RESEARCH ARTICLE

ENSO-driven extreme oscillations in mean sea level destabilise critical shoreline mangroves—An emerging threat

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Abstract

Recent ENSO-related, extreme low oscillations in mean sea level, referred to as 'Taimasa' in Samoa, have destabilised shoreline mangroves of tropical northern Australia, and possibly elsewhere. In 1982 and 2015, two catastrophic Taimasa each resulted in widespread mass dieback of ~76 km^2 of shoreline mangroves along 2,000 km of Australia's Gulf of Carpentaria. For the 2015 event, we determined that a temporary drop in sea level of ~0.4 metres for up to six months duration caused upper zone shoreline mangroves across the region to die from severe moisture deficit and desiccation. The two dramatic collapse events revealed a previously unrecognised vulnerability of semi-arid tidal wetland habitats to more extreme ENSO influences on sea level. In addition, we also observed a relationship between annual sea level oscillations and mangrove forest productivity where seasonal oscillations in mean sea level were co-incident with regular annual mangrove leaf growth during months of higher sea levels (March-May), and leaf shedding during lower sea levels (September-November). The combination of these periodic fluctuations in sea level defined a mangrove 'Goldilocks' zone of seasonal productivity during median-scale oscillations, bracketed by critical threshold events when sea levels became unusually low, or high. On the two occasions reported here when sea levels were extremely low, upper zone mangrove vegetation died *en masse* in synchrony across northern Australia. Such extreme pulse impacts combined with localised stressors profoundly threaten the longer-term survival of mangrove ecosystems and their benefits, like minimisation of shoreline erosion with rising sea levels. These new insights into such critical influences of climate and sea level on mangrove forests offer further affirmation of the urgency for implementing well-considered mitigation efforts for the protection of shoreline mangroves at risk, especially given predictions of future re-occurrences of extreme events affecting sea levels, combined with on-going pressure of rapidly rising sea levels.

Introduction

Mangrove-fringed shorelines are ubiquitous along the extensive, largely low relief coastal areas of tropical northern Australia [1]. For the most part, these forested ecosystems remain relatively pristine and intact owing to their remoteness with its absence of direct anthropogenic stressors. As such, the condition of mangroves across the region have been mostly influenced by prevailing climatic conditions of high temperatures and low rainfall [2, 3] manifest in the distinctive regional features of low biodiversity, low biomass and limited extent of mangroves across broad tidal flats. Given their pristine state, the widely occurring mass dieback around the Gulf of Carpentaria (GOC) in late 2015 (Fig 1) was considered unprecedented, and the cause was unknown [4]. The lethal impact alone was estimated to have been more than 76 km^2 of lost mangrove forests spread along ~2,000 km of shoreline.

Coastal communities in the region were greatly concerned and sought explanations of potential impacts on their livelihoods, as they expected to lose multiple benefits from the lost mangrove ecosystems [5, 6]. For instance, mangroves and tidal wetlands of the region were notably recognised for their economic role in supporting lucrative commercial and recreational fishing, particularly the Australian prawn fishery [7]. Furthermore, local first nations people identify intimately with these coastal ecosystems as valued sea country, providing traditional fishery resources, and protecting culturally significant seagrass habitats and associated megafauna, like dugong and sea turtles, that make-up their homeland landscape.

Post-impact assessments of the mass dieback identified that damaged mangrove trees were impacted by severe moisture stress after a prolonged absence of tidal wetting during a long dry season [8–10]. This contributed to the rapid, synchronous and widespread mortality of shoreline mangroves across the area [4, 11]. Of note, the dieback coincided with an extreme El Niño climatic event that not only delivered extreme high temperatures and prolonged low rainfall, but also unusually low mean sea levels [12, 13]. Investigations also identified a previously undetected earlier occurrence of mass dieback of shoreline mangroves in 1982 across the same region [14, 15]. Both events were synchronous with unusually low sea levels associated with the severe El Niño conditions [11, 14–18].

Given the periodicity of El Niño climatic conditions, it was somewhat surprising that mangroves had responded with such pronounced impacts from extreme low sea levels, as had occurred with the 1982 and 2015 mass mortality events in Australia's GOC. By comparison, it is well established [1, 2] that the position, structure and function of mangrove forests had over millions of years adapted to low water availability from humidity, rainfall, groundwater and river runoff—manifest chiefly within mangrove species distributions in arid and semi-arid climatic zones of individual estuarine systems and tidal profiles [3, 19]. For example, rising sea levels were expected to have forced migration of mangrove habitat upland [20], whilst decreases in longer term rainfall generally led to the contraction of mangrove extent across tidal profiles in favour of tidal saltmarsh and pans, and vice versa when rainfalls had increased [3]. Observed differences in adaptability also appeared influenced by the nature of disturbances, notably where short, extreme low mean sea level events represented large and infrequent pulse disturbances, whilst the lack of rainfall was a mostly regular and seasonal press disturbance [21].

Of further relevance, such periods of extreme low sea level associated with severe El Niño conditions had been recorded elsewhere as 'Taimasa'—a term coined in Samoa describing the stench of dead corals following their prolonged exposure during extended periods of low sea level [22, 23]. While Taimasa are known to kill shallow water corals on Pacific islands, their wider influence on corals and other tidal marine habitats appears less recognised. Therefore, it is significant that our findings [9, 11] now associate Taimasa low sea level events with the

Fig 1. Our investigations of the 2015 mass dieback of mangroves in Australia's Gulf of Carpentaria revealed an additional threat from greenhouse warming [14, 15]. The three images of shoreline mangroves near Limmen Bight River in the Gulf highlight the situation: A) prior to 2015, healthy canopies of largely *Avicennia marina* trees; B) in late 2018, standing dead trees killed after the 2015 desiccation event; and C) in late 2019, catastrophic scouring caused by Category 3 Tropical Cyclone 'Owen' (Image source: photographs by NCD).

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widespread mass dieback of mangroves in Australia's GOC. In consideration of such observations, it seems likely these damaging events may have occurred without recognition in other places, and to have affected other tidal marine habitats, in addition to shoreline mangroves.

Sudden dieback of mangroves associated with extreme lows in sea level were also observed in Mangrove Bay near Exmouth in Western Australia [24, 25] more than 2,500 km west of the GOC. In some ways, this appeared consistent with the wider relevance of extremes in sea level seriously affecting mangroves. However, there were notable points of difference between Mangrove Bay and the GOC, starting with the relatively small area of reported damage being <2 hectares total in Mangrove Bay. At this western site, there were also additional strong events in

1992 and 2003 with short periods of recovery atypical of the trends observed in the GOC [11]. These findings demonstrate considerable variability in the severity and timing of damage by the fluctuations in sea level where specific events might have been localised or widespread.

The timing, severity and extent of dieback appears critical towards understanding the full impact of each damaging event on mangrove forested habitat. For instance, Taimasa events may be classified as pulse disturbances since they deliver abrupt and severe impacts, comparable in some ways with serious flooding and severe cyclones [4, 26, 27]. However, Taimasa impacts differ because they occurred widely across the region. In any case, such pulse impacts on mangrove forests initiates innate natural recovery processes combining both sexual and asexual forest regrowth processes [28]. Accordingly, and most critically, the replacement of dead forested areas was bound to follow a predictable, but slow and risk-adverse trajectory from propagule production, dispersal, recruitment, establishment and growth to maturity, taking upwards of several decades. In this way, sexual recovery involves a lengthy period of replacement of damaged forested stands leaving impacted shorelines exposed to erosion and coastal retreat until new trees become established. By contrast, recovery from sub-lethal disturbance would be considerably faster since trees need only re-sprout to rapidly replace lost foliage [28–30]. In recent decades, the individual influences of climate and sea level variability have combined and increased in magnitude to currently threaten these natural recovery processes [21, 27, 31–34]. Accordingly, recovery processes appear to be at great risk of becoming overwhelmed by more frequent and more severe impacts from various damaging events, raising the real prospect of ecosystem failure and collapse of shoreline mangrove ecosystems as climatic conditions accumulate and worsen [5, 21, 28, 35, 36].

While initial assessments of the 2015 mangrove mass dieback event had focused on the GOC, there were reports of other occurrences in northern Australia. For instance, seemingly comparable impacts on mangroves were reported from Joseph Bonaparte Gulf in western Northern Territory [7] and near Exmouth in northern Western Australia [24, 25]. Therefore, a key aim with this study has been to evaluate whether these more widely-occurring mangrove dieback events might be coincident and comparable with the 2015 Taimasa in the GOC. And if so, we ask how knowledge of such a phenomenon might help us better understand how oscillations in mean sea level normally influence the growth and productivity of mangroves whilst also accounting for specific limits, or tipping points, needed to define their survival zone across the intertidal biome.

