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# Nutrient pollution enhances productivity and framework dissolution in algae- but not in coral-dominated reef communities

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ABSTRACT

Ecosystem services provided by coral reefs may be susceptible to the combined effects of benthic species shifts and anthropogenic nutrient pollution, but related field studies are scarce. We thus investigated in situ how dissolved inorganic nutrient enrichment, maintained for two months, affected community-wide biogeochemical functions of intact coral- and degraded algae-dominated reef patches in the central Red Sea. Results from benthic chamber incubations revealed 87% increased gross productivity and a shift from net calcification to dissolution in algae-dominated communities after nutrient enrichment, but the same processes were unaffected by nutrients in neighboring coral communities. Both community types changed from net dissolved organic nitrogen sinks to sources, but the increase in net release was 56% higher in algae-dominated communities. Nutrient pollution may, thus, amplify the effects of community shifts on key ecosystem services of coral reefs, possibly leading to a loss of structurally complex habitats with carbonate dissolution and altered nutrient recycling.

## 1. Introduction

Coral reefs are among the most productive and biologically diverse ecosystems on Earth, despite generally growing in oligotrophic tropical waters (Hatcher, 1990). Under these conditions, the photo-symbiotic association of corals with dinoflagellate algae (LaJeunesse et al., 2018; Muscatine and Porter, 1977) and the efficient retention and recycling of carbon (C) and nitrogen (N) are critical to maintaining ecosystem functioning and support growth (De Goeij et al., 2013; Odum and Odum, 1955; Wild et al., 2004). As reef organisms are adapted to low exogenous nutrient inputs (Yellowlees et al., 2008), nutrient pollution (particularly excessive N inputs) has been recognized as one of the main local stressors leading to coral reef degradation (D'Angelo and Wiedenmann, 2014; Naumann et al., 2015; Wiedenmann et al., 2013). At the same time, global stressors have led to extensive coral mortality events in recent decades (Hughes et al., 2018a; Newman et al., 2003). The resulting changes in the benthic community composition are often expressed by shifts from formerly coral-dominated to turf and fleshy macroalgae-dominated reefs (Anton et al., 2020; Hughes et al., 2018b; McCook et al., 2001). As a consequence, many extant coral reefs are characterized by a mosaic of co-occurring species (Lin and Denis, 2019; Ninio and Meekan, 2002; Tkachenko et al., 2007), a state with a lower coral cover that may evolve into a stable state supported by coral degradation events worldwide (Bellwood et al., 2019; Birkeland et al., 2017).

Intrinsically, important biogeochemical processes, such as the cycling of C and N or the accumulation of calcium carbonate ($CaCO_3$) within the reef ecosystem, are linked to the community composition of

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the benthos (Wild et al., 2011). For example, coral-dominated communities ensure constant reef accretion through calcification that changes the physical, chemical, and biological environment and provides habitats for associated reef organisms (Graham, 2014). In these communities, low net community production despite high gross productivity warrants that biomass accumulates slowly (Gattuso et al., 1999, 1998), while the release of large amounts of C-rich dissolved and particulate organic materials by corals functions as energy carriers and particle traps that enhance the retention of essential elements within the wider ecosystem (Naumann et al., 2012; Rusch et al., 2006; Wild et al., 2004). In addition, benthic N inputs by microbial dinitrogen ($N_2$) fixation (diazotrophy) of the coral holobiont during nutrient-depleted conditions suggest a strong biogeochemical coupling between diazotrophy and the reef C cycle (Cardini et al., 2016). Algae-dominated communities, on the other hand, display significantly higher net primary productivity (Cardini et al., 2016; Rix et al., 2015) with a greater potential for autotrophic biomass production (Fong and Paul, 2011; Kelly et al., 2017) and a more direct transfer of organic C to higher trophic levels through grazing (Fong and Paul, 2011). Organic material exuded by algae tends to be more labile (Nelson et al., 2013) and can increase the microbial abundance on algae-dominated reefs (Haas et al., 2016).

The differences in biogeochemical processes mediated by these reef organisms and their associated communities may be compounded by distinct responses to environmental change, which, in turn, may promote alterations in the species composition of the impacted reef (e.g., Anton et al., 2020). At a local scale, nutrient pollution is a prevailing anthropogenic stressor (Fabricius, 2005) that can affect the functioning of (co-occurring) reef communities differently (Karcher et al., 2020). Chronic nutrient enrichment can have both positive and negative effects on corals (Fox et al., 2021) depending on the environmental context (Fabricius, 2005; Shantz and Burkepile, 2014). Often, however, nutrient pollution has adverse effects on coral growth (Ferrier-Pages et al., 2000; Hall et al., 2018), calcification (Silbiger et al., 2018), reproductive success (Loya et al., 2004), and increases the susceptibility of corals to bleaching (Burkepile et al., 2020; DeCarlo et al., 2020; Wiedenmann et al., 2013). Moderate N enrichment can also stimulate both $N_2$ fixation and denitrification (El-Khaled et al., 2020), highlighting the sensitivity of important N pathways of corals to altered nutrient conditions. In contrast, other benthic groups present in coral reefs, such as turf and macroalgae benefit from an increased nutrient availability in many cases (reviewed in McCook, 1999), potentially gaining a competitive advantage over corals (Karcher et al., 2020).

Despite the aforementioned studies reporting species-specific effects of excess nutrients on the organism's physiology, there is a limited understanding of how biogeochemical processes mediated by entire reef communities are impacted by nutrient pollution in the natural environment. On the one hand, the cycling of C and N within the reef is not only facilitated by dominant functional groups of the visible reef surface (e.g., corals or algae). Instead, community-wide biogeochemical processes result from the interplay of complex species communities (Roth et al., 2019), including the surrounding benthic and pelagic microbiome (Tout et al., 2014; Walsh et al., 2017) and organisms living in cryptic habitats. For example, cracks and crevices within the reef matrix can encompass about 60%–75% of the total surface area of a reef (Richter et al., 2001; Richter and Wunsch, 1999), with the organisms inhabiting these spaces (e.g., sponges, bryozoans, and tunicates) metabolizing and recycling considerable amounts of C and N (De Goeij et al., 2013; Rix et al., 2018). On the other hand, while experimental exposure to elevated nutrient concentrations in laboratory studies often induce negative responses (see above paragraph and citations therein), several in situ observations failed to reveal direct adverse effects of increased nutrient levels on the physiology of reef organisms or found them only at unnaturally high concentrations (reviewed in D'Angelo and Wiedenmann, 2014; Szmant, 2002). Thus, the results of experimental exposure to elevated nutrient concentrations, particularly from laboratory studies, need to be interpreted carefully. Consequently, measurements under in situ conditions with intact reef communities and under realistic nutrient exposure concentrations are required to better understand how C and N cycles mediated by tropical reef communities will respond to elevated nutrient availability in the natural environment (Fox et al., 2021; Silbiger et al., 2018).

