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Stable isotopes indicate ecosystem restructuring following climate-driven mangrove dieback

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Abstract

Extreme climatic events can trigger sudden but often long-lasting impacts in ecosystems by causing near to complete mortality of foundation (habitat-forming) species. The magnitude and frequency of such events are expected to rise due to anthropogenic climate change, but the impacts that such events have on many foundation species and the ecosystems that they support remains poorly understood. In many cases, manipulative experimentation is extremely challenging and rarely feasible at a large scale. In late 2015 to early 2016, an extensive area of mangrove forest along ~ 1000 km of coastline in the Gulf of Carpentaria, Australia, experienced severe dieback, an event associated with climatic extremes. To assess the effect this dieback event had on the mangrove ecosystem, we assessed benthic faunal assemblages and food web structure using stable carbon and nitrogen isotopes in a comparative experiment of impacted forest and adjacent unimpacted forest. Eighteen months after the dieback, the forest that suffered dieback contained significantly fewer crabs that rely on mangrove litter food source but more crabs that rely on microphytobenthos food source than the unimpacted forest. However, the infaunal biomass was largely unaffected by the mortality effect. This is most likely because microphytobenthos was largely unaffected and consequently, this buffered the food web responses. However, overall, the habitat value for mangrove ecosystem services most likely decreased due to lower physical habitat complexity following tree mortality. Longer-term monitoring could lead to better understanding of biological effects of this extreme event and underlying biological mechanisms that drive changes and recovery.

Extreme climatic events, including droughts, floods, and heatwaves, have a major role in structuring ecological communities via reduction or elimination of foundation species (e.g., canopy-forming plants, reef-building corals) (Silliman et al. 2005; Thomson et al. 2015; Wernberg et al. 2016; Stuart-Smith et al. 2018). The occurrence of these events is anticipated to rise due to climate change (Coumou and Rahmstorf 2012; Stott 2016). However, biological effects of such extreme events remain poorly understood and case studies are limited (Harris et al. 2018). During 2015–2016, extreme climatic conditions including high temperatures, dry conditions, and El Niño–Southern Oscillation-induced low sea level triggered a severe unprecedented mass mortality of mangroves along ~1000 km of coastline in tropical Australia (Duke et al. 2017; Lovelock et al. 2017), the largest known mangrove dieback event from natural causes (Sippo et al. 2018). This coincided with the heat-stressed mass bleaching event of the Australian Great Barrier Reef (Hughes et al. 2017). How the extreme climate-driven loss of mangroves that provide the foundation for habitats and support core ecological processes, can change ecosystem structure remains unclear. It is expected that mangrove tree losses will lead to changes in biological communities due to changes in primary production and associated shifts in nutrients cycling, and to disturbances from physical modifications of habitat structure provided by the mangrove foundation species (Kristensen 2008; Lee et al. 2014; Alongi 2015).

Understanding of individual extreme weather events in human-induced climate change has advanced in the recent decades (Coumou and Rahmstorf 2012; Stott 2016); however, a similar understanding of extreme biological events is limited (Parmesan et al. 2013; Ummenhofer and Meehl 2017; Harris et al. 2018). Climate-driven environmental stresses as well as

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extreme events such as droughts and heatwaves can change benthic communities of estuarine habitats (Dolbeth et al. 2007; Pillay and Perissinotto 2008, 2009; MacKay et al. 2010; Pollack et al. 2011; Veríssimo et al. 2013; Verdelhos et al. 2014). In some cases, investigations of such biological responses to climate-driven environmental stresses and detecting underlying biological mechanisms that drive such responses involve long-term monitoring (Dolbeth et al. 2007; Pollack et al. 2011). The initiation of monitoring after an extreme biological event is therefore essential to interpret these extreme biological events and to anticipate such events in the future (Altwegg et al. 2017). In most cases, "before and after" monitoring is not achievable; however, experimental studies with spatial and temporal controls, for example, comparisons with areas that did not experience the extreme event might produce biological data that can help to identify the mechanisms driving a response. This might also establish casual relationships, possibly detecting other important, non-climatic drivers (Veríssimo et al. 2013; Verdelhos et al. 2014; Bailey and van de Pol 2016; Altwegg et al. 2017).

Stable isotope tracer data that provide biogeochemical source and process information over time help ecosystem analyses, because as elements circulate in the biosphere, stable isotopic compositions can change in predictable ways (Peterson and Fry 1987). Stable isotopes have been widely used in investigations of C and N cycling in mangrove ecosystems (Adame et al. 2018) and mangrove food webs (Fry and Smith 2002; Bouillon et al. 2008). Mangrove faunal communities including infauna that live within the sediment and epifauna that live at the sediment–water interface or on solid substrata generally constitute much of the benthic food web and perform important functions in coastal habitats (Bouillon et al. 2002; Demopoulos et al. 2007). For example, they serve as food for animals at higher trophic levels and stimulate detrital decomposition (Sheaves and Molony 2000; Lee 2008). Disturbances such as losses of mangrove trees can change organic matter inputs and degradation of sediment organic matter (Atwood et al. 2017; Adame et al. 2018) and consequently change overall sediment conditions with consequences to benthic faunal assemblages (Sweetman et al. 2010; Bernardino et al. 2018). However, detailed knowledge of such trophic interactions in mangrove ecosystems is lacking. Therefore, to assess the effects of climate-driven loss of mangroves on mangrove food webs, a careful evaluation of food web structure, including food resource utilization, is needed. In such isotope investigations, it is typically assumed that consumer isotope values resemble those of food resources, with a trophic shift of +0 to 1‰ for $\delta^{13}C$ and +2 to 3‰ for $\delta^{15}N$ (Vander Zanden and Rasmussen 2001; McCutchan et al. 2003).

The study aims to identify changes in ecosystem structure following this climate-driven mangrove dieback. We combined field survey and stable isotope data at impacted mangrove forest and adjacent unimpacted forest (Fig. 1a,b). We hypothesized that (1) changes in benthic faunal assemblages between unimpacted and impacted forests would be evident due to mangrove mortality; and (2) food web structure would be noticeably different between unimpacted and impacted forests as a result of changes in assemblages and on food sources.

Materials and methods

2015–2016 mangrove dieback in the Gulf of Carpentaria, Australia

In late 2015 to early 2016, large areas of mangrove vegetation along ~1000 km of coastline in the Gulf of Carpentaria experienced severe dieback (Duke et al. 2017; Sippo et al. 2018). This led to the complete to near death of mangrove trees. There were coincidental mangrove mortality events that occurred in Exmouth, Western Australia (Lovelock et al. 2017) and Kakadu National Park, Northern Territory (Asbridge et al. 2019). At the time, this region in the Gulf of Carpentaria had not experienced any other significant coincidental disturbances, for example, cyclones and pollution, and was most likely a pristine mangrove forest (Duke et al. 2017). Mangroves in the Gulf region experience harsh environmental conditions such as seasonal aridity, high variability in air and sea surface temperatures, and salinity. Due to these conditions, the extent of mangroves is limited in the Gulf region (Asbridge et al. 2016; Duke et al. 2017). The climate in this region is wet-dry tropical with highly seasonal rainfall driven by the Australian monsoon. This tropical arid region experiences drought annually for 6–8 months with the majority of rainfall occurring between December and March, and receives mean annual precipitation ranging from approximately 600–900 mm (Bureau of Meteorology, see www.bom.gov.au). The cause of the Gulf mangrove dieback is most likely due to a weak monsoon (i.e., drier summer-wet season in 2015–2016) combined with unusual climate/weather events at the time including high air and surface seawater temperatures, and El Niño–Southern Oscillation induced low sea-level. These factors most likely resulted in hypersalinization of mangrove sediments and caused adequate hydric, thermal, and radiant stresses (Duke et al. 2017; Lovelock et al. 2017). The details of causality are documented by Duke et al. (2017) (see their fig. 12 for the meteorological data showing key climatic drivers) and Harris et al. (2018) (*see* their Supplementary Material, S1.52).

