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Coral elementomes diverge for colonies persisting in vegetative lagoons versus reef environments

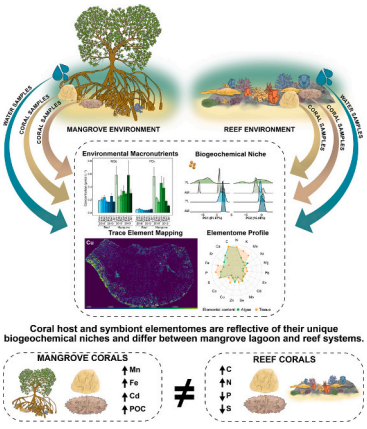
Emma F. Camp [a,*], David Clases [b], David Bishop [c], Annette Dowd [d], Samantha Goyen [a], Raquel Gonzalez de Vega [f], Paige Strudwick [a], David J. Suggett [a,e]

[a] Climate Change Cluster, University of Technology Sydney, Broadway 2007, NSW, Australia
[b] NanoMicroLab, Institute of Chemistry, University of Graz, 8010 Graz, Austria
[c] Hyphenated Mass Spectrometry Laboratory, Faculty of Science, The University of Technology Sydney, Ultimo, NSW 2007, Australia
[d] School of Mathematical and Physical Sciences, University of Technology Sydney, Broadway 2007, NSW, Australia
[e] KAUST Coral Restoration Initiative (KCRI) and Division of Biological and Environmental Science and Engineering (BESE), King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia
[f] TESLA, Institute of Chemistry, University of Graz, 8010 Graz, Austria

HIGHLIGHTS

- Corals living in mangrove lagoons survive in extremely hostile seawater conditions.
- Mangrove waters have higher nutrient content than reef waters.
- Mangrove corals have unique elementomes that reflect a unique biogeochemical niche.
- Corals living in mangroves have different amounts of trace elements than reef corals.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change, in tandem with localised stressors, continues to drive global declines in coral cover worldwide. Identifying where and how corals survive in present day extreme environments, characterised by suboptimum abiotic conditions, has become a key tool to better resolve coral stress tolerance and in turn future reef trajectories. Whilst several reef forming coral species routinely extend their ecological niche into extreme environments, whether corals have a distinct biogeochemical niche reflected by unique elementomes (the stoichiometry and quantity of elements) remains unknown. Here, through quantitative assessment and elemental mapping, we demonstrate that two functionally important Great Barrier Reef coral species, *Acropora millepora* and *Porites lutea* and their algal symbionts (Symbiodiniaceae) exhibit unique elementomes, that reflect a unique biogeochemical

* Corresponding author.
E-mail address: emma.camp@uts.edu.au (E.F. Camp).

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Redfield ratio
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niche of species in the extreme mangrove lagoon compared to a neighbouring reef. Coral elementomes were distinct over multiple years, as were the elementomes of the seawater of each habitat. Furthermore, particulate organic matter was elevated in the mangrove lagoon which could support enhanced rates of heterotrophy. Collectively these findings reveal that vegetative mangrove island waters provide a unique biogeochemical environment for resident corals and that resident corals undergo bioelemental reorganisation, particularly via elevated micronutrient content, when living in extreme vegetative mangrove island lagoons. Results here reaffirm the importance of vegetative island systems in the survival of coral reefs and thus the critical need to ensure conservation efforts consider cross ecosystem protection measures.

1. Introduction

Extreme coral environments are characterised by large deviations from optimal abiotic conditions (sensu Schoepf et al., 2023) and are well recognised as important natural laboratories to further knowledge of how corals can thrive in suboptimal environmental conditions (Camp et al., 2018). Such extreme conditions provide valuable insight towards global efforts forecasting how well corals (Camp et al., 2016) – and in turn potential for reef formation (Cornwall et al., 2018; Tanvet et al., 2023) – can survive rapid environmental change ongoing through the Anthropocene. Systems supporting extreme coral environments are diverse (Camp et al., 2018; Schoepf et al., 2023) but include hot seas and shallow reef systems such as exposed reef flats and mangrove lagoons (Burt et al., 2020). Mangrove systems in particular have now been documented at locations around the world housing corals within complex multi-stressor conditions, where abiotic factors such as temperature, pH, oxygen, light and salinity are extreme and/or highly variable (e.g., Camp et al., 2017, 2019; Maggioni et al., 2021; Stewart et al., 2022). Corals living in such mangrove systems have unique microbiome associations (Camp et al., 2020; Haydon et al., 2021; Tanvet et al., 2023) and altered physiology (Ros et al., 2021; Haydon et al., 2023) that have been suggested to support their survival. However, trade-offs to other key traits underpinning fitness, such as reduced calcification and reduced genetic diversity, have also been documented (Camp et al., 2016; Scucchia et al., 2023). Most importantly, a common observation from extreme coral environments, including mangrove lagoons, has been the ability for corals to diversify their modes of energy acquisition via nutritional plasticity (e.g., shifts from autotrophy to heterotrophy; reviewed in Camp et al. (2018)); a mechanism predicted to provide the elevated energy requirements required to survive the suboptimum abiotic conditions. However, this leads to a fundamental yet unanswered question. Does nutritional plasticity of corals in extreme environments align to unique resource provision in the underlying elemental landscape? Furthermore, do distinct elemental coral phenotypes exist in extreme environments as with organisms in extreme terrestrial systems (Jeyasingh et al., 2014)? Addressing these unknowns will advance our understanding of the mechanisms supporting survival of corals in extreme environments, facilitate conservation efforts, and support new and ongoing active management interventions.