To overcome these constraints and to account for ongoing coral-algal phase shifts worldwide, we used an eight-week in situ nutrient addition experiment and benthic incubation chambers to directly compare community-wide biogeochemical processes of naturally co-occurring coral- and algae-dominated communities in response to nutrient enrichment in a reef of the central Red Sea. Nutrient enrichment (3-fold on average compared to environmental background values) reflected nutrient inputs in the Red Sea from sources such as aquaculture (Loya et al., 2004) or urban wastewater (Peña-García et al., 2014). Using benthic incubation chambers, we quantified in situ community-wide biogeochemical processes such as net and gross productivity, respiration, calcification, and fluxes of dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN), and dissolved organic nitrogen (DON), all of which are central to the balanced C and N dynamics enabling coral reefs to thrive in the oligotrophic waters of the tropics. Thereby, we a) directly compared the magnitudes and directions of key biogeochemical processes of co-occurring coral- and algae-dominated reef communities under ambient nutrient conditions, and b) assessed the responses of the above processes to environmental change induced by enhanced nutrient availability.

## 2. Material and methods

### 2.1. Experimental design

The experiments were conducted at Abu Shosha reef located in the central Red Sea on the west coast of Saudi Arabia (22°18′16.3″N; 39°02′57.7″E) from late January until late March 2018. Both coral- and algae-dominated communities are present at Abu Shosha reef. Thus, this site allows quantifying biogeochemical processes mediated by both communities under identical environmental conditions. Eight distinct natural communities were chosen for in situ investigations at 5 m water depth within an area of 50 × 50 m. The same communities were selected previously for a seasonal study (January 2017 until January 2018) to assess C and N fluxes (Roth et al., 2020). The communities were randomly selected among communities that had the following characteristics: 1) The four coral-dominated communities had at least 40% coral but <10% algae cover; 2) the four algae-dominated communities had >40% algae but <10% coral cover; 3) all communities had to fit into the incubation chambers (max. diameter 50 cm, max. height 39 cm). The community composition at the level of major functional groups was assessed using underwater photogrammetric surveys of each community (n = 8) before and after the experiments. The first timepoint of the community assessment corresponded to the last timepoint of experiments from Roth et al. (2020), where two-factor permutational multivariate analysis of variance (PERMANOVA) discriminated the communities according to coral and algal dominance. There was no significant change in the short time from before to after the nutrient enrichment (details and statistics in Table S1), such as the overall means are presented in Fig. 1.

For the nutrient enrichment experiments, each community was surrounded by four pins with mesh bags containing 70 g of slow-release fertilizer granulate (Osmocote® Plus 15-9-12) (Fig. S1). Osmocote® Plus fertilizer supplies various macronutrients continuously (15% total N, 9% available phosphorus (P) in the form of phosphate ($PO_4^{3-}$), 12% soluble potash; see detailed list of released micronutrients in Table S2), and has been used successfully in many previous nutrient enrichment studies on coral reefs (Falkenberg et al., 2013; Kelly et al., 2017) and other ecosystems (Wheeler, 2003). Whether the polymer coating of the fertilizer was a source of dissolved organic compounds (Lawrencia et al., 2021) to the water column and possibly to the communities remains

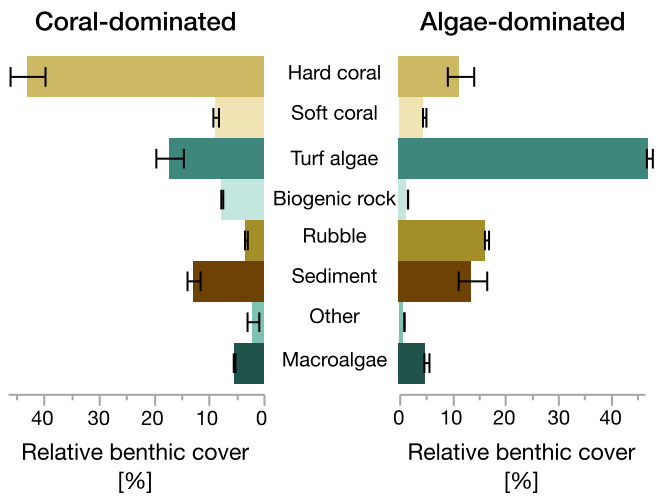


**Fig. 1.** Relative benthic cover of functional groups in the studied coral- and algae-dominated reef communities. The community composition at the level of major functional groups was assessed for each community (n = 8) before and after the experiments. There were no significant changes in the short time (eight weeks) from before to after the nutrient enrichment (details and statistics in Table S1), such as the bars represent the overall mean ± standard error across sampling periods.

unknown and should be considered in future studies. The fertilizer was renewed every two weeks to assure a continuous nutrient supply. Every two weeks, water samples for nutrients were taken directly at the fertilizer pins, 25 cm towards the center of the four pins (roughly corresponding to the center of the communities), and 25 cm and 200 cm away from the investigated communities to test whether the nutrient addition was effective locally. The nutrient enrichment phase lasted for eight weeks. Response parameters were measured on all communities using in situ chamber incubations before the fertilizer pins were deployed (hereafter "before nutrient enrichment"), and after eight weeks of manipulated nutrient conditions (hereafter "after nutrient enrichment"); thus, the experiment followed a quasi-experimental one-group pre-/post-test research design (Marsden and Torgerson, 2012). Limitations of the experimental design: In situ incubation at the scale of whole coral reef communities are both novel and difficult to implement. Due to logistical constraints, no more than the eight incubation chambers (i.e., four per treatment) could be handled during the experiments. Thus, the present study lacks a conventional control group of "unenriched" communities and the results have to be interpreted accordingly. While the lack of an experimental control group is often unavoidable in complex field studies, productivity and the release of DOC may have been enhanced by the slightly increasing temperature during the study period (Roth et al., 2020). However, the large-fold changes and statistical differences emerging after the nutrient enrichment that were greater than the variance associated with the before-enrichment period support that the differences were due to nutrients and not time. In addition, to avoid misinterpretation of the data, we compared the change in metabolic rates from the community incubations (present study) to incubations of individual functional groups of the same communities (data published in El-Khaled et al., 2020). In El-Khaled et al. (2020), specimens from the surrounding, non-fertilized reef communities were taken as a control group. The results show an increased activity of metabolic processes in response to nutrient addition and relative to the control group, thus confirming that the control group did not respond to changes in water temperature during the study period (El-Khaled et al., 2020). Additional isotopic work on the organisms of the same experiment by Karcher et al. (2020) showed that all specimens took up the fertilizer and incorporated it into their tissue. The alignment of the observed patterns in both studies improves the validity of associating any changes described here with the experimental intervention rather than seasonal variability.