To investigate these matters, we considered a series of pertinent questions based on the impacts and processes observed in mangroves during mass dieback events and other abrupt declines in canopy condition across northern Australia [11, 14, 15], specifically:

1. Was the dieback of mangroves, coincident with the 2015 Tiamasa event, synchronous across northern Australia?

2. Does mean sea level across northern Australia experience fluctuations that coincide with ENSO conditions, as quantified in the Southern Oscillation Index (SOI)?

3. Does mangrove condition (as depicted by stand canopy cover) respond to moderate and extreme variations in mean sea level, whilst accounting for concurrent less likely influences from the climate variables of rainfall and temperature?

4. Does the amount of canopy loss influence the time for canopy recovery, following various abrupt declines in mangrove canopy density?

We also planned to evaluate these observations in the context of global climate change, especially where the frequency of extreme environmental drivers, like Taimasa and severe

ENSO, were expected to increase [37]. But, while we consider suggestions for better management to minimise harm to mangroves, our primary goal with this article has been to raise awareness of the implications of the newly recognised impacts of Taimasa and other manifestations of extreme low sea level oscillations (coincident with severe El Niño) on shoreline mangroves.

Methods

The Gulf of Carpentaria (GOC) study area

Much of the northern and western Australian coast is semi-arid with highly seasonal rainfall, moderate temperatures and low relief topography. This is particularly so for the GOC, a large, shallow (<70m depth) coastal gulf of ~330 000 km^2 (Fig 2) whose hydrographic features have been described by Wolanski [38]. This large gulf straddles the border between the Northern Territory and Queensland. Human populations are quite sparse in this remote region, with few direct human impacts, development and infrastructure. Mean ranges in climatic and tidal factors for the GOC are summarised in Table 1.

The majority of impacted shoreline mangroves were characteristically dominated by the Northern Grey Mangrove, *Avicennia marina* var. *eucalyptifolia* (= *A. marina)*. This species type has the reputation of being both a pioneer and one to dominate sites with abnormally high levels of physical disturbance [1, 39]. For GOC areas damaged by the 2015 mass dieback, individual *A. marina* trees ranged in age between 10–15 years and up to a maximum of around 30 years [8, 15].

The study area had been surveyed and assessed in various studies [14, 15], including aerial surveys in 2017 and 2019. Aerial surveys were made using low-flying helicopters to observe and film the entire shoreline, using an adapted version of the shoreline video assessment method (S-VAM) [14, 40]. These studies were comparable with prior surveys of the east coast shoreline of Cape York Peninsula in north-eastern Australia [41], and in Torres Strait [42].
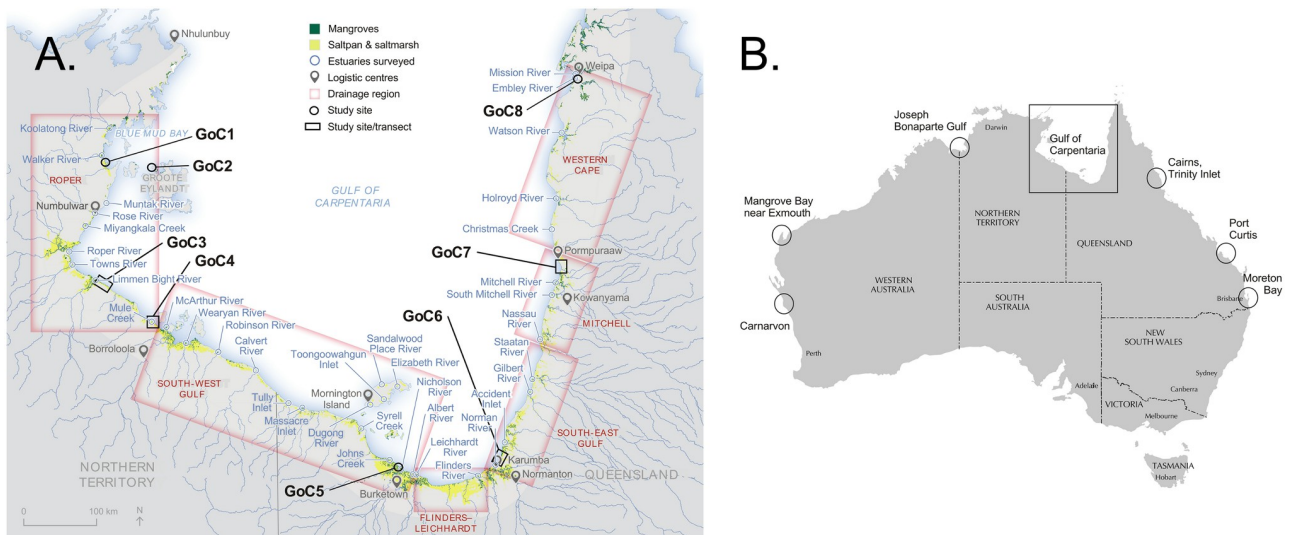
Fig 2. A. Locations of sites across northern Australia both west and east of the main study area of the Gulf of Carpentaria (GOC). See Table 2 for location coordinates. Instances of 2015 dieback of shoreline mangroves occurred from Mangrove Bay near Exmouth to the Gulf. **B**. Gulf sites were spread across six sub-regional areas. Severe damage (75–100% loss of shoreline mangroves) was recorded mostly at four sites (GOC3, GOC4, GOC6 & GOC7) further assessed in the field in 2018, while less severe dieback (25–75%) was observed in 2017 and 2019 during aerial shoreline surveys from Weipa (QLD) to Blue Mud Bay (NT) (Image source: illustration by NCD using basemap from NESP NA Hub).

Table 1. Longer term (25–50 year) climate and sea level averaged conditions for sites across northern Australia. SLSI is the sea level stress index described in the Methods. Data sources include the: Permanent Service for Mean Sea Level (PSMSL)–(https://www.psmsl.org/) and the, Australian Bureau of Meteorology (http://www.bom.gov.au/). Sites in bold are those located in Australia's Gulf of Carpentaria (for site location details, see Fig 2; Table A in S1 Text). The WCI (% Wetland Cover Index) describes the ratio of mangrove area to total area of tidal wetlands (the combination of mangroves, tidal saltmarsh and saltpan) in local estuarine systems [3].

#	Study Site Code	Sea Level Station near Site	Mean Temp degC	Annual Rainfall mm	WCI %	Tidal Range mm	Min SLSI mm	Max SLSI mm
1	W1	Carnarvon, WA	17–28	300	68	900	-200	367
2	W2	Exmouth, WA	18–32	300	20	1700	-212	228
3	W3	Wyndham, WA	21–33	1193	21	5300	-263	291
4–5	**GOC1-2**	**Milner Bay, NT**	**21–33**	**988**	**17**	**1800**	**-370**	**330**
6–10	**GOC3-7**	**Karumba, QLD**	**20–31**	**846**	**11**	**3300**	**-440**	**498**
11	**GOC8**	**Weipa, QLD**	**22–32**	**1825**	**72**	**2100**	**-419**	**363**
12	E1	Cairns, QLD	21–29	2028	72	2000	-362	521
13	E2	Gladstone, QLD	17–29	898	63	3200	-87	157
14	E3	Brisbane, QLD	16–25	1126	85	1800	-77	126

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Surveys in the GOC were complemented with concurrent mapping using satellite imagery to quantify mangrove extent and areas lost during the 2015 dieback [4, 14]. Selection of site locations for this study were made in consideration of this knowledge of the severity and extent of mangrove dieback.

The wider study region of northern Australia

To assess whether mangrove dieback was further widespread across northern Australia, we compared data from 14 broadly spaced sites in tropical and sub-tropical latitudes (Fig 2; Table A in S1 Text), including: eight sites in the GOC, plus three sites further west, and three sites to the east; collectively being Carnarvon (W1), Mangrove Bay (W2), Joseph Bonaparte Gulf (W3), Cairns (E1), Gladstone (E2) and Brisbane (E3).

Broad zonation patterns for mangroves across tidal profiles in this region are depicted in Fig A in S1 Text. This figure further shows the three sea level factors likely to influence mangrove zonation, including: tidal range, rising sea levels, and oscillations in mean sea level.