Vegetative islands (reviewed in De Falco et al., 2022) – which often extend to support mangrove systems – provide important nutrient subsidies to resident coral reefs (island mass effect; Doty and Oguri, 1956). Mangrove systems can provide elevated particulate organic matter (Mejias-Rivera et al., 2023). Nitrogen (N) and phosphorous (P) are found to be enriched around vegetative islands (e.g., Raapoto et al., 2019), where a combination of bird guano and decomposition and recycling of organic matter stimulate primary production and trigger cascading effects throughout food webs (Graham et al., 2018). However, for mangrove systems, N and P input is less understood, due to the high heterogeneity of mangrove systems and the temporal variability of N and P sources, sinks, and transformation pathways (Taillardat et al., 2018). Mangrove systems have the potential to act as an important source of trace elements, as mangroves accumulate trace metal plaques on their prop roots, which upon decomposition, return to the waterway (Ca çador et al., 1996; Machado et al., 2005). Alongside essential macro elements (such as carbon (C), N, P), trace metals play a pivotal role in coral health (Reich et al., 2023). Trace metals are used as cofactors in enzymatic activity and are particularly important for the photosynthetic functioning of Symbiodiniaceae (Raven, 1990; Raven et al., 1999); the algal symbiont of corals. At concentrations outside of homeostasis, trace elements can be toxic (e.g., Golding et al., 2023), but at optimal levels they can facilitate coral fitness (Biscéré et al., 2018; Blanckaert et al., 2022). Laboratory studies of cultured Symbiodiniaceae have shown elevated uptake of trace elements under heat stress, highlighting their potential importance in modulating the holobiont stress response (Camp et al., 2022; Reich et al., 2021). Whether corals persisting in naturally extreme and stressful environments have elevated update of trace metals, however, remains unknown.

Understanding the full suite of elemental requirements of coral is necessary to resolve reef nutrient cycling and trophic transfer (Sterner and Elser, 2017), as well as nutritional health and an individual's biogeochemical niche (Hofmann et al., 2021). As for all other organisms, the nutritional profile for corals includes macronutrients such as N, P and C as well as trace metals and other micronutrients (Grima et al., 2022). Yet for coral reefs, research to date has almost exclusively focused on single elements, or a sub-set of key elements, which cannot capture the complex sum of elemental stoichiometric relationships that are likely to impact organism fitness. Trace elements – spanning their uptake, incorporation and hence organism requirements – in particular remain largely unstudied for corals (Reich et al., 2023), yet have recently been shown to be crucial in defining the biochemical niche where corals thrive (Grima et al., 2022). Under climate change, availability of trace elements may change in ways that could create a mismatch between need and availability (Reich et al., 2023), particularly where increased uptake of trace elements is a strategy employed by both the coral host (Ferrier-Pagès et al., 2018) and algal symbionts (Camp et al., 2022) under thermal stress. It is thus time-critical to determine whether vegetative mangrove island act as a source of trace metals and whether corals residing in mangrove lagoons have a unique elemental phenotype that reflects their biogeochemical niche when surviving in extreme abiotic conditions. We therefore conducted a two-year study at an offshore (15 km from the mainland) vegetative mangrove island and an adjacent reef site on the northern Great Barrier Reef. At these locations, we tracked the particulate organic carbon of seawater and the elemental seawater content alongside the elementome (quantity and stoichiometry of elements) of two coral species *Acropora millepora*, and *Porites lutea* along with their algal symbionts, through C and N analysis and inductively coupled plasma-mass spectrometry (ICP-MS). For *P. lutea* we further applied laser ablation ICP-MS and x-ray fluorescence microscopy to explore elemental allocation within the coral holobiont. Our study enables us to examine, for the first time, how elements are distributed within extreme corals, shedding light on the role of mangrove-based vegetation systems in influencing the "trace element" economy and nutrient environment of reef-building corals.