Experimental design

The main study aim was to assess the effect of climate-driven mangrove tree mortality on mangrove ecosystem structure with particular focus on benthic faunal assemblages and food web structure. Controlled experimentation as well as "before and after" comparisons were not easily achievable. For these reasons, we undertook a comparative experiment of an impacted forest vs. an unimpacted forest. This comparative study was carried out at Karumba in the Gulf of Carpentaria, Queensland, Australia (Fig. 1c). A major field campaign was conducted in August 2017 in the winter dry-season, 18 months after the dieback event. A forest that had suffered dieback, as well as an adjoining

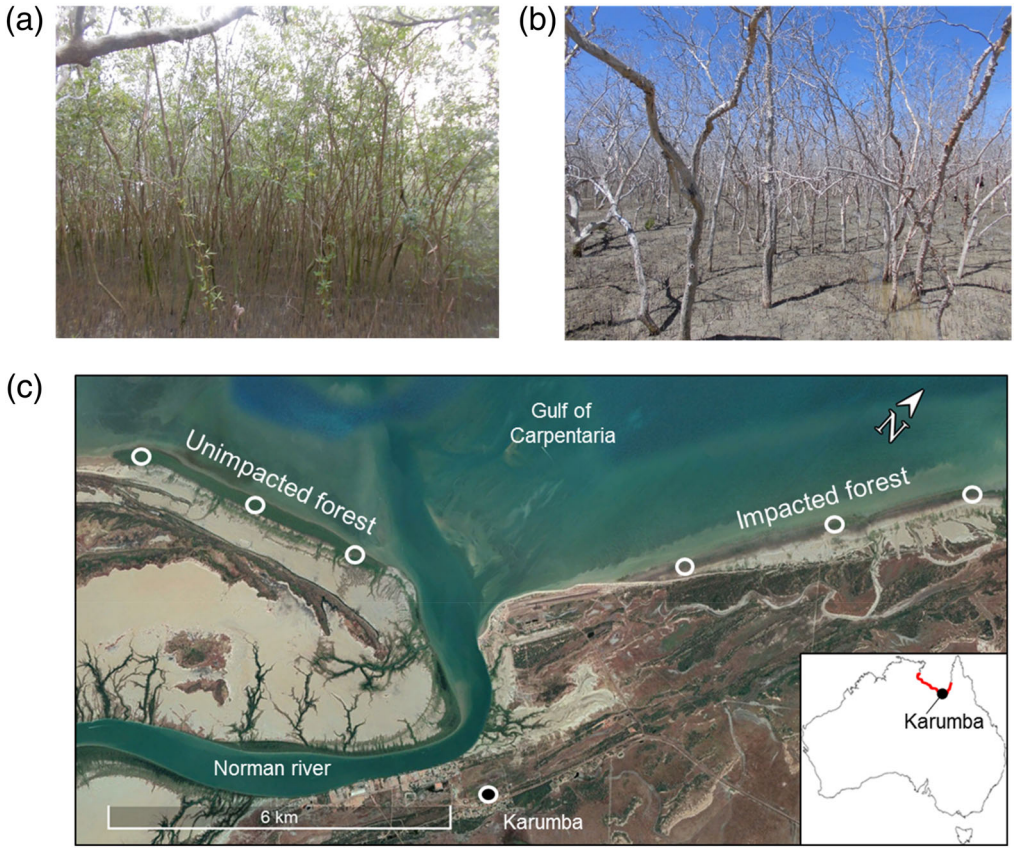

Fig. 1. Comparative experiment of unimpacted (**a**) and impacted (**b**) mangrove forests. (**c**) Study location at Karumba in the Gulf of Carpentaria, Queensland, Australia (–17.435572S, 140.844766E). An aerial image/map shows the mangrove vegetation loss and the extent of mangrove loss along the coastline. There are three sampling areas within the unimpacted forest and three within the impacted forest (shown as white circles). Two sites within each area were independently sampled.

unimpacted forest, provides the settings for a comparative experiment (Fig. 1a,b). *Avicennia marina* was the dominant mangrove species. In this experiment, three areas (2–2.5 km apart) within the unimpacted forest and three within the impacted forest were surveyed (Fig. 1c). At each area, two independent sites (> 50 m apart) were sampled, one site about 20 m from the forest edge (seaward) and one about 70 m from the forest edge (seaward) to cover the general variability across the intertidal zone and ensure that the physical-oceanographic conditions between the two forests were as similar as possible.

Field survey and sampling

The field surveys were carried out during low tide when the forest ground was exposed. At each sampling site, we conducted sampling using quadrats of sizes 4 m^2 (n = 3) and 1 m^2 (n = 3), to quantify the populations of common benthic epifauna (ind. m^{-2}). The location of quadrats was randomly chosen at each sampling site and at least 3 m away from each other. In total, n = 36 quadrats (6 quadrats × 6 sampling sites) were obtained for each forest. We combined data from 4 and 1 m^2 quadrats because the smaller quadrat underestimated low abundant species. Individuals were counted visually throughout the quadrats, and each observation lasted 10–15 min to ensure that burrowing crabs recover from the initial disturbance (a modified method from Nobbs and McGuinness 1999; Skov and Hartnoll 2001; Skov et al. 2002). Although every care was taken to avoid double-counting individuals, this visual estimation method may have overestimated epifaunal densities by over counting individuals and/or underestimated the densities by under counting those that remained belowground, for example, burrowing crabs and very small individuals that are difficult to observe (Skov et al. 2002). Ten species were identified and sorted into five groups based their feeding modes, namely, algae-feeder (crab) = *Tubuca signata*, *Uca flammula* (Kon et al. 2010; Tue et al. 2012), detritivore (crab) = *Paracleistostoma wardi* (Jones and Clayton 1983), grazer (gastropod) = *Telescopium telescopium*, *Terebralia sulcata* (Pape et al. 2008), leaf-feeder (crab) = *Parasesarma moluccensis*, *Episesarma* sp. (Harada and Lee 2016; Kristensen et al. 2017), omnivore (crab) = *Metopograpsus frontalis* (Poon et al. 2010). Populations (ind. m^{-2}) of the five benthic epifaunal groups were estimated for each forest.

Pneumatophores, crab holes, and leaves on the forest floor were quantified using smaller quadrats (size 50 × 50 cm, n = 15–25 per site). In total, n = 161 for the unimpacted forest and

n = 173 for the impacted were obtained to estimate densities (ind. m^{-2}) of pneumatophores, crab holes, and leaves for each forest. In this process, photographs were taken, and counts were made later in the laboratory. To quantify biomass of benthic infauna, sediment core samples (n = 3) were collected independently (> 10 m apart) at each site using a soil corer (15 cm in diameter and 20 cm in depth) following the method modified from Alfaro (2006). The sediment core samples were immediately wet-sieved using a 0.5 mm sieve onsite. For each sample, the residue retained on the sieve was transferred into sealed plastic containers and preserved in 70% ethanol. The preserved animals mainly consisting of burrowing crabs and some clams and worms in the ethanol solution were separated under a binocular microscope and later weighted (wet g) in a laboratory. In total, n = 18 cores ($n = 3 \times 6$ sampling sites) were obtained from each forest to estimate infaunal biomass (g m^{-2}) of each forest. One additional sediment core sample (5 cm in diameter and 20 cm in depth) was collected at each site (total n = 6 each forest) for analyzing total carbon (TC), total organic carbon (TOC), total nitrogen (TN), stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), and particle sizes. Particle sizes were analyzed using a particle size analyzer (Malvern Mastersizer Hydro). At each sampling site, pH and salinity were measured from a water sample obtained by digging bores to the depth of water table (total n = 6 each forest). The top 0.5 cm surface sediment (200 mL) was also collected at each site (total n = 6 each forest) for TC, TOC, TN, $\delta^{13}C$, and $\delta^{15}N$ measurements. One hundred fifty milliliters of each 0.5 cm surface sediment sample was used to extract microphytobenthos (MPB) as described below. Extracted MPB samples were also analyzed for $\delta^{13}C$ and $\delta^{15}N$ values. The chlorophyll *a* (Chl *a*) content of the surface sediment samples was also measured to assess the abundance of MPB. Chl *a* was extracted using 90% aqueous acetone in darkness for 24 h. Chl *a* concentration was measured following the spectrophotometric method (Parsons 2013). In this process, three measurements were made for each sample and the mean of three measurements was determined for each sample for data analysis. Five grams of sediment was used for each measurement.

Stable isotope analysis

To compare stable carbon and nitrogen isotopic compositions of primary producers including mangrove (*A. marina*) and MPB as well as invertebrate consumers from the abovementioned five feeding groups between unimpacted and impacted forests, samples were gathered from each forest. Each forest consists of three sampling areas (2–2.5 km apart) as shown in Fig. 3c. At each sampling area, samples were collected between 20 and 70 m from the forest edge (seaward). Samples were collected by hand and were frozen immediately after the collection. All stable isotope samples were stored separately in sealed plastic containers at −20°C until analysis. In total, 15 mangrove leaves, 6 MPB samples, and > 141 individual invertebrates from the unimpacted forest and 12 mangrove leaves, 6 MPB samples, and > 102 individual invertebrates for the impacted forest were collected and analyzed as described below. Senescent yellow leaves were picked from mangroves (*A. marina*). Leaves samples were washed thoroughly, rinsed with distilled water, and the main vein was removed. Three leaves from the same sampling area were composited for each isotope measurement.

MPB was extracted from the top 0.5 cm soil samples by density gradient centrifugation in colloidal silica (Hamilton et al. 2005; Bui and Lee 2014). The soil was suspended in distilled water and then filtered through a 63 μm sieve to remove larger particles. The filtrate was centrifuged at 4400 rpm for 5 min, and the supernatant was discarded. Pellets were resuspended with 40 mL of 30% Ludox colloidal silica (Sigma) and centrifuged again at 4400 rpm for 5 min. The top layer containing algal cells (mostly diatom and filamentous cyanobacteria), confirmed by microscopic examination, was collected and centrifuged again with distilled water to remove silica. The MPB samples were dried and collected in tin capsules for analysis.