### 2.2. Environmental monitoring and conditions during the experiments

Key environmental variables were monitored at the sampling site. Water temperature was measured continuously (logging interval = 30 min) for the whole study period with Onset HOBO data loggers (accuracy: ±0.2 °C) deployed at the seafloor. Light availability was measured continuously (logging interval = 1 min) on three full days per month with an Onset HOBO Pendant data logger. Light readings were converted from lux to photosynthetically active radiation (μmol quanta $m^{-2}$ $s^{-1}$; 400 to 700 nm wavelengths) by intercalibration and conversion as outlined in Roth et al. (2018), and values are presented as daytime means. Seawater samples for the determination of dissolved nitrate ($NO_3^-$), nitrite ($NO_2^-$), ammonium ($NH_4^+$), phosphate ($PO_4^{3-}$), and monomeric silicate ($Si(OH)_4$) were taken in triplicates every second week from at least 10 m away from the fertilizer pins as an environmental background control. Details for sampling and analysis can be found in Appendix S1 of the supporting information. The sum of $NO_3^-$, $NO_2^-$, and $NH_4^+$ is termed 'dissolved inorganic nitrogen' (DIN) henceforth.

Water temperature increased from 24.8 to 28.1 °C during the in situ manipulation period of 8 weeks. Environmental background DIN concentrations remained stable throughout the experiments at 0.40 ± 0.03 μmol N $L^{-1}$. When nutrient manipulation was initiated, DIN concentrations increased on average 3-fold compared to background values to 1.31 ± 0.14 μmol N $L^{-1}$ (measured directly at the communities; Table S3). $PO_4^{3-}$ around the communities remained stable, despite being present in the fertilizer (Table S3).

### 2.3. In situ incubations and quantification of community functions

In situ incubations with benthic chambers (Fig. S1) were performed to measure fluxes of dissolved oxygen ($O_2$), total alkalinity (TA), dissolved organic carbon (DOC), total dissolved nitrogen (TDN), dissolved organic nitrogen (DON), and dissolved inorganic nitrogen (DIN). Incubations were performed according to an adapted protocol described in Roth et al. (2019), and according to the same procedures outlined in Roth et al. (2020). Briefly, polymethyl methacrylate cylinders with removable gas-tight lids of the same material were used for the experiments. All chambers (n = 8) were equipped with individual water circulation pumps with adjustable flow control, autonomously recording dissolved $O_2$ sensors (HOBO U26), and two sampling ports for discrete water samples. Incubations were carried out on three consecutive days in January (before nutrient enrichment), and March (after nutrient enrichment) 2018, respectively. On day one, divers deployed four chambers on coral-dominated, and four chambers on algae-dominated reef communities. The chambers were left in place without lids until the next morning, reducing the stress response of organisms and allowing for sufficient water exchange. On day two, incubations started at around 9:00 a.m. by tightly securing the lids and closing all sampling ports during natural daylight conditions. The exact incubation start- and end-time were recorded for each chamber. Incubations lasted approximately 2 h. The chambers were then left in place without lids for a second set of incubation on the following day. On day three, benthic communities were incubated at "simulated" darkness (i.e., chambers were covered with thick black PVC covers), starting at around 9:00 a.m. for approximately 2 h. Between deployments, all materials were rinsed with freshwater, washed with 4% hydrochloric acid (HCl), and subsequently rinsed with deionized water for reliable water chemistry measurements that included sensitive DOC samples.

Discrete water samples for TA, DOC, TDN, and DIN were withdrawn from the sampling ports with acid-washed syringes at the beginning and the end of each incubation (Appendix S1). Changes in seawater chemistry between start and end of incubations were used to calculate rates of net community production (NCP), community respiration (CR), gross primary production (GPP), net community calcification (NCC), and fluxes of DOC, TDN, DON, and DIN. All rates/fluxes were normalized to

the water volume (in L) in the respective chamber, the planar reef area (in $m^2$) of the enclosed benthic community, and incubation duration (in h). The exact water volume in each chamber was calculated by subtracting the measured community volume using photogrammetric tools, as well as the volume occupied by the sensors and the pump from the theoretical volume enclosed by the chamber above the sediment line. Details on the methodology are presented in Roth et al. (2019). NCP and CR were calculated based on $O_2$ fluxes from continuous measurements with dissolved $O_2$ sensors. Values from light and dark incubations were used to calculate NCP and CR, respectively. GPP was calculated as GPP $=$ NCP $+ |$CR$|$. Rates were expressed as mmol $O_2$ $m^{-2}$ $h^{-1}$. NCC (in mmol $CaCO_3$ $m^{-2}$ $h^{-1}$) was calculated by concentration differences in TA, which are primarily caused by calcification and dissolution of $CaCO_3$, whereby TA is reduced (increased) by two molar equivalents for every mole of $CaCO_3$ produced (dissolved) (Zeebe and Wolf-Gladrow, 2001). Nutrient fluxes (i.e., $NO_3^-$, $NH_4^+$, $PO_4^3$, and $Si(OH)_4$) that cause a change in TA unrelated to calcification and dissolution were accounted for in calculations according to Zeebe and Wolf-Gladrow (2001) and Wolf-Gladrow et al. (2007). DOC (in µmol C $m^{-2}$ $h^{-1}$), TDN (in µmol N $m^{-2}$ $h^{-1}$), DON (in µmol N $m^{-2}$ $h^{-1}$), and DIN (in µmol N $m^{-2}$ $h^{-1}$) fluxes were calculated from concentration differences between start and endpoints. In addition to the community-wide functions measured with benthic incubation chambers in the present study, individual functional groups and organisms of the communities were also used for additional measurements presented in Karcher et al. (2020) and El-Khaled et al. (2020). Specifically, organic carbon ($C_{org}$) and N contents using elemental and stable isotope analysis, along with organism-specific productivity, $N_2$ fixation and denitrification measurements were performed. While detailed findings can be found in the above studies, we will refer to some of the results in relevant sections of the discussion to complement our findings.