2. Materials and methods

2.1. Study location and sample details

The study was conducted within Woody Isles, a vegetative mangrove

lagoon (herein referred to as the mangrove lagoon site; 16.388° S, 145.566° E) and on the adjacent Low Isles reef (herein referred to as the reef site; 16.390° S, 145.560° E, Fig. 1a. & c.). They are found 15 km from the mainland and can be subjected to terrestrial influences during extreme weather events (see Bartels et al., 2023). Both Woody Isles and Low Isles reef typically experience semi-diurnal tidal cycles. The Woody Isles mangrove lagoon has lower pH, lower oxygen, and higher temperature variation than the adjacent Low Isles reef (see Camp et al., 2019; Haydon et al., 2021, Table 1). The mangroves are predominantly *Rhizophora* sp., and have been documented to be expanding onto the reef flat (Hamylton et al., 2019). The mangrove island has resident bird populations and between November and March has an estimated 25,000 migrating pied imperial pigeons. The mangrove lagoon is comprised primarily of carbonate sediments, and on the outer edge of the sand cay there are muddy sand and mixed coral shingles (Hamylton et al., 2019). In December 2018 within each location, five colonies (15–30 cm maximum diameter) of *Acropora millepora* and *Porites lutea* were marked with a tag secured with a clear plastic cable tie. Previous studies have confirmed the host species identity (Scucchia et al., 2023) and the dominant Symbiodiniaceae genotypes (Camp et al., 2019) for these species in these locations. In brief, *A. millepora* associates with species of the genus *Cladocopium* on the reef and *Durusdinium* in the mangrove lagoon, whereas *P. lutea* in both habitats associated with C15 radiation (*Cladocopium*) taxa (Camp et al., 2019).

Using a plastic chisel, two outer fragments (ca. 5 cm) were collected from each colony of *A. millepora*, whereas two small (3–5 cm) sections were removed from the outer edge of the colony for *P. lutea*. One sample was kept in native seawater for assessment of maximum yield of photo system II (PSII) photochemistry back on the research vessel (measured within 30 mins of sampling). Maximum yield of PSII photochemistry (F_v/fm, dimensionless) was measured to provide a proxy for the corals physiological status, using a pulse amplitude modulation (PAM) fluorometry (Diving PAM, Walz, Effeltrich, Germany) as described previously (Goyen et al., 2019). The second fragment from each coral was placed into a Whirl-Pak bag and immediately flash-frozen. Samples were stored at −80 °C prior to analysis. One year later, in December 2019, each colony was resampled as described for December 2018. At both sites, corals were at a depth of 0.5–1.5 m. Each year at the time of coral collection, $n = 20$-point measurements were taken to characterise the mangrove seawater abiotic conditions (10 within 2 h of sunrise and 10 within 2 h of sunset) using a WTW multi-meter (see Table 1). Each year at the time of coral collection, seawater samples ($n = 10$ per habitat) were collected for particulate organic carbon (POC) concentration as described in Wagner et al. (2011). In brief, 500 mL of seawater was filtered onto a pre-weighted and pre-combusted 47 mm GF/F filters (Whatman, 0.7 um nominal pore size). After filtration the filters were frozen until analysis. The filters were acidified as per (Pike and Moran, 1997) to remove particulate inorganic carbon, followed by 24 h drying at 60 °C prior to analysis conducted by dry combustion with a LECO TruMac Carbon Nitrogen Analyser (LECO Castle Hill, Australia). Furthermore, $n = 3$–7 water samples were also collected (in a polyethylene container 10 cm from coral) for characterisation of both trace elements and macronutrient concentrations of NOx (nitrate (NO_3) and nitrite (NO_2), and phosphate (PO_4^{3-}). Further samples ($n = 5$–10 each sampling time) were collected in the same manner for macronutrients in January 2018 and 2019, February 2018 and 2019 and June 2019. The samples were filtered through a 0.7 μm GF/F filter (Whatman) and stored at −20 °C until analysis (Becker et al., 2020; Xu et al., 2021). All collection vessels were prepared as described below.