For fauna stable isotope analysis, muscle tissues were used. Several individuals (2–10) of the same species from the same sampling area were pooled to efficiently obtain the mean isotope values (Fry 2006). Each sediment sample of < 0.5 cm surface sediment (n = 6 per forest) and 0.5–20 cm deep sediment (n = 6 per forest) as described above were mixed, dried, and homogenized before stable isotope analysis. For sediment $\delta^{13}C$ measurements, samples were acidified with 1 mol L^{-1} HCl to remove inorganic fraction. All samples were dried at 60°C, powdered, homogenized, and collected in tin capsules for stable isotope analysis. Stable isotope analyses of $\delta^{13}C$ and $\delta^{15}N$ were carried out on an elemental analyzer (Europa EA-GSL, Sercon) coupled to an isotope ratio mass spectrometer (Hydra 20-22, Sercon) at Griffith University, Brisbane, Australia. Vienna PeeDee Belemnite (VPDB) and atmospheric air (AIR) were used as standards for C and N, respectively. Stable isotope values are reported in δ-notation (‰), that is, $\delta^{13}C$ or $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1000$, where R is, respectively, $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The elemental compositions, that is, %C and %N, of samples were also provided.

Data analysis

All statistical analyses were undertaken in R version 3.4.3 with RStudio interface version 1.1.414. Differences among group means were tested with ANOVA. Before performing ANOVA, the assumptions of homogeneity of variance and normality were checked using Levene's and Shapiro–Wilk's test, respectively. When the ANOVA assumptions were violated, the data were log-transformed and ensured that the assumptions were met before performing the ANOVAs. For the sediment TC, TOC, TN, $\delta^{13}C$, and $\delta^{15}N$ data, when the ANOVA test was significant, a post hoc Turkey test was performed to check which specific groups differed (< 0.5 cm surface sediment and 0.5–20 cm deep sediment). A generalized linear model (GLM) with Poisson distribution was performed for count data. Permutational Multivariate Analysis of

Variance (PERMANOVA) was performed to compare epifaunal compositions (i.e., abundance of the five feeding groups, ind. m^{-2}) between the two forests and to test whether the compositions between the two forests differ in spread or position in a multivariate space. In this analysis, square-root transformation was applied to minimize influence of the most abundant groups, then the Bray-Curtis index was used as the distance metric. Permutation test of multivariate homogeneity of dispersions was performed to check whether dispersions around the centroids are similar between the two forests. All statistical tests used a significance criterion of 0.05.

Results

Population densities (ind. m^{-2}) of the five epifaunal feeding groups across unimpacted and impacted forests are shown in Table 1. The forest that suffered dieback contained fewer leaf-feeding crabs but more algae-feeding crabs than the unimpacted forest (mean, SE, and GLM statistics provided in Table 1). However, populations of other dominant faunal groups, including omnivores (crab), detritivores (crab), and grazers (gastropod), did not differ significantly (Table 1). Epifaunal species composition (%) for each forest (Fig. 2a) indicates that the impacted forest is dominated by the algae-feeding crabs. PERMANOVA indicated that the two forests differed in the assemblages of five epifaunal feeding groups (df = 1, $r^2 = 0.29$, $F = 27.22$, $p = 0.001$), but the data dispersions did not differ significantly (df = 1, $F = 1.95$, $p = 0.15$; Supporting Information Fig. S1). There was also no significant difference in the total infaunal biomass, that is, mostly burrowing crabs (Fig. 2b and Table 1). Consistent with this, the densities of crab burrows (burrows m^{-2}) did not differ significantly between the impacted (mean = 64.3, SE = 2.0) and the unimpacted forest (mean = 65.2, SE = 2.3) (Table 1). In terms of trophic resource availabilities, leaf litter abundance (leaves m^{-2}) significantly differed, with fewer leaves on the ground in the impacted (mean = 3.8, SE = 1.3) than the unimpacted forest (mean = 76.1, SE = 11.7) (Table 1). The leaves in the impacted forest probably arrived as subsidies from adjacent healthy areas, or minor patches of regrowth. Microphytobenthos (MPB) density estimated by soil chlorophyll content ($\mu g\ g^{-1}$) did not differ significantly between the

Table 1. Summary of values (mean, SE) of ecological components from each forest.

	Forest				
	Unimpacted		Impacted		ANOVA/GLM
	Mean (SE)	*n*	Mean (SE)	*n*	df, *F*, *p*
Algae-feeder (crab) (ind. m^{-2})	3.5 (0.7)	36	10.9 (1.2)	36	1, −1.1, < 0.001
Detritivore (crab) (ind. m^{-2})	0.9 (0.2)	36	0.7 (0.4)	36	1, 0.28, 0.30
Grazer (gastropod) (ind. m^{-2})	0.8 (0.1)	36	0.8 (0.2)	36	1, −0.08, 0.78
Leaf-feeder (crab) (ind. m^{-2})	1.6 (0.2)	36	0.2 (0.04)	36	1, 2.2, < 0.001
Omnivore (crab) (ind. m^{-2})	0.8 (0.1)	36	0.5 (0.1)	36	1, 0.47, 0.11
Crab burrows (burrows m^{-2})	65.2 (2.3)	161	64.3 (2.0)	173	1, −0.014, 0.272
Pneumatophore (pneumatophores m^{-2})	184.5 (8.1)	161	4.4 (0.6)	173	1, −3.74, < 0.001
Leaf litter (leaves m^{-2})	76.1 (11.7)	161	3.8 (1.3)	173	1, 2.91, < 0.001
Infaunal biomass (wet g m^{-2})	63.3 (21.8)	18	87.7 (43.7)	18	1, 0.03, 0.86
Surface < 0.5 cm sediment TC (%)	2.37 (0.44)	6	2.18 (0.16)	6	1, 0.01, 0.92
Surface < 0.5 cm sediment TOC (%)	2.15 (0.61)	6	1.37 (0.29)	6	1, 1.34, 0.28
Surface < 0.5 cm sediment TN (%)	0.15 (0.03)	6	0.11 (0.02)	6	1, 1.43, 0.26
0.5–20 cm sediment TC (%)	2.10 (0.20)	6	2.51 (0.45)	6	1, 0.52, 0.49
0.5–20 cm sediment TOC (%)	1.72 (0.27)	6	1.56 (0.29)	6	1, 0.27, 0.61
0.5–20 cm sediment TN (%)	0.12 (0.01)	6	0.08 (0.01)	6	1, 7.80, 0.02
Soil Chl *a* (μg soil g^{-1})	6.7 (1.1)	6	8.4 (0.9)	6	1, 2.07, 0.18
Mean particle size (μm)	17.3 (5.4)	6	26.8 (3.3)	6	1, 4.27, 0.07
% Clay (<2 μm)	13.7 (1.5)	6	10.4 (0.4)	6	—
% Silt (2–50 μm)	60.5 (3.4)	6	57.8 (1.8)	6	—
% Sand (50–2000 μm)	25.8 (4.6)	6	31.8 (2.2)	6	—
Salinity	58.6 (6.9)	6	56.8 (4.5)	6	1, 0.05, 0.83
pH	6.9 (0.1)	6	6.9 (0.1)	6	1, 0.01, 0.94
Tree density (tree m^{-2})	0.18 (0.03)	3	0.18 (0.04)	3	1, 0.04, 0.99

Tree density (tree m^{-2}) is taken from Jeffrey et al. (2019) (their table 1). The value reported here is an average of three intertidal zones (upper, middle, and lower).

impacted (mean = 8.4, SE = 0.9) and the unimpacted (mean = 6.7, SE = 1.1) forests (Table 1). However, forest floor habitat structure differed between the two forests, with significantly fewer pneumatophores in the impacted (mean = 4.4, SE = 0.6 pneumatophores m^{-2}) than the unimpacted (mean = 184.5, SE = 8.1) forests (Table 1).

TC, TOC, and TN measurements (%) of the two types of sediment (i.e., surface < 0.5 cm and 0.5–20 cm deep) across two forests are provided in Table 1 with the mean values and ANOVA statistics. For the surface sediment samples, TC, TOC, and TN (%) measurements did not significantly differ between the two forests. For the 0.5–20 cm deep sediment, TC and TOC (%) did not differ between the forests, but TN (%) differed, being significantly lower in the impacted forest. $\delta^{13}C$ and $\delta^{15}N$ values of sediment samples are provided in Table 2 and shown in Fig. 3a,b with their C and N elemental compositions (TOC % and TN%) (Fig. 3c,d). While the $\delta^{13}C$ and $\delta^{15}N$ values in the 0.5–20 cm deep sediment samples did not differ significantly between the two forests, the $\delta^{13}C$ and $\delta^{15}N$ values for the surface sediment samples were significantly higher in the impacted forest (Table 2). The surface sediment $\delta^{13}C$ and $\delta^{15}N$ values in the impacted forest were significantly higher than all the other groups including those for the 0.5–20 cm deep samples from both forests (post hoc Turkey test, $p < 0.05$) (Fig. 3a, b). Overall, sediment $\delta^{13}C$ values ranged from −26.3 to −23.8‰ for the unimpacted forest and −25.3 to −21.2‰ for the impacted forest. Sediment $\delta^{15}N$ values ranged from 0.9 to 2.8‰ for the unimpacted forest and 1.3 to 3.7‰ for the impacted forest. Mean particle size (μm) of 0.5–20 cm deep sediment did not differ between the two forests with silt (2–50 μm) being the main component (Table 1). Salinity and pH did not differ between the two forests (Table 1).