### 2.4. Data treatment and statistical analysis

Hourly rates from light and dark incubations (presented in Table S4) were used to calculate daily net fluxes based on the light/dark regime of the exact day of incubations. To minimize the error associated with extrapolating hourly rates, we chose a time window for daylight incubations (from around 9 a.m. to 11 a.m.) that is closest to average daytime irradiation and excludes the "ramping up" phase in the early morning hours and extreme values that can occur during midday. The ratio of GPP to CR (i.e., GPP:CR) was calculated based on daily net fluxes. The C:N molar ratio of dissolved organic matter (DOM; comprised of DOC and DON) was calculated based on the elemental composition of organic matter released by the respective communities. All values are reported as means ± standard error. The dataset was analyzed using the R 'lme4' package (Bates et al., 2015). We fitted linear mixed models (estimated using REML) with repeated measures to predict the response variables (i.e., the various C, $CaCO_3$, and N fluxes) with community type (i.e., coral- and algae-dominated community) and treatment (i.e., before and after nutrient enrichment). The model included the community ID as random effect intercept to account for the repeated measures structure. We performed all pairwise comparisons for all combinations of 'community type' and 'treatment' with the R package 'emmeans' using a Tukey adjustment. Significant relationships between community types (coral- vs. algae-dominated) and treatment (before vs. after nutrient enrichment) are represented with letters in Figs. 2–4, and statistical details can be found in Table S5. Levels not connected by the same letter are significantly different.

## 3. Results

### 3.1. Community-wide biogeochemical processes at the onset of the experiment

Before the nutrient enrichment experiment started, coral- and algae-dominated reef communities exhibited rates of GPP (518 ± 19 and 531 ± 25 mmol $O_2$ $m^{-2}$ $d^{-1}$, respectively; Fig. 2A), CR (−223 ± 28 and −258 ± 14 mmol $O_2$ $m^{-2}$ $d^{-1}$, respectively), and NCP (295 ± 9 and 273 ± 12 mmol $O_2$ $m^{-2}$ $d^{-1}$, respectively) that were not significantly different (Fig. S2; Table S5). As a result, both community types showed similar GPP:CR ratios (2.4 ± 0.3 in coral- and 2.1 ± 0.2 in algae-dominated communities, respectively; Fig. 4A). NCC was one order of magnitude higher in coral- (150.7 ± 13.2 mmol $CaCO_3$ $m^{-2}$ $d^{-1}$), compared to

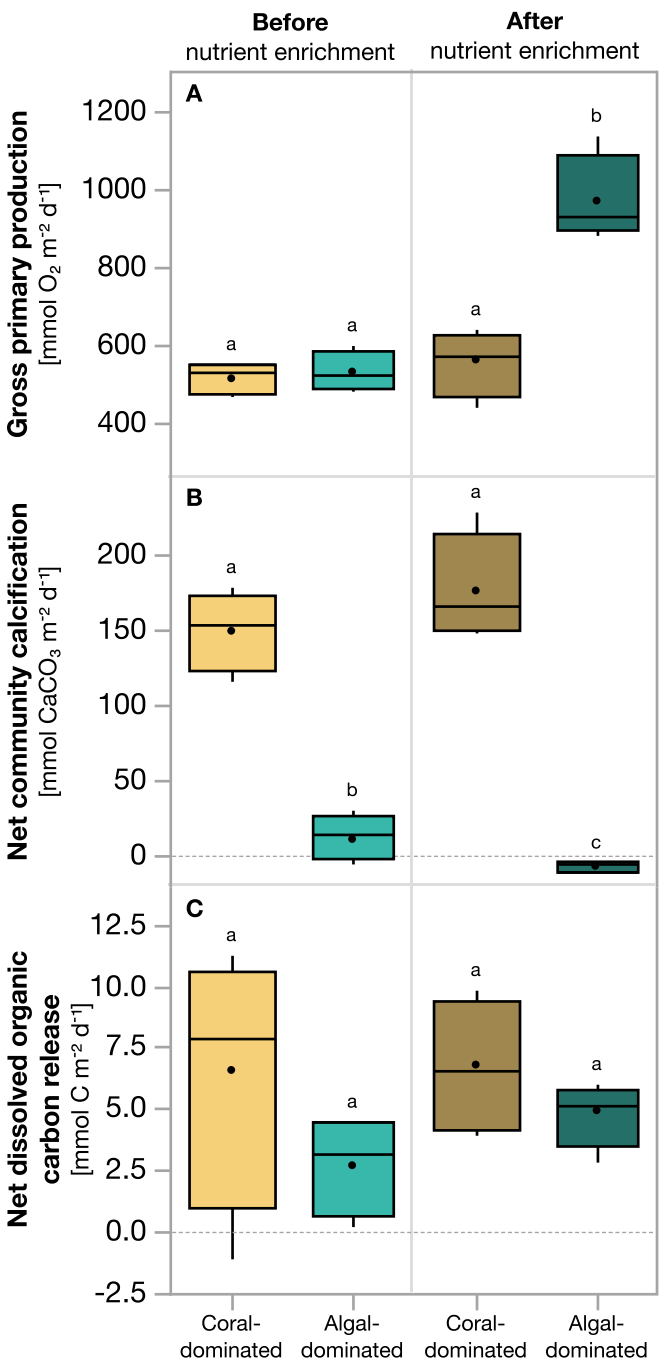


**Fig. 2.** Gross primary production (A), net community calcification (B), and net release of dissolved organic carbon (C) in coral- and algae dominated reef communities, before and after nutrient enrichment. Boxplots show the median (line across a box), mean (dot in the box), first and third quartiles (upper and lower bounds of each box), and the minimum and maximum value (i.e., upper and lower whisker, respectively). Levels not connected by the same letter are significantly different. Statistical details of linear mixed models are presented in Table S5.

