [161]. The flooding occurred between 12th and 14th January 2011 and influenced the lower Brisbane River floodplain and upstream of the confluence with the Bremer River. By June 2011, 5 months after the flood event, 92 % of the mangroves along a 76 km stretch of the Brisbane River were reported dead or partially damaged, with this observed by comparing time-series of aerial photography (Fig. 4). The ongoing siltation is likely to have resulted in further loss, with 95 % of mangroves along the river experiencing dieback. Differential mangrove damage was observed as a function of the depth and period of inundation and river circulation.

The recovery of mangroves along the catchment is likely to occur in future years as mangroves re-establish. However, the spatial variation and time of recovery will depend on seasonal factors such as rainfall, temperature and the availability of propagules. Recovery started to take place quite rapidly in some areas as in June 2011, *E. agallocha* trees were observed with new shoots in areas of mangrove, which previously had 100 % mortality and where *A. corniculatum* and *A. marina* had occurred. *E. agallocha* thrives along estuaries, river banks and on the landward fringe of the community. By exhibiting persistence in this area where erosion has removed other species, it can be assumed that this species is able to anchor itself

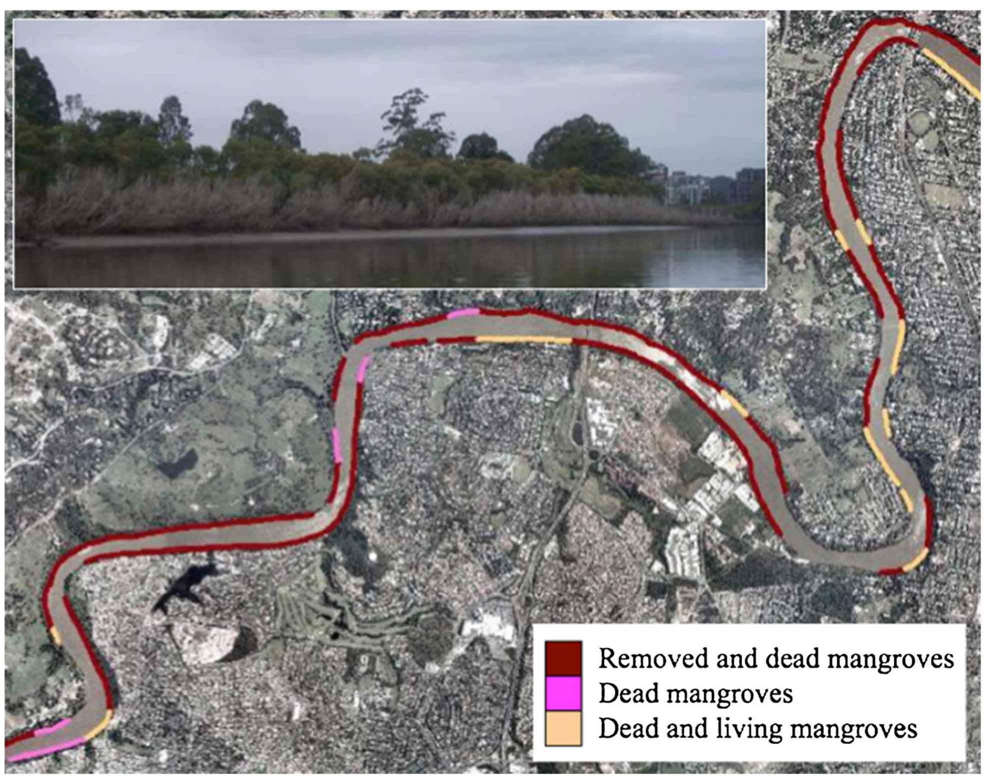

Fig. 4 Mangrove change along the Brisbane River showing the extensive dieback along the banks of the river (*inset*) and categorisation of mangrove death and dieback as determined through time-series comparison of aerial photography [160••]

to underlying bedrock and will be the first species to recover [160••]. The main concern is that extreme and unfavourable weather events are likely to become more frequent and intense as a result of climate change. Therefore, the forests may not be able to recover sufficiently before the next event occurs.

Increased Discharge and Sea Level Rise in the Gulf of Carpentaria, Australia

Sea level around Australia has risen by approximately 10 cm from 1920 to 2000 [2] which equates to around 1.2 mm per annum in the twentieth century [162]. There is significant regional variability with regards to sea level surrounding Australia due to the influence of the El Niño–Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) [26]. For instance, the rates of sea level rise in the east and the south are similar to the global rate (e.g., 1.3 mm/year at Rosslyn Bay, Queensland). However, in the west and the north west the rates are more than double the global rate (e.g., +8.1 mm/year at Hillarys, Western Australia) [163].