$\delta^{13}C$ and $\delta^{15}N$ values of primary producers, including mangrove leaves of *A. marina* and MPB as well as epifaunal consumers from different feeding groups, are reported in Table 2 with the mean, SE values, and ANOVA statistics and shown in Fig. 4. Mangrove leaf $\delta^{13}C$ and $\delta^{15}N$ values did not differ between the two forests. The leaf $\delta^{13}C$ values ranged from −28.4 to −25.6‰ for the unimpacted forest and −26.4 to −25.6 in the impacted forest. The leaf $\delta^{15}N$ values ranged from 2.4 to 4.7‰ for the unimpacted forest and 2.1 to 4.3‰ in the impacted forest. MPB $\delta^{13}C$ values were significantly higher in the impacted forest than the unimpacted forest, but the $\delta^{15}N$ values did not differ significantly. Overall, MPB $\delta^{13}C$ values ranged from −26.5 to −24.7‰ for the unimpacted forest and −22.0 to −18.9‰ in the impacted forest and MPB $\delta^{15}N$ values ranged from 1.5 to 3.5‰ for the unimpacted forest and 2.4 to 3.9‰ in the impacted forest. Overall, consumer $\delta^{13}C$ values ranged from −23.4 to −16.7‰ in the unimpacted forest with lower values (−23.4 to −21.5‰) associated with the leaf-feeders and higher values (−16.7 to −20.9‰) associated with the algae-feeders. Overall, the impacted forest had a relatively higher $\delta^{13}C$ range of −20.1 to −14.4‰. Consumer $\delta^{15}N$ values ranged from 4.6 to 8.7‰ in the unimpacted forest. Compared to this, the impacted forest had a relatively higher range of 3.7–11.2‰. $\delta^{13}C$ and $\delta^{15}N$ measurements of the individual consumer samples were shown in Supporting Information Fig. S2. The individual epifaunal species and the feeding groups showed substantial differences in the $\delta^{13}C$ and $\delta^{15}N$ values between the two forests, except for filter-feeders (bivalve) more reliant on water column resources (Table 2 and Fig. 4). The patterns of isotope difference between the two forests were fairly consistent across all the faunal groups, also mirroring those of the surface sediment and MPB (Fig. 4).

Discussion

Overall, results from our study that compared between the impacted and unimpacted forests suggest that the climate-

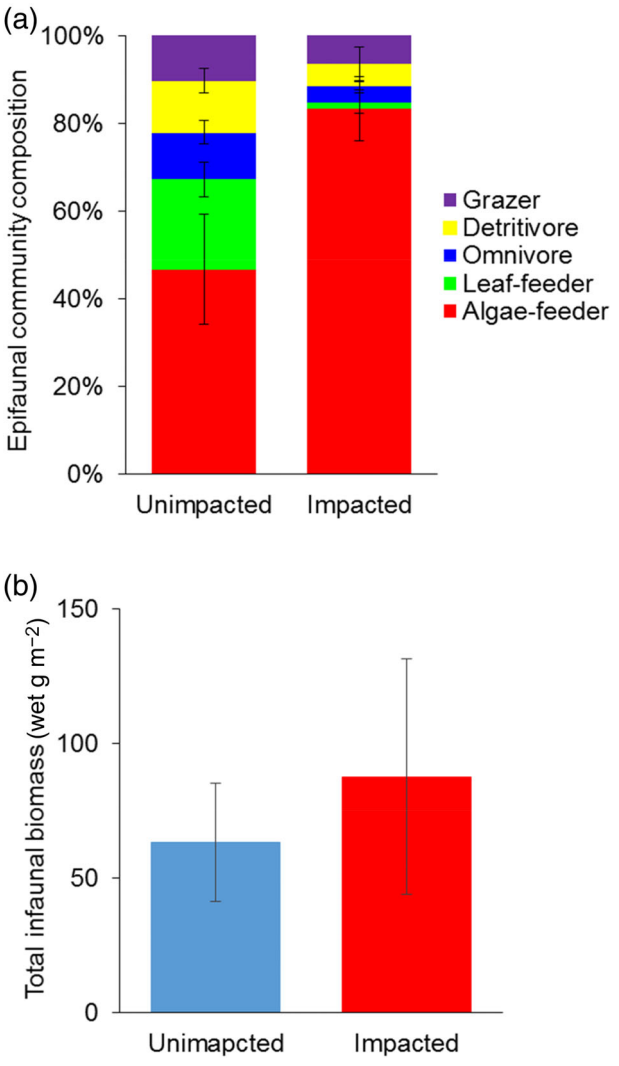

Fig. 2. Observed differences in benthic faunal community between unimpacted and impacted mangrove forests. (**a**) Proportions of dominant epifaunal feeding groups (% mean, SE). (**b**) Total > 0.5 cm size fraction infaunal biomass estimated from coring (mean, SE, $n = 18$ per treatment).

Table 2. C and N isotope values (mean, SE) of primary producers, sediment, and consumers collected from unimpacted and impacted forests.

		Forest							
		Unimpacted			Impacted			ANOVA (df, *F*, *p*)	
Type/taxon		$\delta^{13}C$ (SE), ‰	$\delta^{15}N$ (SE), ‰	*n* (pooled)	$\delta^{13}C$ (SE), ‰	$\delta^{15}N$ (SE), ‰	*n* (pooled)	$\delta^{13}C$	$\delta^{15}N$
Primary producers									
Mangrove	*A. marina*	−28.0 (0.8)	3.8, (0.4)	5 (3)	−25.9 (0.2)	3.3 (0.5)	4 (3)	1, 5.13, 0.06	1, 0.57, 0.48
MPB		−25.3 (0.3)	2.5, (0.3)	6 (1)	−20.7, (0.4)	3.1 (0.2)	6 (1)	1, 85.1, < 0.001	1, 3.00, 0.11
Sediment									
Surface < 0.5 cm		−24.7 (0.4)	2.0 (0.2)	6 (1)	−22.4 (0.4)	2.8 (0.2)	6 (1)	1, 19.1, 0.001	1, 6.57, 0.03
0.5–20 cm		−24.8 (0.3)	1.7 (0.2)	6 (1)	−24.5 (0.2)	1.7 (0.1)	6 (1)	1, 0.63, 0.45	1, 0.01, 0.98
Consumers									
Algae-feeder, crab	*T. signata*	−17.9 (0.7)	6.0, (0.4)	4 (3)	−15.3 (0.6)	7.6 (0.6)	4 (3)	1, 8.42, 0.03	1, 5.23, 0.06
	U. flammula	−20.9	4.6	1 (1)	−14.4 (0.1)	4.3 (0.5)	2 (1)	—	—
Omnivore, crab	*M. frontalis*	−20.0 (0.4)	7.7, (0.9)	2 (2)	−15.9 (0.6)	9.9 (0.7)	4 (3–4)	1, 18.72, 0.01	1, 3.60, 0.13
Detritivore, crab	*P. wardi*	−21.9 (0.5)	6.0, (0.3)	4 (2)	−17.1 (0.8)	8.7 (0.6)	3 (3–5)	1, 26.93, 0.004	1, 18.26, 0.008
Leaf-feeder, crab	*P. moluccensis*	−21.5 (0.4)	7.9, (0.3)	8 (5)	−18.5 (0.2)	9.3 (0.6)	4 (1)	1,22.52, < 0.001	1, 7.25, 0.02
	Episesarma sp.	−22.6	8.0	1 (1)	—	—	—	—	—
Grazer, gastropod	*i. telescopium*	−19.1 (1.3)	6.4, 0.1	3 (4–5)	−17.4 (0.7)	6.9 (0.1)	4 (4–5)	1, 1.52, 0.27	1, 10.59, 0.02
	T. sulcata	−20.3 (1.3)	5.6 (0.3)	4 (2–3)	−16.9 (0.3)	6.5 (0.1)	3 (2)	1, 3.03, 0.14	1, 8.55, 0.03
Filter-feeder, bivalve	Mussel	−20.9 (0.1)	6.8, (0.1)	3 (5–10)	−21.7 (0.1)	6.8 (0.1)	3 (3)	1, 18.48, 0.01	1, 0.07, 0.81
	Oyster *Saccostrea*	−20.0 (0.2)	7.7 (0.2)	4 (10)	−19.9 (0.5)	7.9, (0.3)	4 (10)	1, 0.05, 0.83	1, 0.52, 0.50