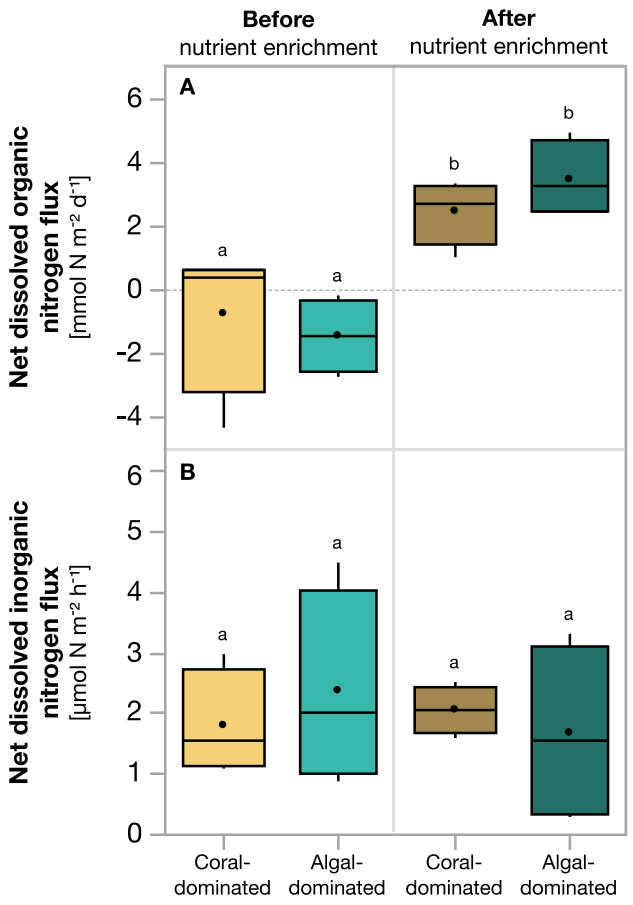


**Fig. 3.** Dissolved organic nitrogen (A) and dissolved inorganic nitrogen (B) net fluxes in coral- and algae dominated reef communities, before and after nutrient enrichment. Boxplots show the median (line across a box), mean (dot in the box), first and third quartiles (upper and lower bounds of each box), and the minimum and maximum value (i.e., upper and lower whisker, respectively). Negative fluxes (<0) indicate a net uptake of nitrogen by the communities. Levels not connected by the same letter are significantly different. Statistical details of linear mixed models are presented in Table S5.

algae-dominated (9.8 ± 7.6 mmol $CaCO_3$ $m^{-2}$ $d^{-1}$) communities (Fig. 2B). Net DOC fluxes (Fig. 2C) ranged from −1.1 to 11.3 mmol C $m^{-2}$ $d^{-1}$ in coral-, and from 0.2 to 4.5 mmol C $m^{-2}$ $d^{-1}$ in algae-dominated communities. Due to the high variability of DOC fluxes between replicates, no significant differences were detected between the two community-types. TDN fluxes were close to zero in both coral- and algae-dominated communities, balanced by the consumption of DON (−0.7 ± 1.2 and −1.4 ± 0.6 mmol N $m^{-2}$ $d^{-1}$, respectively; Fig. 3A) and a concomitant release of DIN (1.8 ± 0.4 and 2.4 ± 0.8 mmol N $m^{-2}$ $d^{-1}$, respectively; Fig. 3B).

### 3.2. Community-wide biogeochemical processes after nutrient enrichment

GPP was 74% higher in algae- compared to coral-dominated communities after nutrient enrichment (968 ± 57 and 556 ± 42 mmol $O_2$ $m^{-2}$ $d^{-1}$, respectively; Fig. 2A). Thereof, CR consumed two-times more $O_2$ in algae- (−502 ± 25 mmol $O_2$ $m^{-2}$ $d^{-1}$) than in coral-dominated (−258 ± 39 mmol $O_2$ $m^{-2}$ $d^{-1}$) communities, while NCP was 55% higher (465 ± 22 compared to 300 ± 14 mmol $O_2$ $m^{-2}$ $d^{-1}$, respectively) (Fig. S2). The resulting GPP:CR ratio was 26% lower in algae- (1.7 ± 0.1) compared to coral-dominated communities (2.3 ± 0.2) (Fig. 4A). In situ nutrient enrichment led to a non-significant increase in NCC in coral-dominated communities, while it caused a significant shift from net calcification to carbonate dissolution in algae-dominated communities (i.e., negative NCC rates; −6.8 ± 1.6 mmol $CaCO_3$ $m^{-2}$ $d^{-1}$; Fig. 2B). In both community types, nutrient enrichment neither affected the magnitude nor the direction of net DOC fluxes (Fig. 2C). In contrast, TDN fluxes were significantly altered by nutrient addition, mainly driven by changes in net DON fluxes (Fig. 3A). Nutrient enrichment caused both communities to shift from being DON sinks to sources (after nutrient enrichment: 3.6 ± 0.3 and 2.5 ± 0.1 mmol N $m^{-2}$ $d^{-1}$ in coral- and algae-dominated communities, respectively); however, the average increase in DON released from before to after nutrient enrichment was 56% higher in algae- (+5.0 ± 0.8 mmol N $m^{-2}$ $d^{-1}$) compared to coral-dominated (+3.2 ± 0.7 mmol N $m^{-2}$ $d^{-1}$) communities. Due to the high variability in DIN fluxes across replicates, neither significant changes from before to after nutrient enrichment nor between the community-types were detected (Fig. 3B). The imbalanced changes in the released amount of DOC and DON caused a small (~10%) but significant reduction of the C:N molar ratio of DOM released by coral- and algae-dominated communities (Fig. 4B).