Table 2. The sites (see Table A in S1 Text) where a changepoint is likely to occur (probability >0.66) in the fractional canopy cover anomaly (1987–2020) at a time proximal to the Taimasa occurring in 2015, including the credible date interval, as predicted by Bayesian time series decomposition [46]. ND indicates no likely changepoint.

Site	Probability of occurrence	Earliest credible date	Latest credible date
W1	ND	ND	ND
W2	0.999	06/2015	10/2015
W3	0.669	02/2015	01/2016
GOC1	0.922	03/2015	09/2015
GOC2	0.923	01/2015	08/2015
GOC3	0.937	11/2014	06/2015
GOC4	0.999	01/2015	05/2015
GOC5	0.967	09/2014	05/2015
GOC6	0.989	01/2015	06/2015
GOC7	0.857	07/2014	02/2015
GOC8	0.895	01/2014	04/2016
E1	0.919	09/2015	11/2015
E2	ND	ND	ND
E3	ND	ND	ND

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Two major types of mangrove dieback discussed in this article are described in the Supporting Information with this article, including Figs B & C in S1 Text, respectively for 'desiccation dieback' and 'drowning dieback'.

Mangrove canopy condition data

At each site, we assessed the long-term canopy condition using Landsat-derived fractional canopy cover (green fraction) estimates from 1987–2021 from the site locations across the study area (Fig 2; Table A in S1 Text). Fractional canopy cover data were derived from multiple Landsat scenes, as described by Lymburner et al. [43]. Cover estimates were taken from homogenous patches of mangrove forests near to both field and reference sites in the GOC and across northern Australia (Fig 3; S1 Data). For each plot, zonal statistics representing an area of 3x3 Landsat pixels were extracted from each image and the mean green fractional cover value was calculated. When less than three pixels were available for a given image date (due to masking of cloud, cloud shadow and water) the mean green fractional cover value was not calculated and those dates were not included in the timeseries data used.

Fig 3 depicts numerous instances of abrupt declines in mangrove canopy condition, including those in 2015. For many earlier instances, there was also apparent recovery with 'maximal' canopy levels restored subsequently over a number of years. We evaluated 45 such earlier declines with recovery, measuring in each case, the initial mean loss in canopy condition (~3–4 months afterwards), and the number of years until 'maximal' canopy conditions were restored. We note that canopy condition maxima measured in green fraction data most likely equate to canopy closure rather than stand maturity [28]. In any case, these data and our determination of the likely cause in each instance of abrupt decline, are summarised in Table E in S1 Text.

Climatic and sea level data

For ten of the 14 sites, having meteorological and sea level data recording stations in close proximity, we obtained records of monthly temperature, rainfall and the Southern Oscillation Index (SOI) from the Australian Bureau of Meteorology (BoM; http://www.bom.gov.au/), and records of monthly sea levels from the Permanent Service for Mean Sea Level (PSMSL; https://www.psmsl.org/). The sites and the stations used in these investigations are listed in Table B in S1 Text. The other four sites in the GOC were considered too distant between respective monitoring stations for specific statistical comparison.

Assessment of the timing of mass dieback across northern Australia

At all sites in Fig 2 (also Table A in S1 Text), Bayesian time series decomposition was used to identify abrupt changes in the canopy fractional cover estimated from Landsat imagery. Changepoints were detected using the 'beast' function in the Rbeast package v0.9.4 in R 4.0.5 [44, 45], using default values and seasonal patterns modelled as a harmonic curve, which implements the methods described in Zhao et al [46]. Rbeast identified likely changepoints (and credible intervals) and the estimated probability of occurrence. The IPCC Likelihood Scale indicates an event is 'likely' to occur when the probability of occurrence is greater than 0.66, 'very likely' with probabilities above 0.9 and 'virtually certain' when the probability is above 0.99 [47].
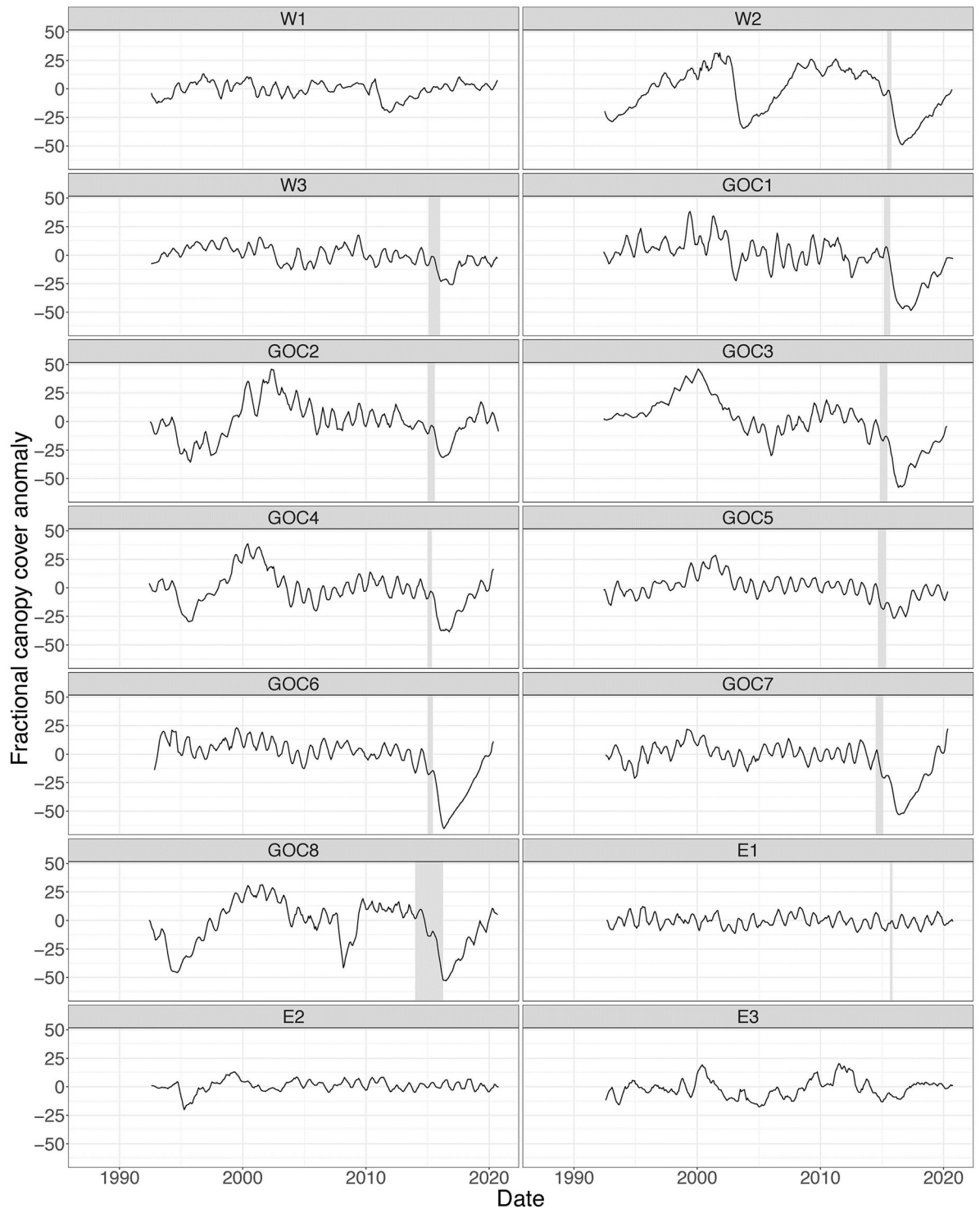
Fig 3. Timeseries of the green fraction anomaly in 14 sites across northern Australia (see Fig 2) from 1987–2020. These plots depict changes in mangrove canopy densities and their relationship with each site, particularly in showing the 2015 mass dieback event (vertical shaded bars) as synchronous in all sites from W2 to E1 across most of tropical, northern Australia (Image source: illustration by NCD).

Statistical assessment of timeseries data of mass mangrove dieback, ENSO, mean sea level, rainfall and temperature

At all 10 fractional green cover monitoring sites with nearby sea level and climate monitoring stations (Table A in S1 Text), we calculated anomaly indices and used multivariate regression with autocorrelated errors to evaluate the following relationships:

1. Sea level anomaly is correlated with the SOI anomaly and time.

2. Fractional green cover anomaly is correlated with the sea level anomaly, rainfall anomaly, the temperature anomaly and time.