2.2. Materials, solutions, and glassware

All acids/reagents used in this investigation, such as HNO_3 (67–69 % *w*/w, Seastar Chemicals, BC, Canada), H_2O_2 (30–32 % w/w, Seastar Cemicals) and Milli-Q water (18.2 MΩ cm) obtained from a Sartorius 611 arium® pro water generation system (Sartorius Lab Instruments GmbH & Co. KG, Goettingen, Germany) were of analytical grade purity and used without further purification. All glassware and plastics used in the sample tagging and sampling procedure were immersed in a Micro-90 solution (2 % for 24 h), rinsed with Milli-Q water, followed by an acid-wash solution (10 % hydrochloric acid for 24 h), before a final Milli-Q rinse and atmosphere dry (Rodriguez et al., 2016). Containers used for field sample collection were double bagged and stored in a polyethylene container cleaned as described above.

2.3. Coral and water elemental quantification

\Methods were conducted on a bench with class 100 laminar flow, following the Clean laboratories and clean rooms for analysis of radionuclides and trace elements protocol (IAEA, 2003). From each coral fragment a ~1 cm^2 nubbin was removed and air picked in sterile 0.1 N TRIS buffer to quantify cell counts using a Neubauer Haemocytometer, (Fisher Scientific, Loughborough, UK) under a Nikon Ti microscope at 10× magnification. Cell density was obtained by standardising the values to fragment surface area using the single wax dipping technique (Stimson and Kinzie, 1991; Veal et al., 2010).

The remainder of the fragment was divided into two, one part was air picked in 10 mL 0.1 N sterile TRIS buffer to remove host tissue, mucus, and algal symbionts from the skeleton (as per Grima et al., 2022) for ICP-MS. The other coral fragment part was air picked into filtered seawater for total C and N analysis. The residual slurry of each was decanted into new 15 mL centrifuge tubes and centrifuged for 5 min at 27 °C and 3500 RPM in a Rotanta 460R centrifuge (Hettich, Germany). The supernatant (host tissue and mucus) fractions were poured into separate 15 mL centrifuge tube. The remaining algal pellets had 5 mL of the respective buffer (TRIS or filtered seawater) added and were re-suspended before repeat centrifugation – where this wash step was repeated once more to ensure the host tissue fraction was removed from the algal pellet fraction. Both the host and algal fractions were stored at −80 °C after processing prior to being freeze dried (Alpha 2–4 LDplus freeze dryer (CHRIST, Germany).

Total C and N was determined by dry combustion with a LECO TruMac Carbon Nitrogen Analyser (LECO Castle Hill, Australia). Approximately 40 mg of algal pellet was used. Manufacturer methods for soil and plant material when utilising a furnace temperature of 1200 °C were followed. A calibration standard (LECO) was used, and sample blanks and standards were utilised prior to sampling, and every 15–20 samples through a sampling run to check for instrument drift. Second, the quantity of other macronutrients (calcium (Ca), phosphorus (P), potassium (K), sulphur (S)) and trace elements (cadmium (Cd), cobalt (Co), copper (Cu), iron (Fe), lead (Pb), magnesium (Mg), manganese (Mn), molybdenum (Mo), nickel (Ni), tin (Sn), selenium (Se), strontium (Sr), vanadium (V) and zinc (Zn)) present in the sample were determined. An average of 30 mg and 15 mg of host tissue and algal symbiont fraction, respectively, were used for ICP-MS analysis. Host tissue samples were digested overnight in 200 μL of each ultra-pure HNO_3 (67–69 % *w*/w, Seastar Chemicals, BC, Canada) and H_2O_2 (30–32 % w/w, Seastar Cemicals), whilst 100 μL of both HNO_3 and H_2O_2 were added to each algal symbiont sample. Varying volumes were used for greater biomass tissue samples which required more acid to complete the digestion. Following the digestion step, 4 mL and 2 mL of Milli-Q water (18.2 MΩ cm) obtained from a Sartorius 611 arium® pro water generation system (Sartorius Lab Instruments GmbH & Co. KG, Goettingen, Germany) was added to the tissue and algal symbiont samples, respectively. To avoid adsorption effects, only sample containers and filters made of polypropylene were used. For external calibration, high purity ICP-MS standard calibration solutions purchased from Choice Analytical (Thornleigh, NSW, Australia), were diluted in aqueous solution of 3.4 % HNO_3 and 1.5 % H_2O_2. Procedural blank samples (TRIS) were also run to check for potential contamination in the methodological process and came back negligible (<1 %). Digested samples were analysed by flow injection analysis using an Agilent 1200 Series HPLC