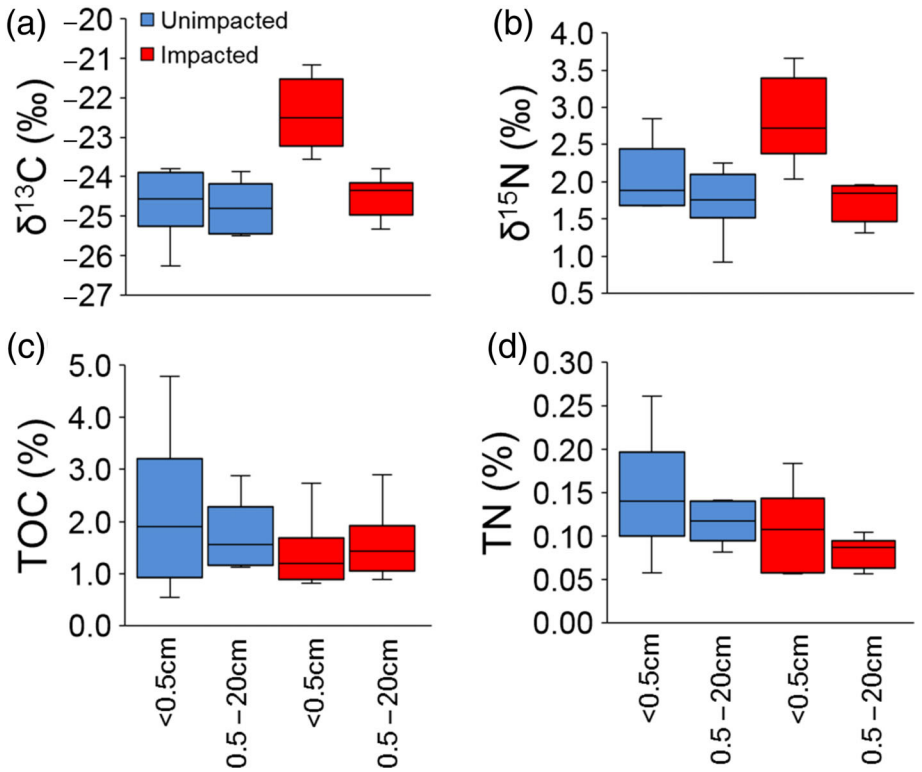

Fig. 3. $\delta^{13}C$, $\delta^{15}N$, TOC, and TN measurements from surface < 0.5 cm sediment and 0.5–20 cm deep sediment in unimpacted and impacted mangrove forests. Box plots present the median, 68% credible interval, and 95% credible interval. *n* = 6 per treatment. See Tables 1, 2 and the text for mean, SE values, and ANOVA statistics.

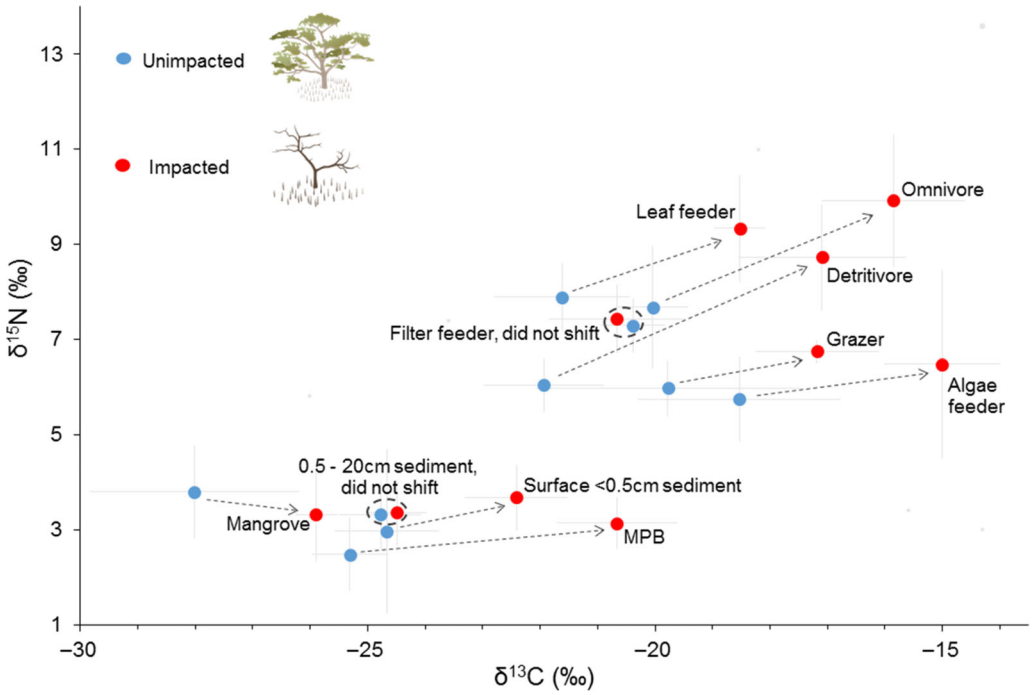

Fig. 4. Patterns of $\delta^{13}C$ and $\delta^{15}N$ values (mean, SD) of dominant epifaunal groups and trophic resources across unimpacted and impacted mangrove forests. Patterns of isotope differences between the two forests shown as arrows were similar between all the faunal groups and correspond to shifts of surface < 0.5 cm sediment and MPB samples. 0.5–20 cm deep sediment samples and filter-feeder samples (mussels and oysters) did not show large shifts. See Table 2 for taxonomic details, mean values, and ANOVA statistics.

driven mangrove mortality has most likely changed the epifaunal species composition, that is, increased population densities of algae-feeders (*Tubuca* and *Uca*) and decreased population densities of leaf-feeders (Sesarmidae). However, it did not have a significant effect on the total infaunal biomass, that is, mostly burrowing crabs and some clams and worms. Consistent with this, the densities of crab burrows did not differ significantly between the impacted and unimpacted forest. Overall, such findings generally suggested that epifauna as well as infauna in the impacted forest (mostly burrowing crabs and gastropods) are fairly abundant, regardless of the mangrove loss. In most cases, epifaunal as well as infaunal communities in mangrove ecosystems are controlled by various factors, including tidal regime, sediment (grain size, pH), trophic resource availability, habitat complexity, and predation (Lee 2008; Nagelkerken et al. 2008). One explanation for our results is that MPB, an important food source in many mangrove ecosystems (Mazumder and Saintilan 2010; Oakes et al. 2010; Larsen et al. 2012) was largely unaffected and consequently, this buffered the food web responses, maintaining overall abundance/biomass of mangrove fauna. In many cases, disturbances such as loss of mangrove trees can change abiotic factors including light intensity and temperature (Granek and Ruttenberg 2008) as well as organic matter inputs and sediment conditions with consequences to benthic assemblages (Sweetman et al. 2010; Bernardino et al. 2018). In some cases, after clearing of mangroves, MPB biomass can increase due to changes in abiotic factors such as light intensity and temperature (Granek and Ruttenberg 2008). In our case, MPB (sediment Chl *a*) did not differed between the two forest, but it may be possible that feeding ground for MPB may have increased in the impacted forest where there are now relatively less canopy cover and pneumatophores with more open cleared spaces (i.e., more space for foraging MPB).

While the effects of the climate-driven mangrove mortality and those of other deforestation events may differ, consistent with our case, similar patterns in faunal communities have been observed in mangrove ecosystems that experienced deforestation. For example, while benthic faunal assemblages changed after clearing of mangroves, the total abundance and biomass did not respond to the mangrove removal effect (Bernardino et al. 2018) or they even increased (Alfaro 2010). Similar to our case, in cleared areas of mangrove forest (due to typhoon), relative abundances of algae-feeding crabs (i.e., fiddler crabs, *Tubuca* and *Uca*) increased whereas leaf feeding crabs (Sesarmidae, typical forest species) were less abundant in the cleared gaps than in the forest (Diele et al. 2013). The increased relative abundance of *Tubuca* and *Uca* spp. in the cleared gaps may relate to improved availability of MPB, its main food source (Kon et al. 2007). In general, these algae-feeder crabs (*Tubuca* and *Uca*) may also prefer more open areas than closed forests due to enhanced visibility that facilitates their visual communication through claw waving for mating and antagonistic interactions (Nobbs 2003; Crane

2015). In contrast, the leaf-feeding crabs (Sesarmidae) are generally associated more with mangrove trees and prefer sheltered areas of mangrove forests (Lee 2008; Diele et al. 2013). The dominance of algae-feeder crabs in our impacted site is shown in Supporting Information Fig. S3.