All regressions were carried out using the 'gls' function within the 'nlme' package in R 4.0.5 [44, 48]. The 'gls' function fitted linear models using generalized least squares by maximum likelihood with an autoregressive process of order 1 correlation structure.

Derived anomaly indices used included:

1. 'Fractional green cover anomaly' as the six-month running average of the difference from the five-year running average of the monthly average fractional green cover.

2. 'SOI anomaly' as the six-month running average of the difference from the five-year running average of the monthly average SOI.

3. 'Sea level anomaly' as the six-month running average of the difference from the five-year running average of monthly mean sea level. We also refer to this as the 'Sea Level Stress Index (SLSI)'.

4. 'Temperature anomaly' as the six-month running average of the difference from the five-year running average of monthly mean daily-maximum temperatures.

5. 'Rainfall anomaly' as the six-month running average of the difference from the five-year running average of monthly rainfall totals.

Using the SLSI, longer-term oscillations in mean sea levels were characterised in three GOC sea level recording stations at Milner Bay (GOC2), Karumba (GOC6) and Weipa (GOC8) (Fig 2). During May-Nov 2015, each port gauge recorded the more extreme levels in respective SLSI minima, being concurrent with the onset of 2015 mangrove mass dieback [9, 14, 15]. Of these three ports, only Karumba with the lowest SLSI minimum was in close proximity to a site of severe (90–100%) loss of shoreline mangroves. The 6-month averaged records of SLSI for respective sites, provided an indication of the relationship between changes in mangrove canopy condition and sea levels up to late 2015 (Table 3).

Results

Mangrove dieback in 2015 occurred synchronously across northern Australia

Synchronicity between sites in 2015 events were shown in the fractional green cover anomaly between 1987–2021 (see Fig 3). While 'desiccation dieback' in 2015 was evident in sites from Exmouth in Western Australia to Weipa in Queensland, there was little indication of similar impacts on the Australian east coast. For instance, mangrove canopies in Cairns showed no declines below 50%, however there was a small reduction leading up to October 2015 with recovery afterwards, suggesting moisture availability may have been only slightly limited at the time. However, other occurrences of mangrove canopy damage were evident in some sites. For example, in Port Curtis in Queensland (E2), the dieback around 1994/1995 was believed to

Table 3. Comparison between extreme lows in port sea level records and nearby mangrove canopy condition between 1987 and 2019. The table shows key instances of low sea level stress index (SLSI) recorded in sea level stations in Gulf of Carpentaria (GOC) ports of Milner Bay (NT), Weipa and Karumba (Qld) (see Figs 2 & 4). Karumba was a site of notably severe mangrove dieback in 2015 while no dieback was observed there in 1997, and less so at the other locations or dates.

Date of Minimal SLSI	GOC Sea Level Station	Site Code	Sea Level Stress Index (SLSI)	Mangrove Condition in the Vicinity
1997/11	Milner Bay	GOC2	-252	No loss
1997/11	Weipa	GOC8	-273	No loss
1997/10	**Karumba**	**GOC6**	**-398**	**No loss**
2002/11	Milner Bay	GOC2	-262	No loss
2002/10	Weipa	GOC8	-258	No loss
2002/10	**Karumba**	**GOC6**	**-345**	**No loss**
2006/11	Milner Bay	GOC2	-197	No loss
2006/11	Weipa	GOC8	-233	No loss
2006/10	**Karumba**	**GOC6**	**-339**	**No loss**
2012/11	Milner Bay	GOC2	-198	No loss
2012/10	Weipa	GOC8	-220	No loss
2012/10	**Karumba**	**GOC6**	**-337**	**No loss**
2014/10	Milner Bay	GOC2	-266	No loss
2014/10	Weipa	GOC8	-288	No loss
2014/10	**Karumba**	**GOC6**	**-348**	**No loss**
2015/10	Milner Bay	GOC2	-370	20–50% loss
2015/10	Weipa	GOC8	-369	20–50% loss
2015/10	**Karumba**	**GOC6**	**-416**	**90–100% Loss**

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be the impact of a severe hail storm in October 1994 [49]. Another example, in Carnarvon in Western Australia (W1), the dieback in 2010 correlated with extreme high sea levels (see Figs D & E in S1 Text), indicative of 'drowning dieback' (Fig C in S1 Text). And, for sites south of the tropics on both east and west coasts of Australia there were no indications of dieback in 2015, implying there were different relationships with sea level in temperate waters.

Accordingly, it was notable that most sites in tropical latitudes had significant changepoints occurring around the time of the 2015 Taimasa (i.e., within the credible interval) and in each case the probability of occurrence was greater than 0.66 (Table 2; see Methods). Specifically, this applied to all eight GOC sites, two out of three western sites, and one eastern site. Note further, that there was a common date amongst changepoint periods around 6/2015.

Taimasa low sea level events in 1982 and 2015 were co-incident with major ENSO extreme lows

Eight of the ten sites with nearby sea level and SOI records demonstrated a significant correlation between anomalies of mean sea level and the SOI between 1987 and 2021 (see Fig 4; Table C in S1 Text; Figs D & E in S1 Text). This relationship applied to tropical sites, and the two sub-tropical sites (W1 and E3) showed non-significant relationships. These findings were indicative of the broad influences of ENSO processes on tropical shoreline mangroves, as well as showing the proxy value of SOI in predicting sea level at these latitudes. In this way, the unusually low 12-month SOI anomaly levels in 1982 (Fig 4C) were both consistent with the earlier Taimasa, and definitive in identifying the specific months of occurrence of that dieback event in the absence of local sea level data. In summary, the two unusually extreme low sea level (Taimasa) periods in the western Pacific region in 1982/83 [16–18] and 2015/16 [9, 27, 37], were consistent with each event causing widespread mass dieback of mangroves [11].
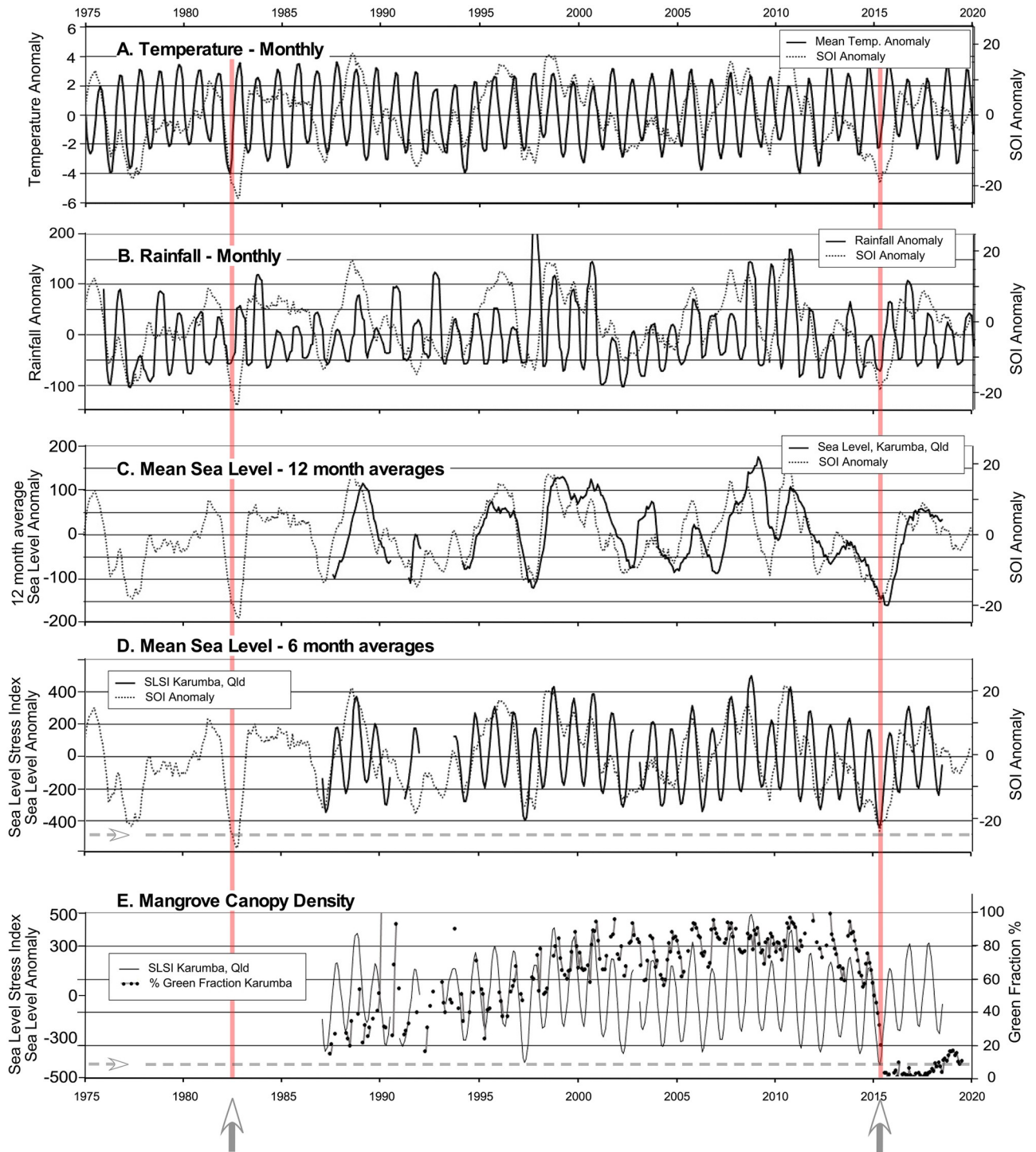
Fig 4. Timelines of influencing variables shown in climate (A & B), sea level change anomaly (C) and the SLSI (D) compared to the SOI anomaly and changes observed in green fraction (= mangrove canopy condition) for the severely impacted site near Karumba in the Gulf of Carpentaria (E). Vertical red lines indicate major desiccation events in 1982 and in 2015 (Image source: illustration by NCD).