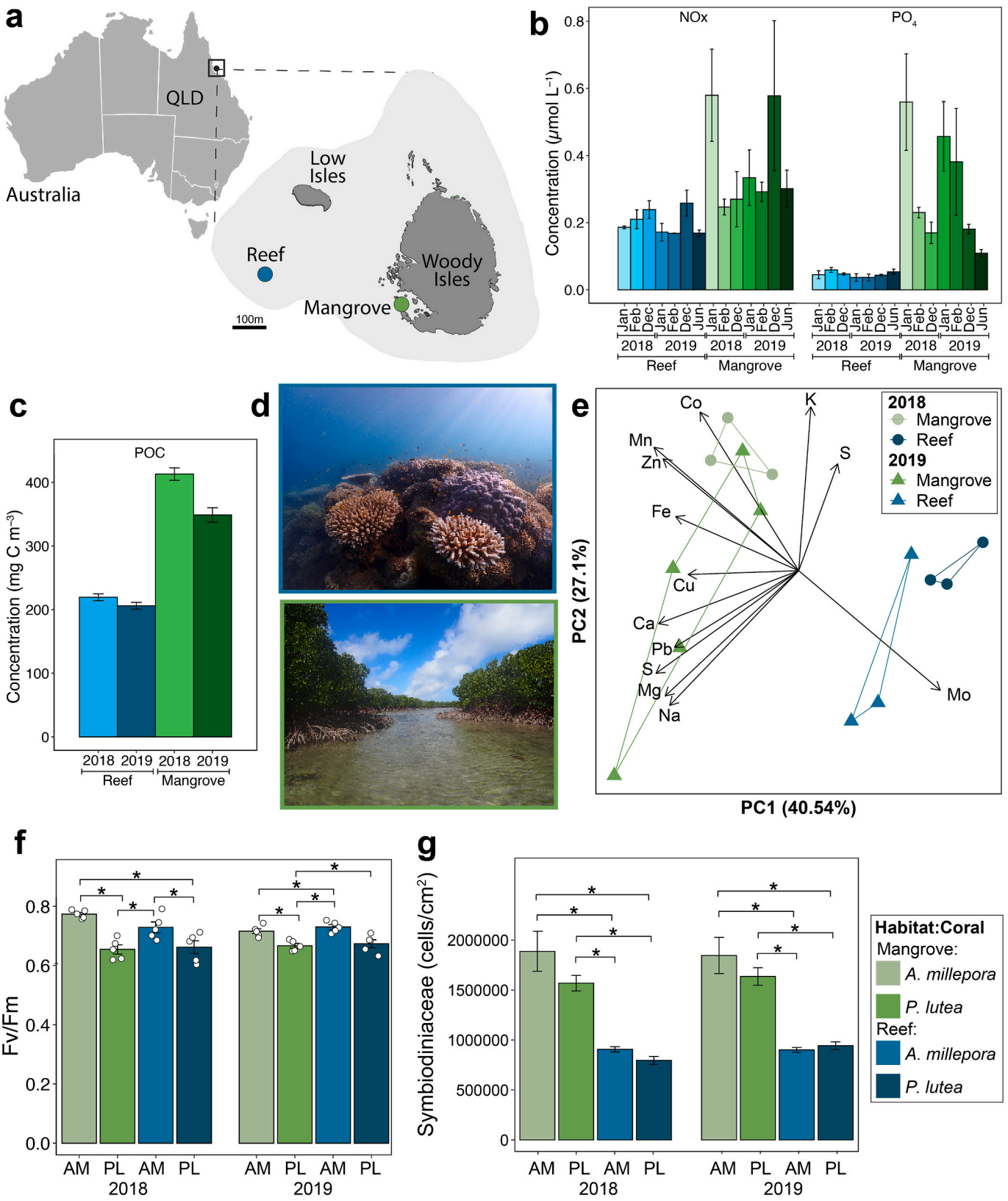

Fig. 1. The Low Isles reef and Woody Isles vegetative mangrove lagoon. (a) A map of the study locations, showing the Low Isles reef site (blue) and the Woody Isles mangrove location (green). (b) Concentration of nutrients NOx and PO_4^{3-} for the reef and mangrove seawaters for both 2018 and 2019 (average with standard error, n = 3-10 spatially collected; see Table S3). (c) Concentration of particulate organic carbon (POC) for the reef and mangrove waters (n = 10 spatially collected; see Table S3), (d) Figure of Low Isles reef (top) and the Woody Isles mangrove lagoon (bottom). (e) Seawater elementome data for each site and year, with major loadings illustrated as vectors. 13 elements were included in the PCA (of the 19 elements measured) as they were present above detection limits in all sample groups (see Table S7). (f) *Fv/Fm* of the corals in both habitats at the time of sampling with SE and * denotes significant differences between groups ($p < 0.05$) while the circles represent individual data points, (g) Symbiodiniaceae cell counts for the corals with SE and * denotes significant differences between groups ($p < 0.05$).