There is evidence to suggest that a combination of sea level rise and increased discharge from rivers is causing both a seaward and landward expansion of mangroves within the Gulf of Carpentaria, northern Australia. The Gulf of Carpentaria covers an area of approximately 23,775 km^2 between the latitudes of 11° S and 17.5° S and longitudes of 136°E and 142°E and is a semi-enclosed epicontinental sea bordered on three sides by northern Australia and limited in the north by the Arafura Sea. The expansive and sheltered region has a total mangrove area of 1609 km^2 with an estimated 36 species. Changes in the extent of mangrove have been observed using a time-series of Landsat imagery from 1987 to 2014 (Fig. 5). Such changes are most noticeable because there is an absence of anthropogenic disturbance due to low population density, remoteness and inaccessibility and hence changes observed in the mangrove distribution, extent and species composition can be attributed to changes in the climate and environment. The seaward expansion of mangroves can be attributed to the increase in the frequency and intensity of rainfall and thus flood events, with this resulting in a large influx of fluvial sediments into the near shore, upon which stabilisation provides a larger and more seaward area for propagule establishment. The landward expansion may be due to the freshwater flooding inland which reduces the landward salinity and increases the mortality of saltmarsh species. In this way, mangroves can extend into this area due to a lack of terrestrial competition and a more favourable salinity. In addition, sea level rise is likely to be a contributing factor to landward movement of mangroves as the forests seek reduced inundation. The impact of a rising sea level in northern Australia is likely to be exacerbated with the influence of increased storm surges as a consequence of more intense storms and cyclones [2]. However, a series of multifaceted interactions need to be understood (e.g., temperature, availability of propagules) in order to effectively predict the future mangrove ecosystem changes in the Gulf of Carpentaria.

Conclusions

Mangroves are complex and dynamic ecosystems that continually change in response to a wide variety of biological, chemical and physical drivers. It is therefore difficult to unambiguously attribute one single change in the forest to one or several climate-related factors. Changes in mangrove variables (primarily extent, structure, biomass, diversity and function) may therefore be more or less pronounced depending on the relative influence of different factors and interactions between these.

The main implications of a changing climate on mangroves are:

a. Changes in extent and distribution; mangroves are likely to extend to higher latitudes due primarily to higher temperatures and reduced frost severity or move in a landward and/or seaward direction in response to changing sediment dynamics and inundation stress (e.g., as a result of increased rainfall, changes in salinity and rising sea levels).
b. Modification of structure and changing productivity; a range of environmental factors (e.g., rainfall, temperature) will be influential but cyclonic activity and storms in particular will lead to a sudden alteration of forest structure and function (e.g., photosynthesis) through mechanical damage (e.g., loss of canopy height, basal area, tree density and foliage amount).
c. Changes in species composition; those tolerant of conditions such as prolonged inundation, higher or lower salinity and high temperature will respond well and species that are able to recover quickly from extreme events through tree sprouts and reserve meristems are likely to dominate forests following dieback events.
d. Phenological changes; increases in temperature will favour some species in terms of propagule, flower and fruit production. Phenological processes will, however, be limited under stressful conditions such as reduced temperatures, prolonged inundation and extreme salinities.

The paper has reviewed evidence of how climate-related phenomena may be manifested within remote sensing data. In Australia, changes associated with climate-related phenomena were observed by comparing time-series of aerial photography (for inland intrusion and degree of inundation), Japanese L-band SAR data (for cyclone damage) and time-series of Landsat sensor data (for seaward/landward expansion and cyclone damage). In each case, changes in mangroves were