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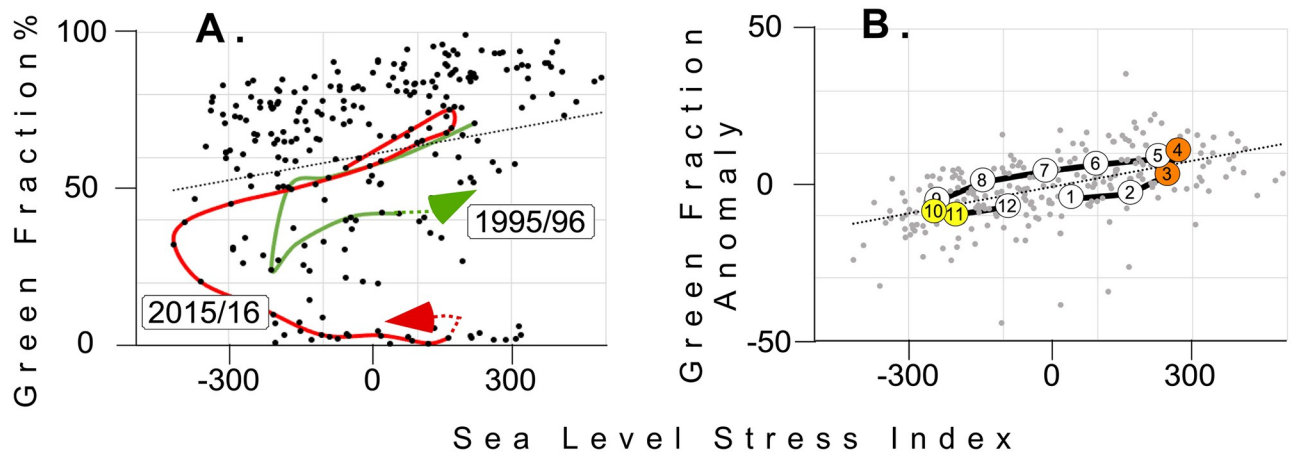
Fig 5. Relationships between the SLSI for Karumba in Australia's Gulf of Carpentaria between July 1987 and December 2018 and measures of mangrove canopy condition (Site 9—GOC6, see Tables 1–3), in A. as green fraction (%), and B. the green fraction anomaly ($r^2 = 0.227$, n = 251, P<0.001; see Methods). For A, the red arrow line depicts the loss in canopy condition between January 2015 to June 2016. Note the point of inflection of canopy decline corresponds to minimum negative values of SLSI ~-400 mm SLSI, marking the major desiccation event in October 2015. For B, numbers in circles show ensemble averaged data for each month of the year (1 = Jan to 12 = Dec) during the period ($r^2 = -0.500$, n = 12, P<0.02); noting March and April (shaded orange, peak wet season) and October and November (shaded yellow, peak dry season). Refer to 'S1 Text' for records from all 14 study sites (Image source: illustration by ADC).

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Relationship between canopy cover and sea level, temperature and rainfall

Further multivariate regression analyses indicated that for all 10 sites, except GOC8 (Weipa), the fractional green cover anomaly showed significant relationships with the mean sea level anomaly, accounting for rainfall, temperature and potential autocorrelation errors (Table D in S1 Text; Figs F & G in S1 Text). Note that coefficients for the sea level anomaly were positive, while those for the mean temperature anomaly were negative. Fig 4 shows data from the Karumba site (GOC6) that exemplified the relationships between fractional green cover, sea level, SOI, temperature and rainfall between 1987 and 2021. Fractional canopy cover showed a long-term interannual cycle and an annual cycle fluctuating between highs in April-May (4–5) and lows in October-November (10–11). Fig 5 shows the comparisons between fractional green cover and its anomaly with the sea level anomaly (= the Sea Level Stress Index), where the later displays a clear positive correlation ($r^2 = 0.227$; n = 251; P<0.001). It was notable further that averaged data for each calendar month (Fig 5B; circled numbers 1 to 12), displayed a linear trend depicting the common timing and regularity of annual highs and lows. These observations applied more widely to sites across tropical northern Australia (see Fig E in S1 Text).

Recovery of damaged mangrove canopies

We further compared fractional green cover data for the 14 sites between 1987 and 2021, quantifying abrupt losses in canopy density with the number of years it took to restore maximal canopy condition. Data displayed in Fig 6 show a significant linear regression (r2 = 0.7943, n = 45, P< 0.001). These 'abrupt decline' occurrences represent at least three categories of dieback type groupings, including: 23 desiccation events (with unusually low sea levels), 18 drowning events (with unusually high sea levels) and 4 storm damage events. We were unable to detect appreciable differences between recovery times for each, nor their location, implying that recovery processes were independent and innate.
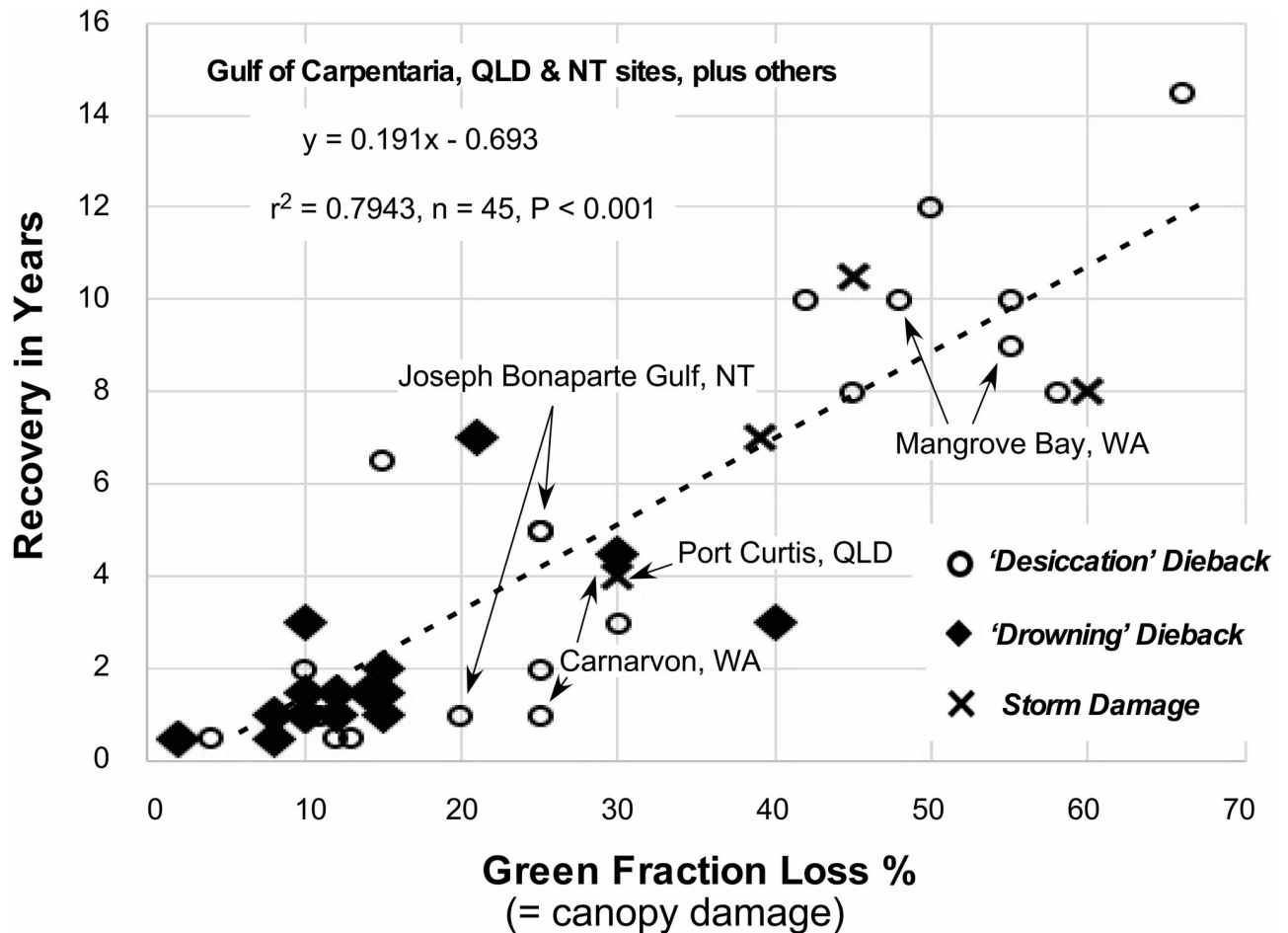
Fig 6. Plot of recovery times deduced from notable declines in canopy condition (impacted) observed in green fraction plots of shoreline mangrove sites across northern Australia (see Fig 3). Whilst recovery times were mostly independent of the type of impact, they were dependent on the severity of canopy loss. Storms and 'desiccation dieback' caused the most severe damage, but storms were considered localised impacts affecting up to 100–500 kilometres of shorelines on each occasion (Image source: illustration by NCD).