Table 1
Summary of abiotic conditions at Woody Isles mangrove lagoon demonstrating the extreme and highly dynamic nature of the site. Data presented are reported ranges in mean values from prior published studied. The data for the present study is mean ± standard error ($n = 20$).

Study	Temperature (°C)	pH	O_2 (mg L^{-1})	Salinity	Dates
Camp et al. 2019	22.6–28.3	7.828–7.871	3.02–3.19	32.5–33.9	2017–2018
Haydon et al. 2021	28–28.2	7.74–7.81	2.5–4.1	33.9–34.2	2018–2019
Chiara et al. In review	15.1–35	5.83–8.81	NA	NA	2022–2023
Present study	28.48 ± 0.20	7.789 ± 0.17	3.04 ± 0.03	33.5 ± 0.02	2018
Present study	28.92 ± 0.15	7.695 ± 0.01	3.28 ± 0.06	33.8 ± 0.03	2019

system coupled on-line with an Agilent 8900 series ICP-MS/MS instrument (Santa Clara, CA, USA). The injection volume was 20 μL and blanks were run periodically to ensure the absence of carry over and cross-contamination. Limits of detection were calculated according to the 3-sigma criterion.

Water samples (10 mL) were processed by ALS Analytical laboratories, Sydney, Australia. Trace elements were acidified overnight with ultra-pure HNO_3 prior to ICP-MS analysis on Agilent 7700/7900× ICPMS instrument. If dilutions were required, they were done in ultra-pure water. For every 20 samples run, a method blank, laboratory control, duplicate sample comparison, and one matrix spike sample were undertaken to ensure quality control of the analysis.

Macronutrient concentrations of NOx, NH_4^+ and PO_4^{3-} were analysed using a Flow Injection Analyser (Lachat Quikchem, 8500MkII) at the University of Technology Sydney. Duplicates were run on each sample (14 mL).

2.3.1. Coral elemental mapping

Elemental maps of select coral samples were collected to investigate the distribution of elements within each sample. At the UTS lab, corals were washed with filtered seawater to remove any mucus of potential debris. Coral samples were cut with a diamond saw and washed again prior to being embedded in epoxy resin and polished to ensure optimum analysis conditions. LA-ICP-MS analyses were performed on an Elemental Scientific Lasers ImageBIO 266 (Kennelec Scientific, Mitcham, Victoria, Australia), connected to an Agilent Technologies 7900 Series ICP-MS (Agilent Technologies, Mulgrave, Victoria, Australia). The laser ablation and ICP-MS conditions were optimised on NIST 612 Trace Element in Glass CRM to achieve maximum sensitivity while minimising oxide formation (ThO/Th < 0.3 %, as shown in Table S1), employing H_2 as a collision gas to mitigate interferences. Pew^2 was used to reconstruct the images (https://doi.org/10.1021/acs.analchem.1c02138). For synchrotron x-ray fluorescence microscopy, the coral was thin sectioned without embedding in epoxy and polished with SiC papers into free-standing 400 μm sections. Samples were analysed at the Australian Synchrotron using an 18.5 keV beam focused to 6 μm. The x-ray fluorescence emitted from the coral sections was collected with Maia 384 channel detector. The elemental maps were reconstructed from the full emission spectra with GeoPIXE v6.6 (CSIRO, Australia).