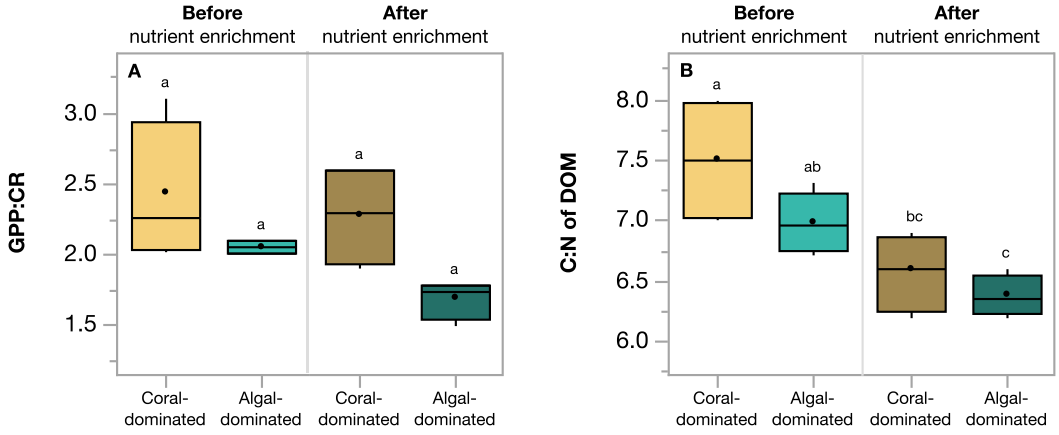


**Fig. 4.** Ratio of gross primary production to community respiration (A), and the molar carbon to nitrogen (C:N) ratio of dissolved organic matter (DOM) (B) from coral- and algae-dominated communities, before and after nutrient enrichment. Boxplots show the median (line across a box), mean (dot in the box), first and third quartiles (upper and lower bounds of each box), and the minimum and maximum value (i.e., upper and lower whisker, respectively). Abbreviations: GPP = gross primary production; CR = community respiration; DOM = dissolved organic matter. Levels not connected by the same letter are significantly different. Statistical details of linear mixed models are presented in Table S5.

## 4. Discussion

### 4.1. Similar biogeochemical processes in coral- and algae-dominated reef communities under ambient nutrient conditions

The present study suggests similar directions and magnitudes of major biogeochemical processes of coral- and algae-dominated communities at Abu Shosha reef in January 2018 (i.e., before nutrient enrichment was initiated). Specifically, both community types showed similar GPP, CR, and NCP rates. Although the rates are in line with the literature (Albright et al., 2015, 2013; Roth et al., 2020), they are in contrast with some studies reporting significantly higher organic C turnover with a greater potential for autotrophic biomass accumulation per planar square meter of the reef for algae- compared to coral-dominated communities (Fong and Paul, 2011; Kelly et al., 2017). These differences may arise from varying rates of turf algae productivity that is shaped by multiple factors, including species composition, study depth, standing biomass, and season (Tebbett and Bellwood, 2021). In the central Red Sea, comparable rates of productivity in coral- and algae-dominated communities were observed previously, particularly during winter and spring (Roth et al., 2020), which corresponds to the current study period. Further, we observed that both community types were net sources of DOC, suggesting that the production of extracellular photosynthates outpaces its consumption (Nelson et al., 2013; Quinlan et al., 2018). However, while coral-dominated communities were net sources of DOC during both light and dark incubations, algae-dominated communities were strong sources of DOC during the light, and sinks of DOC during the dark (Table S4). The consumption of algal-derived C can be promoted by heterotrophic bacterioplankton (Haas et al., 2013; Nelson et al., 2011; Silva et al., 2021) or sponges and other filter feeders that are commonly associated with degraded reef habitats and feed on DOC or algal debris (Rix et al., 2017, 2018; Wooster et al., 2019). In coral-dominated communities, we measured high net community calcification rates, consistent with the accretion of carbonate structures typical for tropical coral reefs (Atkinson and Falter, 2003; Gattuso et al., 1999, 1998). Algae-dominated communities exhibited low rates of net calcification, which indicates a shift in the relative proportion of calcifying to non-calcifying organisms (Albright et al., 2013; Takeshita et al., 2016).

Quantifying N pathways in coral reefs is crucial to understand how productivity is supported despite low ambient nutrient concentrations (D'Elia and Wiebe, 1990). Both coral- and algae-dominated communities were net sources of DIN. The present study's flux rates generally fell within the range of in situ measurements elsewhere (Atkinson and Falter, 2003). Thereby, the effects of assimilation are likely masked by multiple concurrent community-wide processes that produce DIN in situ. For example, cavities within coral reefs can be considerable DIN sources as sponges and other filter feeders utilize and remineralize DOM (Richter et al., 2001). Also, microbial communities can consume and transform organic N compounds (Moulton et al., 2016; Pfister and Altabet, 2019; Yahel et al., 2003), potentially increasing the community-wide DIN release into the environment. Other pathways, such as $N_2$ fixation (Cardini et al., 2016) or heterotrophic feeding on particulate materials (Houlbrèque and Ferrier-Pagès, 2009; Ribes et al., 2003) may also produce dissolved N that potentially masks the DIN uptake. The net production of DIN may also be ascribed to the mineralization of dissolved or particulate N. In support of this, we here report that both coral- and algae-dominated communities were, in fact, net sinks of DON. Corals, for example, use multiple ways to supply their N needs: they can efficiently take up and retain DIN (Grover et al., 2003, 2002), but also use DON in the form of amino acids and urea (Ferrier, 1991; Hoegh-Guldberg and Williamson, 1999). In addition, a substantial fraction of DOC and DON produced by both corals and algae can be assimilated by sponges which subsequently convert it into, and release it as, particulate detritus (Rix et al., 2017). The relative contribution to the observed N fluxes by organisms that were not captured by our visual benthic surveys (i.e., sponges, bryozoans, and tunicates in cryptic spaces, as well as microbial communities) remains to be explored. Overall, however, the balance between DIN production and DON consumption within both community types highlights a balanced N cycle and the efficient reuse of resources in the studied reef under ambient nutrient conditions.

### 4.2. Varying responses of biogeochemical processes to nutrient enrichment in coral- and algae-dominated communities

In situ nutrient enrichment had distinctive effects on benthic C, $CaCO_3$, and N dynamics in coral- and algae-dominated communities (Fig. 5), as has been suggested from a previous mesocosm study (Silbiger et al., 2018). Thereby, the responses of the major biogeochemical processes to excess nutrients (N, specifically) were likely both a direct physiological reaction by N-limited key primary producers and an indirect response to shifts in the availability and quality of dissolved organic compounds for remineralization by bacteria and cryptic species within the communities.