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Discussion

Our investigations present three discoveries concerning the recent influences of the apparently wider amplitude in ENSO-driven oscillations affecting sea level and impacting shoreline mangroves of tropical northern Australia. We summarise these findings in three key conclusions.

1. *A causal relationship* between mass 'desiccation dieback' of mangroves and ENSO-driven Taimasa as instances of extreme lows in mean sea level [22, 23]. While these impacts were synchronous across much of tropical northern Australia, they were particularly severe in the GOC (Fig 3). The two instances of mass 'desiccation dieback' in 1982 and 2015, further initiated a collapse-recovery cycle likely to have contributed to accelerated coastal retreat across the region.

2. *Two previously undescribed types of mangrove dieback* caused by extreme lows (Taimasa events) and extreme highs in sea level resulted in widespread damaging events of 'desiccation dieback' (see Fig B in S1 Text) and 'drowning dieback' (see Fig C in S1 Text), respectively. These damaging events are each believed to degrade the stability of shoreline vegetation and their zonal distribution across the tidal profile.

3. ***Mangrove canopy condition is influenced by both long and short term oscillations in mean sea level***. While the relationship described in (1) explained the lethal impacts of mass dieback events in northern Australia, there were also sublethal impacts. In addition, short-term annual oscillations in mean sea level were coincidental with seasonal growth dynamics of mangrove canopies. We propose that annual oscillations in mangrove inundation highs cause moisture conditions that influence seasonal leafing and leaf fall phenologies. This is most apparent in semi-arid areas, like the GOC. Furthermore, these oscillations are likely also to affect upper and lower elevation ecotone positions and accordingly help constrain and define the zonation of common mangrove vegetation units across the tidal profile.

Mass dieback of mangroves and the resulting collapse–recovery cycle

Shoreline mangroves of Australia's GOC suffered catastrophic damage in both 1982 and 2015 with the loss of ~76 km^2 of mangrove forests, arguably on each occasion—but definitely in 2015 [14, 15]. Despite the counter-intuitive idea of severe impacts being caused by low sea levels, during this period of rapid sea level rise [20, 50], our investigations found each catastrophic Taimasa event was coincident with abrupt periods of extreme low sea level. During mid-late 2015, sea levels dropped temporarily (over a 6 month period) by ~ 0.4 m on average in southern GOC coastal areas (Figs 2 & 4). The prolonged lack of tidal inundation appears to have caused severe 'desiccation dieback' of shoreline mangroves [4, 11]; Fig B in S1 Text). At the time, severe El Niño conditions caused a Taimasa event and climatic conditions across the Western Pacific region [35].

The Tiamasa, in 1982 and 2015 had caused catastrophic 'desiccation dieback' of shoreline mangroves that initiated a long-term cycle of collapse and recovery throughout the GOC (Fig 7). With this cycle, we recognised overall, three distinct phases, including: collapse events; a recovery trajectory; and a period of maximal growth. Whilst recovery after 1982 was seemingly successful with canopy closure after ~15 years, recovery after 2015 appears setback and threatened by additional damaging events making future recovery less likely [11]). For example, additional damaging events affecting GOC mangroves [14, 15], included severe localised cyclonic storms (see Fig 1), extensive flooding, the widespread influences of rising sea levels [20, 50], and the direct damaging impacts of feral pigs, introduced weeds and uncontrolled bush fires [11].
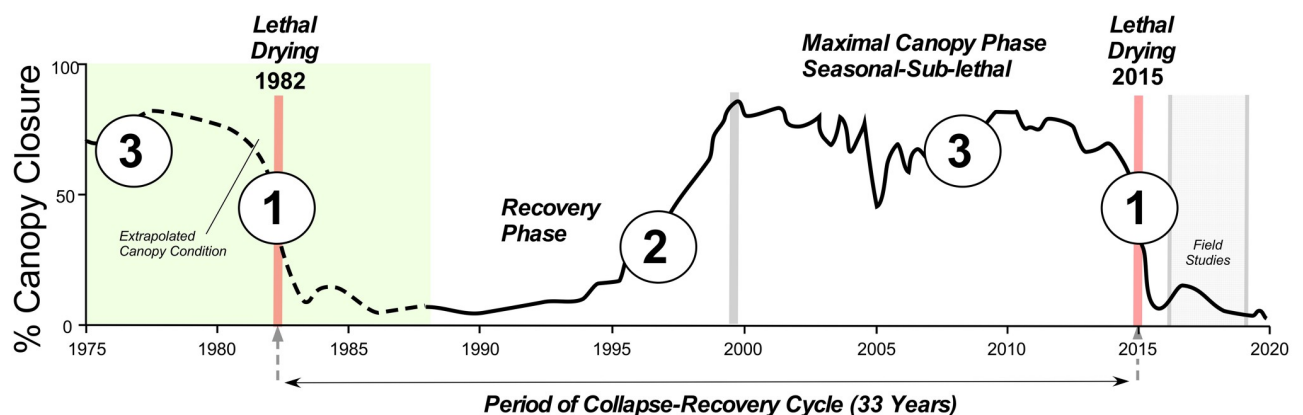
Fig 7. The collapse-recovery cycle affecting shoreline mangroves of Australia's Gulf of Carpentaria derived from various observations, and based on the 1987–2020 timeseries of canopy condition of site GOC6 Karumba (cs. Fig 4E). Note the three cyclical phases of canopy condition from 1) collapses in 1982 and 2015 (vertical red lines), 2) recovery, to 3) maximal canopy density (Image source: illustration by NCD).

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Across the region, declines in mangrove canopies were observed more broadly across northern Australian sites (see Fig 3). In view of the numerous 'abrupt declines' shown, we assessed the respective trajectories of canopy recovery. For example, where there was maximal damage in GOC sites of 80–90% canopy loss, recovery took at least 15 years for canopy closure (see Fig 6). Shorter periods were observed at less damaged sites with recovery from ~70% canopy loss taking ~10 years, and recovery from ~30% damage taking ~5 years. The overall comparisons between severity of canopy damage and recovery time (Fig 6) described a significant linear relationship (r^2 = 0.794; n = 45; P<0.001), depicting canopy recovery dependant on the severity of initial damage. These findings reveal a key feature of innate recovery potential for damaged mangrove forests, for at least the establishment phase to canopy closure [28].