2.3.2. Quantification and statistical analysis

All statistical analyses were conducted in R (version 4.2.3, (R Core Team, 2013). Prior to statistical analyses, elemental content data were square root transformed to reduce heteroscedasticity of the data, outliers were identified in each sample (Grima et al., 2022; Reich et al., 2021) with the *rstatix* package (version 0.7.2, (Kassambara, 2023) and subsequently the value for that element was removed from the corresponding sample (tissue: $n = 62$ and algae: $n = 54$, water: $n = 13$, detailed in Table S2). If an element was below the detection limit of the quantification equipment the value was regarded as $1E^{-10}$. Missing values generated by the removal of outliers were imputed by applying a principal component method with the *imputePCA* function of the *missMDA* package (version 1.18, (Josse and Husson, 2016). For each year (2018, 2019) and for both species (*P. lutea*, *A. millepora*) and habitats (mangrove lagoon, reef) a principal component analysis (PCA) was conducted on the elemental content of the algal symbiont and host tissue separately using the *prcomp* function of the *stats* package (version 4.2.3, (R Core Team, 2013). The PCAs were visualised with the *autoplot* function in the *ggplot2* package (version, 3.4.4, (Wickham et al., 2016) by plotting the first two principal components (PC1 and PC2). The significance of PC1 and PC2 was tested using an Analysis of Variance (ANOVA; *stats* package version 4.2.3, R Core Team, 2013) or Aligned Rank Transformed ANOVA (ART-ANOVA; *art* function of the *ARTool* package, version 0.11.1, (Wobbrock et al., 2011) (dependent on the normality and variance of each element) for tissue and algae in 2018 and 2019 separately. Complementary density plots for PC1 and PC2 were generated to display the biogeochemical niche for each coral species' algal symbiont and host fractions in both habitats. The overlapping coefficient of the PC1 and PC2 density plots for each coral species' algal symbiont and host fractions in both habitats was calculated with the *overlap* function of the *overlapping* package (version 2.1, (Pastore, 2018).

Elementome profiles for the algal symbiont and host tissue for both species in both habitats (for each of 2018 and 2019) were further visually represented with radar plots using the *radarchart* function from the *fmsb* package (version 0.7.5, (Nakazawa, n.d.). Differences in content between algal symbiont and host tissue for each element were assessed with fold change analysis of host to symbiont elemental concentration. For radar plot and line graph visualisations element concentration and fold change ratios were $\log_{10}$ transformed to homogenise variance between macro- and micronutrients.

To test for differences in elemental content (μg/cm^2 or ng/cm^2) between coral species (*P. lutea*, *A. millepora*), habitats (mangrove lagoon, reef) and combination of both, ANOVA or ART-ANOVA analysis were applied (dependent on the normality and variance of each element) for both tissue and algae in 2018 and 2019 separately. Normality and homogeneity of variance was assessed for each element using Shapiro-Wilk and Levene's tests respectively. Post-hoc analysis was then conducted via Tukey's Honestly significant difference (HSD) test or ART-contrasts (ART—C) for parametric and non-parametric data respectively. To test significance of differences in elemental content (μg/cm^2 or ng/cm^2) between years (within a habitat or within a species) Dunn's test with Benjamini Hochberg *p*-value correction was used.

Finally, we assessed whether the ratio of each element in seawater from the reef to mangrove lagoon was comparable to the difference in cellular elemental content of both symbiotic algae and host tissue for each coral species between habitats (reef:mangrove_lagoon). With this analysis we examined whether differences in environmental elemental content matched differences in coral elementome between habitats.

3. Results

3.1. Mangrove lagoon waters are nutrient rich compared to the reef location

Across both years, and all months of sampling, the mangrove lagoon waters were enriched in PO_4^{3-} and NOx relative to the reef water, although differences in NOx were non-significant in 2018 (Fig. 1b, Table S5). The mangrove lagoon water was also enriched in Ca, and organic C (Tables S4 & S6) characteristic of a more eutrophic system compared to the reef. POC was also higher in the mangrove lagoon

waters relative to reef waters across both years ($p < 0.01$, Tables S3, S5, Fig. 1c). Furthermore, four trace metals (Fe, Co, Mn, Zn) were also enriched in the mangrove waters, while the remaining elements had similar concentrations between habitats (Tables S4 & S6). Across the two years, elemental composition was consistent for the reef water with few elemental or nutritional differences (Fig. 1e, Table S4). In contrast, the mangrove lagoon waters were characterised by higher dissolved organic C in 2019 compared to 2018 (Fig. 1e, Tables S4 & S6). Despite this intra-site annual variation, distinct seawater elementomes were still apparent for each habitat across years (Fig. 1e), driven by elevated Mo in the reef system, and elevated trace elements (e.g., Mn, Zn) in the mangrove system (Table S7). Across both years, significant separation between habitats occurred on Principle Component 1 (PC1, ART-ANOVA, $p < 0.05$, Table S7).