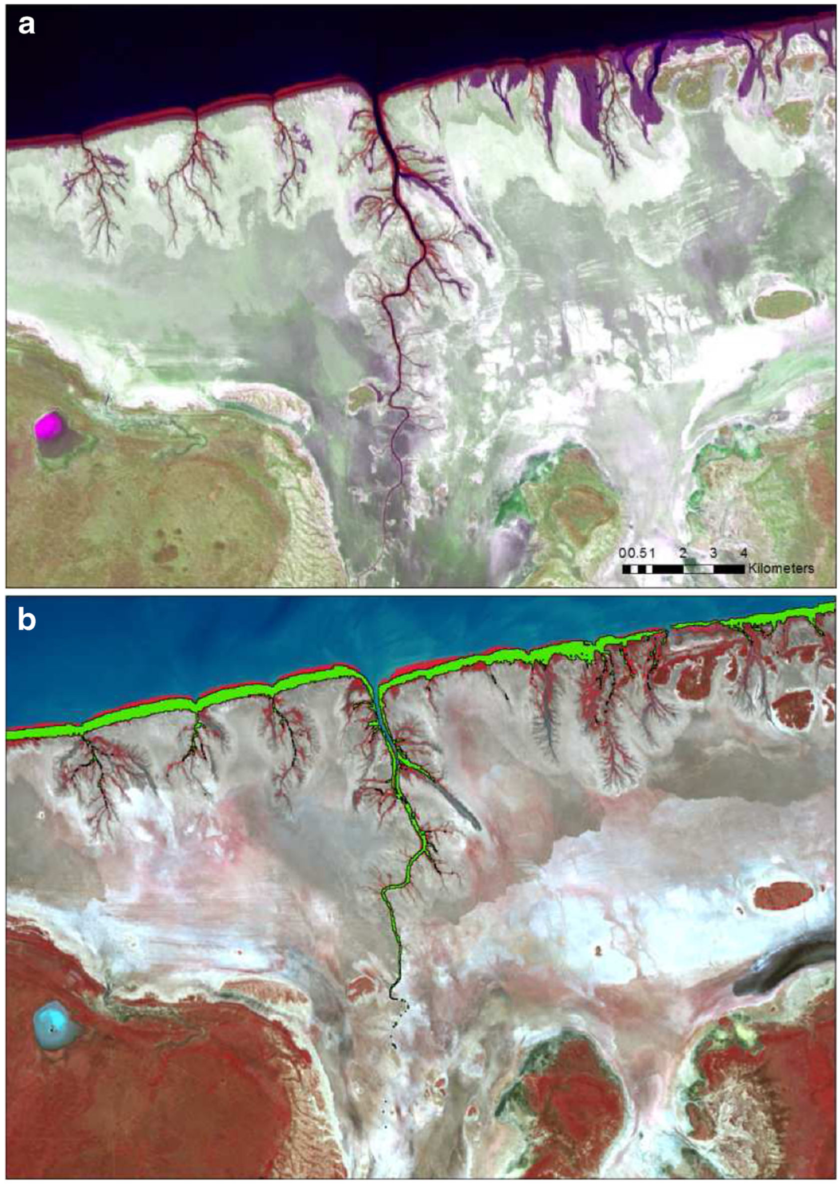

Fig. 5 Seaward and landward expansion of mangroves between (**a**) 1987 and (**b**) 2014 observed in the Gulf of Carpentaria using colour composites of Landsat sensor imagery (near infrared, shortwave infrared and *red* in RGB). The overlay (*green*) in (**b**) represents the extent of mangrove, as classified using a supervised maximum likelihood algorithm. Areas in *red* on the landward and seaward margins in (**b**) represent expanding mangroves

detected, but several (e.g., inland intrusion) warranted the use of finer (<3 m) spatial resolution data. The study conveyed how these changes might be manifested within remote sensing data, thereby providing examples that can be referenced by individuals or organisations charged with monitoring impacts on coastlines.

Changes associated with climatic events and processes are likely to be most evident within areas that are not subject to anthropogenic change, with these often located in developed countries (e.g., Australia, USA) because of the greater protection afforded. However, significant expanses of undisturbed mangrove also occur in developing countries (e.g., within National Parks); as such, they should be monitored long-term to establish whether climate-related changes are occurring. In many cases, monitoring requires the use of finer spatial resolution imagery, such as from spaceborne sensors (e.g., Worldview-2) or aerial photography, as exemplified by the Brisbane River example. However, at regional to global levels, time-series of Landsat sensor data and SAR data are increasingly providing observations of mangroves that can be used to detect and quantify change in extent but also a range of attributes (e.g., biomass, structure, species composition, growth stage, productivity). These data should therefore be used to monitor gains and losses in mangroves and changes in condition that result from climate-related phenomena, with focus on differentiating such changes from those induced by human activities. In this way, the user community (ranging from local residents, to planning and management authorities, scientific organisations and national/international governments) can act to ensure the long-term viability of mangroves and the resources they provide in the face of climate change.

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Compliance with Ethics Guidelines

Conflict of Interest The authors of this paper declare that they have no conflicts of interest.

Human and Animal Rights and Informed Consent This article contains no studies with human or animal subjects performed by the author.

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