Specifically, we observed significantly enhanced productivity by nutrient enrichment in algae-dominated communities, while no such changes were apparent in co-occurring communities dominated by corals. The increased productivity of algae-dominated communities with nutrient enrichment aligns with many previous findings (Burkepile and Hay, 2009; Littler et al., 2006; McCook, 1999). Complementing these results, Karcher et al. (2020) highlighted concomitant increases of N (+39%) and $C_{org}$ (+33%) content in turf algae (the dominant key

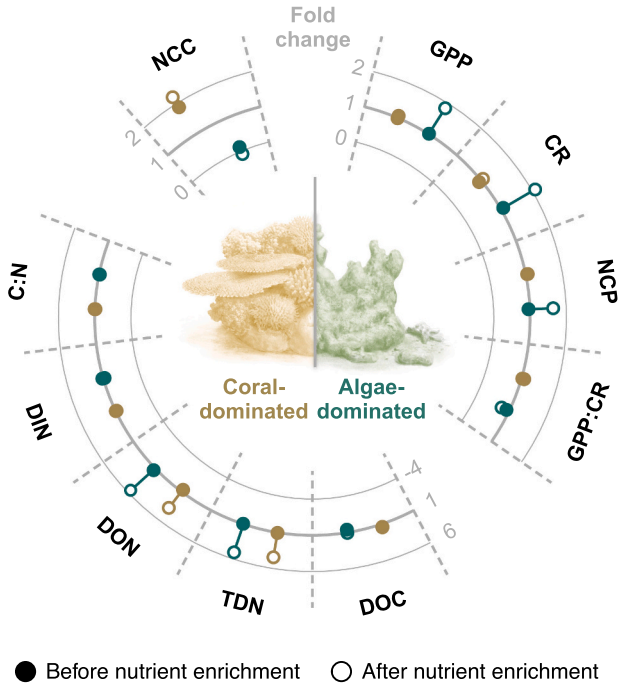


**Fig. 5.** Summary of changes of major biogeochemical response parameters in coral- (brown) and algae-dominated (green) reef communities before (full circle) and after (empty circle) nutrient enrichment. All changes are expresses as "fold change" relative to the combined mean of both communities before nutrient enrichment. Abbreviations: GPP = gross primary production; CR = community respiration; NCP = net community production; DOC = net dissolved organic carbon fluxes; TDN = net total dissolved nitrogen flux; DON = net dissolved organic nitrogen flux; DIN = net dissolved inorganic nitrogen flux; C:N = molar ratio of carbon to nitrogen of dissolved organic matter released by the communities; NCC = net community calcification. Empty circles (after nutrient enrichment) can be masked behind closed circles (before nutrient enrichment). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Reefscape by Xavier Pita, scientific illustrator at KAUST, adapted from Roth et al. (2020) under the CC-BY 4.0 License.

functional group within the "algae-dominated" communities) after eight weeks of the same in situ nutrient enrichment. These results suggest that N was indeed a limiting nutrient for algal growth in the current experiments (Hatcher and Larkum, 1983; McCook, 1999) (potential P limitation discussed at the end of this section). In otherwise oligotrophic reef environments, benthic algae can have high uptake rates of nutrients per unit biomass, benefiting from episodic inputs of N to coral reefs (Den Haan et al., 2016). However, while NCP increased by >50%, an even stronger response in CR (100% increase) was apparent. As a result, algae-dominated communities had a greater potential for autotrophic biomass accumulation both in absolute numbers and relative to the "before nutrient enrichment" measurements. However, the proportionally greater increase in CR resulted in a lowered GPP:CR ratio, indicative of an overall faster turnover of organic C through respiratory processes. Algae-dominated reef structures provide habitat for numerous heterotrophs that rely on algal biomass, fueling community-wide respiration. Particularly heterotrophic bacteria within these communities remineralize labile DOC released by algae (Haas et al., 2013; Nelson et al., 2011; Silva et al., 2021), and sponges and other filter feeders within the reef matrix feed on algal debris and DOC (Rix et al., 2018, 2017). Although we did not observe any change in the net DOC flux integrated over 24 h, previous in situ studies at the community level report DOC production during the light and DOC consumption in the dark in algae-dominated reef communities (Roth et al., 2020). Concordantly, we measured an increase in DOC production during light incubations, and a concomitant increase in DOC consumption during dark incubations, such as the release in the light was effectively balanced by consumption in the dark (Table S4). In coral-dominated communities, neither GPP, CR, nor NCP responded to excess N. Although this is in contrast to previous reports (e.g., Koop et al., 2001), El-Khaled et al. (2020) showed that individual corals of the same experiment indeed did not increase primary production during single organism incubations. Likewise, Karcher et al. (2020) showed that these corals incorporated excess N into the host tissue, however, that corals did not utilize N for the production of $C_{org}$. These results support that N was not a limiting factor for coral productivity in the present experiments. We find two plausible explanations for this observation. Firstly, additional nutrient sources may have contributed to supporting photosynthesis even under low ambient nutrient concentrations (<0.5 μmol DIN $L^{-1}$). Corals and other benthic organisms contribute to benthic N inputs by $N_2$ fixation during nutrient-depleted conditions, suggesting a strong biogeochemical coupling between diazotrophy and the reef C cycle (Cardini et al., 2016). In addition, heterotrophic feeding may complement N demands by corals (Gustafsson et al., 2013). Secondly, the previously observed P limitation in coastal Red Sea waters (Ezzat et al., 2016; Silva et al., 2021, 2019) may cause coral-dominated communities to be limited by P rather than N (Ezzat et al., 2016), restraining the zooxanthellae's N uptake and subsequent coral growth (Godinot et al., 2011; Karcher et al., 2020). In contrast to the evident increase in N availability in our experiments, P provided by the fertilizer did not alter the $PO_3^{-4}$ concentration in the seawater surrounding the communities. While we cannot reconstruct the fate of P from the fertilizer pins with the current experimental design, the communities themselves, reef sediments (Millero et al., 2001) or organisms in the water column and the surrounding benthos could have contributed to the rapid depletion of P (Cuet et al., 2011).