In many cases, organic matter within in mangrove sediment decreases following mangrove forest loss (Otero et al. 2017; Adame et al. 2018). In our study site, TOC and TN (%) did not differ statistically between the two forests except for 0.5–20 cm deep sediment N, but those mean values were consistently lower in the impacted forest, most likely suggesting some degradation of sediment organic matter and lower mangrove organic matter input with the low leaf litter availability. Overall, stable C and N isotope values from sediment, MPB, and consumers were generally higher in the impacted forest, suggesting that the impacted ecosystem had relatively lower mangrove carbon fixation input that generally shows lower $\delta^{13}C$ values near −27‰ (Bouillon et al. 2008). The higher $\delta^{15}N$ values may be associated with lower N fixation input, generally near 0‰ (Fogel et al. 2008) as well as degradation of organic matter that can enrich available N with ^{15}N (Natelhoffer and Fry 1988; Adame and Fry 2016). The $\delta^{13}C$ and $\delta^{15}N$ values in the 0.5–20 cm deep sediment did not differ significantly between the two forests. Although, bioturbation can transport surface organic matter to the range of > 0.5 cm deep sediment, one explanation for such consistency in 0.5–20 cm sediment $\delta^{13}C$ and $\delta^{15}N$ values between the two forests can be that the C and N cycle of the two forests were fairly consistent previously. Furthermore, distinctively high surface (< 0.5 cm) sediment $\delta^{13}C$ and $\delta^{15}N$ values in the impacted forest compared to those of other sediment including those of 0.5–20 cm deep sediment as well as those of the unimpacted forest suggest that there was a probable effect of recent mangrove mortality on the surface sediment compositions. This may be because the surface sediment layer (surface < 0.5 cm) can be more likely to be oxidized than the 0.5–20 cm deep sediment layers. Similar to our case, increase in sediment $\delta^{13}C$ and $\delta^{15}N$ values were observed in mangrove forests in Malaysia that experienced deforestation (Adame et al. 2018), an effect likely due to decomposition of organic matter (Natelhoffer and Fry 1988; Adame and Fry 2016) as well as lower mangrove C input following mangrove losses.

There were also substantial differences in epifaunal $\delta^{13}C$ and $\delta^{15}N$ values among the two forests, with those from the impacted forest generally having higher $\delta^{13}C$ and $\delta^{15}N$ values, fairly consistent with the differences observed in sediment and MPB $\delta^{13}C$ and $\delta^{15}N$ values. The individual epifaunal groups show substantial isotope differences except for filter-feeders (bivalve) more reliant on water column resources such as phytoplankton that may be unaffected by the mangrove mortality. However, MPB $\delta^{13}C$ values largely differed between the forests. This may reflect differences in respiratory inputs from mangrove organic matter (Maher et al. 2013). Mangrove leaf $\delta^{13}C$ values did not significantly differ between the forests, but showed substantial variability with the impacted forest having relatively higher values. Such C isotope pattern may be due to reduced stomatal conductance that causes lower internal carbon dioxide concentrations and lower carbon isotope fractionation (Farquhar et al. 1989; Lin and Sternberg 1992*a*,*b*).

Overall, there were high variabilities in $\delta^{13}C$ values of trophic resources (mangrove and MPB) that limit interpretation of our epifaunal consumer isotope data set. However, a simpler explanation for the large difference in epifaunal $\delta^{13}C$ values between the two forests is that the impacted food web had a lower mangrove C input but substantial inputs from MPB and phytoplankton. Similar to our case, increases in mangrove fauna $\delta^{13}C$ and $\delta^{15}N$ values were observed in mangrove ecosystems in eastern Brazil that experienced deforestation, suggesting a shift of the nutrient sources with more food web reliance on marine carbon sources after clearing of mangroves (Bernardino et al. 2018). In a more quantitative sense, overall primary producer (mangrove and MPB) $\delta^{13}C$ values ranged from −30.5 to −24.7‰ in the unimpacted forest and −26.4 to −18.9‰ in the impacted forest, whereas epifaunal consumer $\delta^{13}C$ values ranged from −23.4 to −16.7‰ in the unimpacted and −20.1 to −14.4‰ in the impacted forest. So that there were substantial isotope mismatches between the end-member food resources and consumers suggesting that our characterization of end-members were generally weak. However, in many cases, such isotope mismatches can occur and characterization of end-members in mangrove detrital food web interactions is often not easily achieved (Bui and Lee 2014). Due to these reasons, we could not confidently conduct stable isotope mixing analysis using our current isotope data set with typical assumptions that consumer isotope values resemble those of food resources, with a trophic shift of +0 to 1‰ for $\delta^{13}C$ and +2 to 3‰ for $\delta^{15}N$ (Vander Zanden and Rasmussen 2001; McCutchan et al. 2003). Additional tracers such as $\delta^{34}S$ (Fry and Smith 2002) as well as $\delta^{13}C$ of individual amino acids (Larsen et al. 2012) may be needed to resolve such isotope mixing problems. However, in a more qualitative sense, the algae-feeder that displayed the mean $\delta^{13}C$ value of −15.5 ‰ (SE = 0.6) was the dominant feeding group in the impacted forest with the population contributing to 83% (SE = 13) of the community total (Fig. 2a). Therefore, it is likely that the epifaunal community in the impacted forest is largely supported by MPB than mangrove detritus food resources that generally show $\delta^{13}C$ values of near −27‰.

In many cases, more nutritious MPB as well as phytoplankton contribute substantially to mangrove food webs, with consumers generally showing lower importance of low quality mangrove leaf litter in their diet (Mazumder and Saintilan 2010; Oakes et al. 2010; Larsen et al. 2012). Consistent with this, in our study, the mangrove epifauna as well as infauna were fairly abundant in the impacted forest and they did not greatly respond to the reduced mangrove leaf litter food availability following the mangrove mortality. This is probably

because nutritious trophic resources such as MPB and phytoplankton were largely unaffected and such food resources were probably highly available in this fringe and narrow mangrove ecosystem adjacent to an extensive mudflat habitat. It is also possible that this ecosystem in the Gulf region (tropical-arid Australia) with probable low tree density relative to forests of similar latitudes (Sanders et al. 2016; Jeffrey et al. 2019) formerly had a high food web reliance on MPB. This is partially evident from our isotope data that the patterns of isotope difference in most epifaunal groups between the two forests corresponded to those of MPB. Furthermore, it may be possible that such large difference in epifaunal $\delta^{13}C$ values between the two forests was largely driven by the difference in MPB food values, rather than differences in nutritional reliance on food resources (e.g., mangrove vs. MPB). Although the overall isotope difference (i.e., high $\delta^{13}C$ values in the impacted forest) is most likely related to the mangrove mortality effect (e.g., low leaf litter and low mangrove respiratory inputs), our current data could not confirm the changes in the nutritional dependency on food resources (mangrove vs. MPB) and could not eliminate the possibility that there is high importance of MPB in the unimpacted forest. More detailed isotope investigations are required to elucidate whether nutritional dependency of consumers on food resources have changed due to the mangrove mortality. In such isotope investigations, stable carbon isotopic compositions in essential amino acids (e.g., Larsen et al. 2012) may be useful.

It is most likely that this mangrove dieback will impact the provision of key ecosystem services, including food and habitat provision, carbon sequestration, and coastal protection. While this study did not characterize meiofaunal fractions as well as larvae that could be affected by mangrove mortality, given that benthic macrofaunal fractions were fairly abundant after the mangrove mortality, trophic contribution by the mangrove ecosystem to adjoining coastal communities (e.g., fish that forage in mangrove forests during high tide) might be sustained. However, animals that rely more on mangroves for habitat structure (e.g., juvenile nekton) might suffer from physical habitat modifications (e.g., reduced shade and habitat complexity). Changes in fish assemblage and decreases in fish abundance especially smaller schooling species were observed in mangrove ecosystems that experienced mangrove losses, an effect likely due to reduced habitat complexity (Shinnaka et al. 2007; Taylor et al. 2007). Our study also captured substantial changes in C and N dynamics including decomposition and loss of mangrove organic matter. A recent study shows rapid losses of sediment C and N stocks after clearing of mangroves (Adame et al. 2018), suggesting that losses of the C and N stocks (including underground roots) following the mangrove mortality are expected with changes to carbon outwelling to the coastal ocean (Sippo et al. 2019). The loss of pneumatophore root structure suggests reduced sediment stability leading to higher risk of erosion. Considering that there is a large amount of dead mangrove materials slowly decaying in the forest, and the recovery of mangrove vegetation to the original state probably takes decades (Adame et al. 2018), the full impact of the 2015–2016 mangrove dieback needs to be further monitored.