Mangrove dieback by extreme low or high sea levels across northern Australia

Our investigations of shoreline mangrove dieback across northern Australia found damage levels were less severe in other areas, although there were synchronous, less lethal impacts in sites west to Joseph Bonaparte Gulf in the Northern Territory and Mangrove Bay near Exmouth in Western Australia (Fig 3). In sites with higher rainfall like those on the east coast, few if any comparable impacts were observed [3]. These findings were consistent with sites on Australia's east coast having alternate sources of moisture (like high rainfall and groundwater flow; see Table 1) during periods of critically low sea levels. These conditions are likely to have prevented 'desiccation dieback' in relatively wetter conditions. Furthermore, the lack of this kind of dieback in southern, sub-tropical sites, notably Carnarvon in central Western Australia and Brisbane in Moreton Bay in south-eastern Queensland, may be due to other influences present at higher latitudes. For mangroves in semi-arid tropical areas, we found that 'desiccation dieback', linked to Taimasa events, had shifted the upper ecotone of the shoreline mangrove zone [15]; see Supporting information). While this ecotone had likely been established by longer-term trends in exposure and drying with rainfall patterns as well as rising sea levels, damage by the Taimasa pulse event had profoundly altered this process, greatly increasing the vulnerability of these impacted shorelines.

Our studies were further indicative of shoreline mangroves being alternately impacted further during extreme high sea level events. For example, seaward fringing mangroves near Carnarvon suffered abrupt severe dieback in 2010–2011 (see Fig 3; Fig E in S1 Text). In that instance, dieback was coincident with a period of extreme high sea levels and severe La Niña conditions [51]. We consider this to be an instance of 'drowning dieback' (Fig C in S1 Text). This kind of dieback pattern had been recognised as 'inner fringe collapse' [14, 41, 42] in shoreline surveys of Torres Strait islands, eastern Cape York Peninsula, and the GOC. We deduced that 'drowning dieback' was consistent with these abruptly impacted mangroves at seaward fringing, lower elevation mangroves, where they corresponded with severe La Niña conditions of extreme high sea levels. We further note that 'drowning dieback' is the same type of dieback most likely associated with rising sea levels [20].

We further propose that highs and lows in mean sea level act to limit and constrain the extent of mangroves and other intertidal vegetation across the tidal profile, especially for mangroves of the shoreline zone (Fig A in S1 Text). While these uniquely salt-tolerant trees displayed a finely-tuned dependence on regular seawater wetting of roots and sediments, this process was expected to have abrupt and finite limits defined by periods of exposure or inundation. And, these types of changes would largely occur at ecotones at either upper or lower elevation zone margins (Fig 1; also S1 Text).

Accordingly, we recognise two indicative ecotones of shoreline mangroves, being: 1) sea edge mangroves at lower elevations around mean sea level, limited by inundation durations less than 50%; and 2) the shoreline mangrove to saltmarsh-pan boundary at upper elevations (Fig A in S1 Text), influenced also by longer term rainfall (Duke et al. 2019). Where mangroves of the shoreline zone would normally be constrained by rainfall, mean sea level and tidal range [11], these particular ecotones appear occasionally to be further influenced by abrupt extremes in mean sea level during severe ENSO conditions.

During El Niño conditions, mangroves at the upper ecotone of the shoreline zone have been shown to be highly vulnerability to exposure and desiccation when sea levels were unusually low. This had largely explained why mangroves died *en masse* along this ecotone during the extreme low mean sea levels associated with severe El Niño conditions in 2015 [4]. However, whilst dieback at this ecotone could also be a response to longer-term declines in rainfall, termed 'ecotone-shift', the latter dieback type differed by being a longer-term pressure response, applied incrementally over many years [14]. In contrast, 'desiccation dieback' described with this study was a pulse response, being sudden, abrupt, widespread and catastrophic [4, 14]. Another significant influence at this upper ecotone had been rising sea levels, although this too was a pressure response. Notably, while rising sea levels in the GOC had progressively forced upland migration of the ecotone over 2–3 decades until 2015 [15], the mass dieback events had overwhelmed that steady incremental process by wiping out entire shoreline stands (see Fig 1).

During La Niña conditions, mangroves at the sea edge ecotone were occasionally impacted by excessive inundation when sea levels were extremely high. As noted, such a pulse instance of 'drowning dieback' was observed at Carnarvon. This type of dieback combined with locally-severe pulse events, like cyclonic storms, are likely to reduce the resilience of mangroves at the sea edge ecotone, further destabilizing the shoreline mangrove zone by reducing its capacity to accommodate the incrementally progressive pressure of rising sea levels.

Regular oscillations in mean sea level drive annual growth cycling in mangroves

Our investigations further revealed a close relationship between seasonal variations in mangrove canopies and sea levels. Relatively moderate, annual oscillations in mean sea level were observed in sites across northern Australia (see Figs 3 & 4; Fig D in S1 Text). The common patterns were consistent with there being a primary level influence of sea level on mangrove ecosystems and forest development [11]. Together with regular tidal flushing, annual oscillations in mean sea level notably influenced both the position of shoreline mangroves across the tidal profile, as well as their seasonal growth and productivity.

Evidence of these influences were depicted in the correspondence between annual oscillations of mean sea level and phenological events of two locally dominant mangrove species, *Avicennia marina* and *Rhizophora stylosa*, in northern Australia. For *A. marina*, leafing (leaf flushing, appearance, production) was observed during wet season months of February to April, and leaf senescence (leaf fall, shedding, loss) during dry season months May to October [52]. This pattern was comparable with that for *R. stylosa* [53] seen in multiple locations across the region [54]. Such common seasonal patterns of these two quite different mangrove genera suggests that mangrove stands, irrespective of species composition and climatic conditions, were influenced by a moisture availability primarily from sea level inundation. While the full implications of these findings are yet to be fully appreciated or explored, these influences were consistent with the unusually pronounced seasonal patterns observed in these largely tropical, forested ecosystems [55].

These observations may also be useful in explaining why mangroves have formed extensive, closed-canopy forests throughout tropical, semi—arid and arid regions. This unique trait is little known in other forested ecosystems in semi-arid to arid regions. The presence of closed mangrove forests in such relatively dry settings, implies they have a specialised ability to access moisture from seawater inundation. While this concept has in some ways been accepted generally, our observations now explain its unique application and function. While mangrove forests flourish (biomass, biodiversity and extent) in regions of higher rainfall [3, 19], they also occur commonly in arid areas where moisture from atmospheric sources like humidity, rainfall, catchment runoff and groundwater are less available and erratic. We propose that shoreline mangrove ecosystems have a default reliance on regular seawater wetting manifest in the seasonal regulation of growth form, composition and phenological cycles, as well as their shoreline zonation [11].

## A schematic depicting the influences of sea level oscillations on mangroves

We summarise key findings from these investigations in a schematic diagram (Fig 8). At its centre (green shaded box) are the newly-discovered influences of moderate sea level oscillations on mangrove forests driving seasonal canopy growth (y-axis, vertical) with regular annual highs and lows (x-axis, horizontal). These annual oscillations in sea level specifically correspond to vegetative phenoevents during the same months each year with mangrove canopies adding leaves during March-April-May, and shedding leaves during September-October-November. The respective median limits in mean sea level define an optimal 'sweet spot' for mangrove growth, a mangrove 'Goldilocks Zone' of normal seasonal variability in mean sea level.

When oscillations become extreme (pink shaded boxes left and right of the green box), exceeding the 'Goldilocks Zone', there would be abrupt and catastrophic impacts on shoreline mangroves (black shaded arrows). These alternate pulse impacts are depicted as 'desiccation dieback' and 'drowning dieback' depending on sea levels being exceptionally low or high, respectively. 'Desiccation dieback' occurs when sea levels are unusually low during strong El Niño conditions (Fig 5, left side) resulting in prolonged drying. Alternately during unusually high sea levels during strong La Niña conditions (Fig 5, right side) prolonged inundation results in 'drowning dieback'. The most damaging of these impacts appears to be 'desiccation dieback' [10], known as 'Taimasa' events in Samoa, where intertidal corals had been left exposed [22, 23].

As shown, damage to mangroves in northern Australia's GOC were particularly severe. This was possibly because of the shallow bathymetry affecting tidal flows within the GOC [38, 56, 57] coupled with the predominance of ambient semi-arid, dry season conditions [9] when sea levels were lowest. For both extreme events in 1982 and 2015, it appears that moisture levels from seasonal rainfall and below ground aquifers were deficient during the dry season, and concurrent with the severe El Niño conditions of extreme low sea levels.