We observed neither a change in the direction nor magnitude of DOC fluxes from coral-dominated communities after nutrient enrichment. This aligns with the common assumption that the release of DOC is closely coupled to productivity (Haas et al., 2011) (although, in corals, DOC release can also be stimulated by stress or as a protective mechanism (Niggl et al., 2009)). Moreover, and unlike previously suggested (Silbiger et al., 2018), we did not observe any change in calcification of coral-dominated communities with moderate nutrient enrichment, neither during light nor dark incubations. The increased competition for dissolved inorganic carbon (DIC) between the coral host and its endosymbionts under elevated nutrient concentrations can directly drive the reported lower calcification rates in other studies (Marubini and Davies, 1996). Drawing from the same DIC pool will result in one process being enhanced (likely productivity), while the other is suppressed (i.e., calcification). However, here, we did not see a positive effect of nutrients on productivity, and, likewise, there was no associated change in calcification. In stark contrast to that, we not only observed a decrease in calcification rates in algae-dominated communities but a shift from net calcification to net dissolution with nutrient enrichment. The observed net dissolution corroborates with results from an experimental mesocosm study with algae-dominated communities under similar nutrient enrichment scenarios (Silbiger et al., 2018). The decline in calcification in response to nutrient addition could be induced by a combination of decreasing calcification rates from encrusting algae and invertebrates, increasing bioerosion or metabolic dissolution (Andersson, 2015). Under field conditions, high bioerosion rates can correlate with high nutrient conditions, likely because many bioeroders are filter-feeding invertebrates or photosynthetic endoliths (DeCarlo et al., 2015; Lubarsky et al., 2018). Dissolution of $CaCO_3$ could also occur due to local $CO_2$-induced acidification caused by natural respiration of benthic fauna and flora at night, as observed in other coastal habitats (Kwiatkowski et al., 2016; Saderne et al., 2020). The doubling of respiration rates within algae-dominated communities may support the latter, especially.

To the best of our knowledge, we here present the first results of the impacts of short-term nutrient enrichment on major N fluxes (specifically TDN, DIN, and DON) of intact reef communities in the natural environment. Our findings indicate that increases in environmental N can alter the critical balance of nitrogenous compounds being taken up and released by both types of reef communities. Specifically, nutrient enrichment caused a reversal of DON fluxes, that is, coral- and algae-dominated communities shifted from being net DON sinks (before nutrient enrichment) to net DON sources (after nutrient enrichment). The absolute increase was, however, significantly higher in algae-dominated communities. We find several possible explanations for how DON was produced in excess, or how its consumption was hampered. First, the export of organic N by reef biota can be enhanced by primary production and the availability of N relative to P. This is supported by results from a study measuring the distribution and partitioning of DON on a Pacific reef showing that DON in the water column increases when productivity and the DIN:DIP ratio are high (Miyajima et al., 2007). Secondly, DIN from anthropogenic sources (in our case, the fertilizer) can increase internal N availability (shown by the complementary study by Karcher et al. (2020)) and induce DON release (Thibodeau et al., 2013). Likewise, as a secondary effect, increased environmental N availability can enhance $N_2$ fixation (El-Khaled et al., 2020), which in turn increases the internal N availability and induces DON release (Thibodeau et al., 2013). Lastly, degradation experiments of reef organic matter showed that DON degradation could be slower than that of DOC, and, therefore, the C:N ratio of organic matter decreases (Suzuki and Casareto, 2011). Indeed, we detected significant reductions of the C:N ratio of DOM retrieved from the communities after nutrient enrichment, indicating that DOC relative to DON may have been consumed faster or released less. It has to be noted, however, that the reduced C:N ratio of DOM may also be the result of more N in the system, i.e., N fertilization and uptake by organisms increased the cellular N content, thereby decreased the C:N ratio in the biomass, as has been suggested by Karcher et al. (2020). In conclusion, after nutrient enrichment, the reversal of DON fluxes led to benthic reef communities being TDN sources rather than having balanced DIN and DON fluxes that leaves the overall TDN flux close to zero. The observed imbalance of the uptake of inorganic and release of organic nitrogenous compounds grants further investigation, especially with regards to cascading microbially-mediated, bottom-up effects on the reefs trophodynamics (Rix et al., 2017; Silveira et al., 2015).

### 4.3. Ecological implications and outlook

We showed that in situ nutrient enrichment did not directly affect organic C budgets and calcification of coral-dominated communities in their natural environment. In contrast, excess nutrients significantly enhanced productivity, respiration, and caused a dissolution of the carbonate framework in co-occurring algae-dominated communities of the same reef. These results may have important implications for the competitive relationship of coral- and algae-dominated communities and the ecosystem services these communities can provide. Specifically, on reefs where the two community-types co-occur, algae-dominated communities may have a higher potential for biomass accumulation that can enhance space occupation and rapid succession on bare reef substrates (Roth et al., 2015; Stuhldreier et al., 2015). The loss of the structurally complex $CaCO_3$ reef framework and an increased space occupation by algae may hamper the replenishment of adult coral populations due to recruitment inhibition through limited habitat complexity and grazing pressure. Together, this may restrain reef recovery (Roth et al., 2018) and the high biodiversity characteristic of tropical coral reef ecosystems (Bellwood, 2001). However, some of the results also open questions for future research directions, particularly highlighting the complexity of and the limited knowledge about reef processes at a community level. For example, the underlying mechanisms of the net dissolution of the reef framework in algae-dominated communities after nutrient enrichment remain highly speculative (e.g., local $CO_2$-induced acidification due to higher microbial respiration rates; Kwiatkowski et al., 2016; Saderne et al., 2020) and should be addressed in the future. Moreover, the increased DOC turnover (increased release during light and concomitant increased consumption in the dark) in algae-dominated communities may indicate a higher activity of opportunistic microbes and other heterotrophs feeding on DOC. Future studies should, thus, assess if nutrient enrichment in coral reefs dominated by algae can shift the microbial community towards opportunistic pathogens, which can further adversely influence the coral-algal competition (Haas et al., 2016). Also, intriguingly, both coral- and algae-dominated communities were sources of DIN at all times, even before experimental nutrient addition. Whether DIN producing processes masked N uptake by autotroph organisms of the communities, or if other elements (e.g., P) limited their growth remains unresolved from the current experiment. However, it reflects a general knowledge gap on organic and inorganic N and P fluxes from whole reef communities in their natural environment; particularly so under the influence of anthropogenic nutrient addition. Overall, the results highlight that complex interactions of community shifts and nutrient pollution occur in the natural environment, which can likely not be resolved by laboratory or mesocosm studies. Nutrient pollution may amplify the effects of community shifts on key ecosystem services of coral reefs, possibly leading to a loss of structurally complex habitats with carbonate dissolution and altered nutrient recycling.

## CRediT authorship contribution statement

FR, YEK, SC and CW conceptualized and designed research. FR, YEK, DBK and LS performed research. FR, YEK, NR, MLC analyzed data. CMD, XAGM, CRV, and BHJ contributed to research materials, logistics and to interpreting data. FR wrote original draft of the manuscript. All authors read and approved the final manuscript.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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