We faced limitations and challenges in this investigation of an extreme biological event and these also apply to single-event studies elsewhere. First, "before and after" comparisons are rarely possible and experimentation is extremely difficult; therefore, investigations largely rely on spatial comparisons (e.g., impacted vs. unimpacted) (Altwegg et al. 2017; Harris et al. 2018). Second, extreme events are rare, so that inference from such single-event studies cannot be simply made under the typical statistical paradigm that depends on replication and control (Altwegg et al. 2017). The inference of our observational data from this experimental study largely relies on an assumption that the unimpacted and impacted forests were comparable and similar before the dieback event. The experimental and control conditions in our study were determined by nature, so we cannot rule out natural variability as an explanation for some of our observational data. However, some of the trends we detected seem to be driven by mangrove mortality, and are consistent with observations from mangrove ecosystems that experienced deforestation (i.e., mangrove removal) and with the general ecology of mangrove faunal communities (Lee 2008). Long-term monitoring would support interpretation of this extreme event and multiannual observational data could help to understand how the mangrove ecosystem may recover from this climate-driven disturbance and underlying biological mechanisms. Experimental studies, for example, Adame et al. (2018) that used a chronosequence of mangrove forests in Matang Mangrove Forest Reserve in Malaysia to test the effect of mangrove clearing and recovery would help to compare and validate observational data from such single-event study. Initiation of monitoring after an extreme biological event is an important contribution to our understanding of biological effects of extreme climatic events.

References

Adame, M., and B. Fry. 2016. Source and stability of soil carbon in mangrove and freshwater wetlands of the Mexican Pacific coast. Wetl. Ecol. Manag. **24**: 129–137. doi:10.1007/s11273-015-9475-6

Adame, M., and others. 2018. Loss and recovery of carbon and nitrogen after mangrove clearing. Ocean Coast. Manag. **161**: 117–126. doi:10.1016/j.ocecoaman.2018.04.019

Alfaro, A. C. 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuar. Coast. Shelf Sci. **66**: 97–110. doi:10.1016/j.ecss.2005.07.024

Alfaro, A. C. 2010. Effects of mangrove removal on benthic communities and sediment characteristics at Mangawhai

Harbour, northern New Zealand. ICES J. Mar. Sci. **67**: 1087–1104. doi:10.1093/icesjms/fsq034

Alongi, D. M. 2015. The impact of climate change on mangrove forests. Curr. Clim. Change Rep. **1**: 30–39. doi:10.1007/s40641-015-0002-x

Altwegg, R., V. Visser, L. D. Bailey, and B. Erni. 2017. Learning from single extreme events. Philos. Trans. R. Soc. B **372**: 20160141. doi:10.1098/rstb.2016.0141

Asbridge, E., R. Lucas, C. Ticehurst, and P. Bunting. 2016. Mangrove response to environmental change in Australia's Gulf of Carpentaria. Ecol. Evol. **6**: 3523–3539. doi:10.1002/ece3.2140

Asbridge, E. F., R. Bartolo, C. M. Finlayson, R. M. Lucas, K. Rogers, and C. D. Woodroffe. 2019. Assessing the distribution and drivers of mangrove dieback in Kakadu National Park, northern Australia. Estuar. Coast. Shelf Sci. **228**: 106353. doi:10.1016/j.ecss.2019.106353

Atwood, T. B., and others. 2017. Global patterns in mangrove soil carbon stocks and losses. Nat. Clim. Chang. **7**: 523. doi:10.1038/nclimate3326

Bailey, L. D., and M. van de Pol. 2016. Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events. J. Anim. Ecol. **85**: 85–96. doi:10.1111/1365-2656.12451

Bernardino, A. F., L. E. D. O. Gomes, H. L. Hadlich, R. Andrades, and L. B. Correa. 2018. Mangrove clearing impacts on macrofaunal assemblages and benthic food webs in a tropical estuary. Mar. Pollut. Bull. **126**: 228–235. doi:10.1016/j.marpolbul.2017.11.008

Bouillon, S., N. Koedam, A. Raman, and F. Dehairs. 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia **130**: 441–448. doi:10.1007/s004420100814

Bouillon, S., R. M. Connolly, and S. Y. Lee. 2008. Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies. J. Sea Res. **59**: 44–58. doi:10.1016/j.seares.2007.05.001

Bui, T. H. H., and S. Y. Lee. 2014. Does 'you are what you eat' apply to mangrove grapsid crabs? PLoS One **9**: e89074. doi:10.1371/journal.pone.0089074

Coumou, D., and S. Rahmstorf. 2012. A decade of weather extremes. Nat. Clim. Chang. **2**: 491–496. doi:10.1038/nclimate1452

Crane, J. 2015. Fiddler crabs of the world: Ocypodidae: Genus Uca. Princeton Univ. Press.

Demopoulos, A. W., B. Fry, and C. R. Smith. 2007. Food web structure in exotic and native mangroves: A Hawaii–Puerto Rico comparison. Oecologia **153**: 675–686. doi:10.1007/s00442-007-0751-x

Diele, K., and others. 2013. Impact of typhoon disturbance on the diversity of key ecosystem engineers in a monoculture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam. Glob. Planet. Change **110**: 236–248. doi:10.1016/j.gloplacha.2012.09.003

Dolbeth, M., P. G. Cardoso, S. M. Ferreira, T. Verdelhos, D. Raffaelli, and M. A. Pardal. 2007. Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. Mar. Pollut. Bull. **54**: 576–585. doi:10.1016/j.marpolbul.2006.12.005

Duke, N. C., and others. 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: A severe ecosystem response, coincidental with an unusually extreme weather event. Mar. Freshw. Res. **68**: 1816–1829. doi:10.1071/MF16322

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Biol. **40**: 503–537. doi:10.1146/annurev.pp.40.060189.002443

Fogel, M., and others. 2008. Unusually negative nitrogen isotopic compositions ($\delta^{15}N$) of mangroves and lichens in an oligotrophic, microbially-influenced ecosystem. Biogeosci. Discuss. **5**: 937–969. doi:10.5194/bgd-5-937-2008

Fry, B. 2006. Stable isotope ecology. Springer-Verlag.

Fry, B., and T. J. Smith. 2002. Stable isotope studies of red mangroves and filter feeders from the Shark River Estuary, Florida. Bull. Mar. Sci. **70**: 871–890. Available from https://www.ingentaconnect.com/content/umrsmas/bullmar/2002/00000070/00000003/art00006

Granek, E., and B. I. Ruttenberg. 2008. Changes in biotic and abiotic processes following mangrove clearing. Estuar. Coast. Shelf Sci. **80**: 555–562. doi:10.1016/j.ecss.2008.09.012

Hamilton, S. K., S. J. Sippel, and S. E. Bunn. 2005. Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. Limnol. Oceanogr.: Methods **3**: 149–157. doi:10.4319/lom.2005.3.149

Harada, Y., and S. Y. Lee. 2016. Foraging behavior of the mangrove sesarmid crab *Neosarmatium trispinosum* enhances food intake and nutrient retention in a low-quality food environment. Estuar. Coast. Shelf Sci. **174**: 41–48. doi:10.1016/j.ecss.2016.03.017

Harris, R. M. B., and others. 2018. Biological responses to the press and pulse of climate trends and extreme events. Nat. Clim. Chang. **8**: 579–587. doi:10.1038/s41558-018-0187-9

Hughes, T. P., and others. 2017. Global warming and recurrent mass bleaching of corals. Nature **543**: 373–377. doi:10.1038/nature21707

Jeffrey, L. C., and others. 2019. Are methane emissions from mangrove stems a cryptic carbon loss pathway? Insights from a catastrophic forest mortality. New Phytol. **224**: 146–154. doi:10.1111/nph.15995

Jones, D., and D. Clayton. 1983. The systematics and ecology of crabs belonging to the genera cleistostoma de Haan and Paracleistostoma de Man on Kuwait mudflats. Crustaceana **45**: 183–199. doi:10.1163/156854083X00613

Kon, K., H. Kurokura, and K. Hayashizaki. 2007. Role of microhabitats in food webs of benthic communities in a

mangrove forest. Mar. Ecol. Prog. Ser. **340**: 55–62. doi:10.3354/meps340055

Kon, K., H. Kurokura, and P. Tongnunui. 2010. Effects of the physical structure of mangrove vegetation on a benthic faunal community. J. Exp. Mar. Biol. Ecol. **383**: 171–180. doi:10.1016/j.jembe.2009.11.015

Kristensen, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. **59**: 30–43. doi:10.1016/j.seares.2007.05.004

Kristensen, E., S. Y. Lee, P. Mangion, C. O. Quintana, and T. Valdemarsen. 2017. Trophic discrimination of stable isotopes and potential food source partitioning by leaf-eating crabs in mangrove environments. Limnol. Oceanogr. **62**: 2097–2112. doi:10.1002/lno.10553

Larsen, T., M. J. Wooller, M. L. Fogel, and D. M. O'Brien. 2012. Can amino acid carbon isotope ratios distinguish primary producers in a mangrove ecosystem? Rapid Commun. Mass Spectrom. **26**: 1541–1548. doi:10.1002/rcm.6259

Lee, S. Y. 2008. Mangrove macrobenthos: Assemblages, services, and linkages. J. Sea Res. **59**: 16–29. doi:10.1016/j.seares.2007.05.002