Implications of more frequent and more severe oscillations in sea level

These investigations have identified a substantive and previously unrecognised, widespread and severe pulse threat to shoreline mangrove ecosystems from increasingly extreme oscillations in mean sea level, as Taimasa events. In recent decades, these notably abrupt extreme lows in sea level have on two occasions, at least, resulted in severe desiccation and catastrophic mass dieback of shoreline mangroves in northern Australia [11]. The underlying drivers responsible have been the unusually severe El Niño events in 1982 and 2015, the two most severe such events in recent centuries, depicted in the 400 year coral record [37]. Of
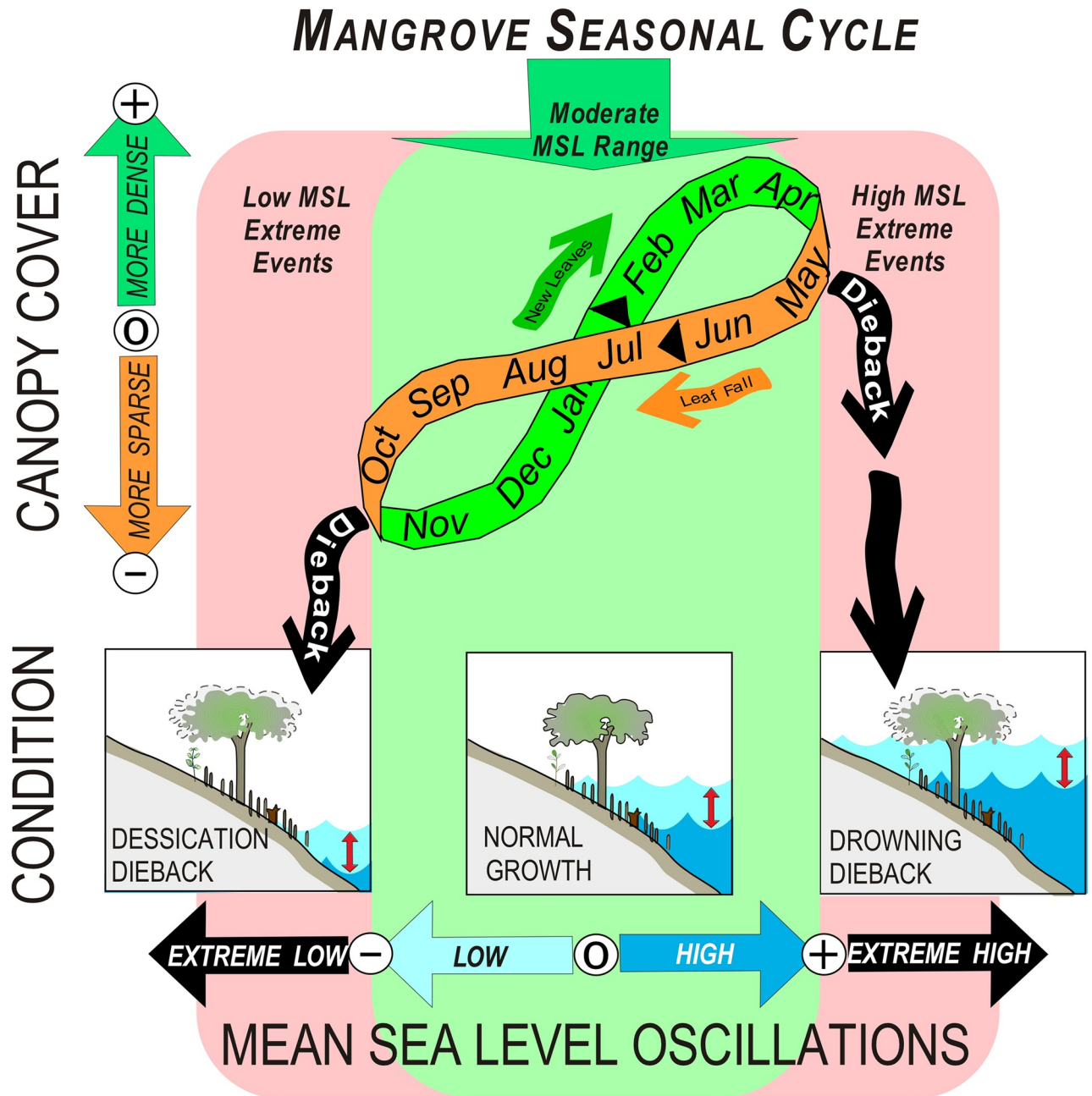
Fig 8. The relationships between canopy condition of tropical, semi-arid shoreline mangroves and mean sea level (MSL) identified during this study. When conditions exceeded the mangrove Goldilocks zone (central green shaded block) of normally moderate annual oscillations in mean sea level, severe destructive impacts occurred as a result of high or low extreme events (drowning or desiccation dieback respectively; pink shaded blocks). Moderate oscillations appear to drive natural seasonal cycles of leafing and leaf fall where low levels (less inundation) correspond with leaf fall (maximal in Sept-Nov), and high levels (more inundation) with new leaf production (maximal in Mar-May) (Image source: illustration by NCD).

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further concern, such occurrences have been predicted to re-occur as greenhouse warming escalates [58].

Over the last half century, changing ocean atmospheric conditions have led to more energised ENSO processes [34, 59], driving more extreme oscillations in mean sea level [22, 23, 58,

60]. Our findings extend upon these observations with confirmation of the recently recognised impacts on mangrove ecosystems caused by such events, identifying relationships between: 1) oscillations in mean sea level linked to ENSO processes and the condition of mangroves; 2) the increased amplitude of oscillations in sea level and increased severity of 'Tiamasa' events; and, 3) the widespread abrupt, mass dieback of shoreline mangroves [4, 11, 14, 15]. Of notable importance also, our studies reveal the profound influence of sea level oscillations as a major driver of seasonal growth processes of mangrove forests. These circumstances highlight an innate and fundamental reliance by mangroves on seawater inundation, possibly explaining how these uniquely salt-tolerant forests dominant the decidedly harsh environmental conditions at the sea edge.

In summary, our studies show how mangroves, like coral reefs [35] are profoundly influenced by ENSO processes. Damage to mangroves and corals were both coincident with unusually severe El Niño events in 1982 and 2015 [35, 57, 61]. This relationship is likely to extend further to include kelp and seagrass beds [27, 62], along with extended implications for dependant fisheries like the Australian prawn industry [7], as well as a number of other natural ecosystems [21, 27, 31–34].

In view of these newly recognised threats from extreme sea level oscillations on shoreline mangroves, there are a number of environmental management initiatives being planned and undertaken, including: -

1. to better inform government managers of current threats and imminent risks to further validate increased international efforts to reduce the impacts of climate change, and by supporting inclusion of informative ecological indicators into national shoreline environmental monitoring programs;

2. to support local governments, catchment management agencies, indigenous custodians and community groups to engage in local shoreline and estuarine monitoring programs documenting and evaluating each type and instance of notable damage and change, assisting local management agencies in raising the resilience of natural mangrove ecosystems at risk, by reducing localised threats like feral pigs, weed infestations and bush fires; and

3. by giving serious consideration to innovative, well-considered, mitigation strategies for reducing the deadly severity of future occurrences of catastrophic mass dieback of mangroves—especially since these events are partly predictable, and possibly preventable.

Supporting information

S1 Text. PDF-document with Tables A-E, Figs A-G. Content includes: sea level influences on tidal mangroves; two types of mangrove dieback attributed to extremes in sea level; study site additional information; post impact assessments of mangrove canopy recovery; timeseries plots for the sea level stress index (SLSI); comparisons between green fraction indices and SLSI; timeseries plots for climate data; comparative assessment of sea level and southern oscillation index data; comparative assessment of green fraction with climate and sea level data; green fraction data used to quantify mangrove condition.
(PDF)

S1 Data. Data file containing data used for the analysis. The raw data are open access. Relevant data used in this analysis for 14 sites across northern Australia for the period 1987 to 2022 (see Table A in S1 Text). Description of variables used: 'FCC_anomaly'; 'SL_anomaly'; 'SOI_anomaly'; 'Rainfall_anomaly' and 'Temp_anomaly'.
(CSV)

S1 File.
(DOCX)

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