Lee, S. Y., and others. 2014. Ecological role and services of tropical mangrove ecosystems: A reassessment. Glob. Ecol. Biogeogr. **23**: 726–743. doi:10.1111/geb.12155

Lin, G., and L. Sternberg. 1992*a*. Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA. Aquat. Bot. **42**: 303–313. doi:10.1016/0304-3770(92)90050-S

Lin, G., and L. D. S. Sternberg. 1992*b*. Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Funct. Plant Biol. **19**: 509–517. doi:10.1071/PP9920509

Lovelock, C. E., I. C. Feller, R. Reef, S. Hickey, and M. C. Ball. 2017. Mangrove dieback during fluctuating sea levels. Sci. Rep. **7**: 1680. doi:10.1038/s41598-017-01927-6

MacKay, F., D. Cyrus, and K.-L. Russell. 2010. Macrobenthic invertebrate responses to prolonged drought in South Africa's largest estuarine lake complex. Estuar. Coast. Shelf Sci. **86**: 553–567. doi:10.1016/j.ecss.2009.11.011

Maher, D. T., and others. 2013. Novel use of cavity ring-down spectroscopy to investigate aquatic carbon cycling from microbial to ecosystem scales. Environ. Sci. Technol. **47**: 12938–12945. doi:10.1021/es4027776

Mazumder, D., and N. Saintilan. 2010. Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands **30**: 375–380. doi:10.1007/s13157-010-0021-2

McCutchan, J. H., W. M. Lewis Jr., C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos **102**: 378–390. doi:10.1034/j.1600-0706.2003.12098.x

Nagelkerken, I., and others. 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. **89**: 155–185. doi:10.1016/j.aquabot.2007.12.007

Natelhoffer, K. J., and B. Fry. 1988. Controls on natural Nitrogen-15 and Carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. **52**: 1633–1640. doi:10.2136/sssaj1988.03615995005200060024x

Nobbs, M. 2003. Effects of vegetation differ among three species of fiddler crabs (*Uca* spp.). J. Exp. Mar. Biol. Ecol. **284**: 41–50. doi:10.1016/S0022-0981(02)00488-4

Nobbs, M., and K. A. McGuinness. 1999. Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: *Uca*) in mangrove habitats. Aust. J. Ecol. **24**: 43–49. doi:10.1046/j.1442-9993.1999.00945.x

Oakes, J. M., R. M. Connolly, and A. T. Revill. 2010. Isotope enrichment in mangrove forests separates microphytobenthos and detritus as carbon sources for animals. Limnol. Oceanogr. **55**: 393–402. doi:10.4319/lo.2010.55.1.0393

Otero, X. L., and others. 2017. High fragility of the soil organic C pools in mangrove forests. Mar. Pollut. Bull. **119**: 460–464. doi:10.1016/j.marpolbul.2017.03.074

Pape, E., A. Muthumbi, C. P. Kamanu, and A. Vanreusel. 2008. Size-dependent distribution and feeding habits of *Terebralia palustris* in mangrove habitats of Gazi Bay, Kenya. Estuar. Coast. Shelf Sci. **76**: 797–808. doi:10.1016/j.ecss.2007.08.007

Parmesan, C., and others. 2013. Beyond climate change attribution in conservation and ecological research. Ecol. Lett. **16**: 58–71. doi:10.1111/ele.12098

Parsons, T. R. 2013. A manual of chemical & biological methods for seawater analysis. Elsevier.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320. doi:10.1146/annurev.es.18.110187.001453

Pillay, D., and R. Perissinotto. 2008. The benthic macrofauna of the St. Lucia Estuary during the 2005 drought year. Estuar. Coast. Shelf Sci. **77**: 35–46. doi:10.1016/j.ecss.2007.09.004

Pillay, D., and R. Perissinotto. 2009. Community structure of epibenthic meiofauna in the St. Lucia Estuarine Lake (South Africa) during a drought phase. Estuar. Coast. Shelf Sci. **81**: 94–104. doi:10.1016/j.ecss.2008.10.014

Pollack, J. B., T. A. Palmer, and P. A. Montagna. 2011. Long-term trends in the response of benthic macrofauna to climate variability in the Lavaca-Colorado Estuary, Texas. Mar. Ecol. Prog. Ser. **436**: 67–80. doi:10.3354/meps09267

Poon, D. Y. N., B. K. K. Chan, and G. A. Williams. 2010. Spatial and temporal variation in diets of the crabs *Metopograpsus frontalis* (Grapsidae) and *Perisesarma bidens* (Sesarmidae): Implications for mangrove food webs. Hydrobiologia **638**: 29–40. doi:10.1007/s10750-009-0005-5

Sanders, C. J., and others. 2016. Are global mangrove carbon stocks driven by rainfall? Eur. J. Vasc. Endovasc. Surg. **121**: 2600–2609. doi:10.1002/2016JG003510

Sheaves, M., and B. Molony. 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. **199**: 97–109. doi:10.3354/meps199097

Shinnaka, T., M. Sano, K. Ikejima, P. Tongnunui, M. Horinouchi, and H. Kurokura. 2007. Effects of mangrove deforestation on fish assemblage at Pak Phanang Bay, southern Thailand. Fish. Sci. **73**: 862–870. doi:10.1111/j.1444-2906.2007.01407.x

Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science **310**: 1803–1806. doi:10.1126/science.1118229

Sippo, J. Z., C. E. Lovelock, I. R. Santos, C. J. Sanders, and D. T. Maher. 2018. Mangrove mortality in a changing climate: An overview. Estuar. Coast. Shelf Sci. **215**: 241–249. doi:10.1016/j.ecss.2018.10.011

Sippo, J. Z., and others. 2019. Carbon outwelling across the shelf following a massive mangrove dieback in Australia: Insights from radium isotopes. Geochim. Cosmochim. Acta **253**: 142–158. doi:10.1016/j.gca.2019.03.003

Skov, M., and R. Hartnoll. 2001. Comparative suitability of binocular observation, burrow counting and excavation for the quantification of the mangrove fiddler crab *Uca annulipes* (H. Milne Edwards). Hydrobiologia **449**: 201–212. doi:10.1023/A:1017598616178

Skov, M., M. Vannini, J. Shunula, R. Hartnoll, and S. Cannicci. 2002. Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. Mar. Biol. **141**: 725–732. doi:10.1007/s00227-002-0867-9

Stott, P. 2016. How climate change affects extreme weather events. Science **352**: 1517–1518. doi:10.1126/science.aaf7271

Stuart-Smith, R. D., C. J. Brown, D. M. Ceccarelli, and G. J. Edgar. 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature **560**: 92–96. doi:10.1038/s41586-018-0359-9

Sweetman, A., and others. 2010. Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments. Biogeosciences **7**: 2129–2145. doi:10.5194/bg-7-2129-2010

Taylor, D. S., E. A. Reyier, W. P. Davis, and C. C. McIvor. 2007. Mangrove removal in the Belize cays: Effects on mangrove-associated fish assemblages in the intertidal and subtidal. Bull. Mar. Sci. **80**: 879–890. Available from https://www.ingentaconnect.com/content/umrsmas/bullmar/2007/00000080/00000003/art00026

Thomson, J. A., and others. 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: An example from an iconic seagrass ecosystem. Glob. Chang. Biol. **21**: 1463–1474. doi:10.1111/gcb.12694

Tue, N. T., H. Hamaoka, A. Sogabe, T. D. Quy, M. T. Nhuan, and K. Omori. 2012. Food sources of macro-invertebrates in an important mangrove ecosystem of Vietnam determined by dual stable isotope signatures. J. Sea Res. **72**: 14–21. doi:10.1016/j.seares.2012.05.006

Ummenhofer, C. C., and G. A. Meehl. 2017. Extreme weather and climate events with ecological relevance: A review. Philos. Trans. R. Soc. B **372**: 20160135. doi:10.1098/rstb.2016.0135

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. **46**: 2061–2066. doi:10.4319/lo.2001.46.8.2061

Verdelhos, T., P. Cardoso, M. Dolbeth, and M. Pardal. 2014. Recovery trends of *Scrobicularia plana* populations after restoration measures, affected by extreme climate events. Mar. Environ. Res. **98**: 39–48. doi:10.1016/j.marenvres.2014.03.004

Veríssimo, H., M. Lane, J. Patrício, S. Gamito, and J. C. Marques. 2013. Trends in water quality and subtidal benthic communities in a temperate estuary: Is the response to restoration efforts hidden by climate variability and the Estuarine Quality Paradox? Ecol. Indic. **24**: 56–67. doi:10.1016/j.ecolind.2012.05.028

Wernberg, T., and others. 2016. Climate-driven regime shift of a temperate marine ecosystem. Science **353**: 169–172. doi:10.1126/science.aad8745

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Author Contribution Statement

The study was conceptualized by all authors. Writing was led by Y.H. and contributed to by all. Field surveys were executed by D.T.M., J.Z.S., and Y.H. Data compilation and analysis was coordinated by Y.H. and contributed to by all.

Conflict of Interest

None declared.

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