3.2. Physiological condition of mangrove lagoon and reef corals

In 2018, there was no difference in F_v/F_m values at the time of sampling for either coral species between habitats ($p > 0.05$, Fig. 1e). In 2019, a small reduction in F_v/F_m of mangrove corals (*A. millepora* difference of 0.015, *P. lutea* difference of 0.007) relative to the reef corals was evident at the time of sampling ($p < 0.05$, Fig. 1e). Consistent with previous studies (Camp et al., 2019), corals from the mangrove lagoon had a higher density of Symbiodiniaceae cells (ca. 2–4 fold) compared to their reef counterparts ($p < 0.05$, Fig. 1f). However, elemental data were not normalised to per cell for the following analysis to allow direct comparisons between the symbiont and host tissues fractions for biogeochemical niche analysis (e.g., presented as ng cm^2) and to remain consistent with prior studies (e.g., Blanckaert et al., 2022). Interpretation of the following data relative to other datasets should consider the normalisations undertaken as discussed in detail by Matthews et al. (2024).

3.3. Corals have a distinct elementome in the mangrove lagoon

Both *A. millepora* and *P. lutea* exhibited distinct elementomes in the mangrove lagoon compared to Low Isles reef, for both their Symbiodiniaceae (Fig. 2a, c) and tissue (Fig. 2b, d) fractions, and across both 2018 and 2019 (Fig. 2, Figs. S1-S3). The elementomes of corals consistently (across years) differed between habitats for both the host tissue and their Symbiodiniaceae fractions along the Principle Component 1 axis (PC1, ART-ANOVA, $p < 0.05$, Table S8). The elementome tissue fraction for both coral species had separation based on habitat which was driven by higher concentrations of C and N, and lower concentrations of P, S and trace metals (e.g., Fe, Mn, Cd) in the reef corals tissue. The Symbiodiniaceae fraction for both coral species also had elementome separation evident based on habitat (Fig. 2a & c.), with Symbiodiniaceae elementome separation between the two habitats largely due to differences in concentrations of C, K and S (Fig. 2a & c., Supplementary Table S8). Across both years, significant differences in Symbiodiniaceae elementomes between coral species was documented, with PC1 significantly different in 2018, and PC2 in 2019 (ART-ANOVA, $p < 0.05$, Fig. 2, Table S8). Collectively, these findings indicate species-specific and habitat-specific elementomes are consistently present.

Absolute values of elemental content recorded in this study were typically within the same order of magnitude for values previously recorded for corals on the Great Barrier Reef (Blanckaert et al., 2022). Both the tissue and Symbiodiniaceae fractions exhibited the highest elemental content per cm^2 for C and the lowest for the trace metals (e.g., Mo, Sn, Pb, Figs. S1 & S2). Reef coral host fractions had less absolute Mn and Cu and Fe than the mangrove coral host fractions, with some species-specific differences (Fig. 3, Tables S9-S12 and Figs. S1 & S2). The Symbiodiniaceae fraction of reef corals were characterised by less Fe, Ni, Zn across both years, and in 2019, they also had less Ca, Mn, Sr, Se, Co, and Pb than the mangrove Symbiodiniaceae fraction (Fig. 3, Tables S9-S12 and Figs. S1 & S2). Carbon content of both the host tissues and Symbiodiniaceae fractions were consistently higher in the reef corals than the mangrove corals (Fig. 2, Tables S9-S12). Consideration of common stoichiometric ratios (e.g., Redfield ratio; Redfield, 1934), revealed a lower C:N:P of the tissues fractions in both habitats (mangrove corals: 22:8:1, reef corals: 260:27:1) than the Symbiodiniaceae fractions (mangrove corals: 1002:206:1, reef corals: 3574:541:1). For both the tissue and Symbiodiniaceae fractions, C:N and N:P were higher in the reef corals (host: C:N = 5.7, N:*P* = 46, Symbiodiniaceae: C:N = 6.8, N:*P* = 541) than the mangrove corals (host: C:N = 5.6, N:*P* = 8.0, Symbiodiniaceae: C:N = 4.9, N:*P* = 250).

Radar plots were used to assess the proportional elemental content in the two fractions and revealed that elemental content was not consistently greater for either the host or Symbiodiniaceae fractions for either coral species in 2018 or 2019 (Fig. 3). This finding highlighted differences between resource sharing within the holobiont across years and for each coral species. A notable observation was high Cu in the tissue rather than Symbiodiniaceae fraction of the mangrove corals (Fig. 3). LA-ICP-MS mapping of the elemental content for *P. lutea* revealed highly heterogeneous distribution of elements, such as Cu, across the coral colony (skeleton to host tissue layers) but also within regions (e.g., within the host tissue layer (Fig. 4b-d). XFM analysis also confirmed heterogeneity of elements across a region (Fig. 4e-f), with the higher resolution imagery supporting the ICP analysis, whereby many trace metals were concentrated in the Symbiodinicaeae cells rather than the host tissue or skeleton layers (Fig. 4g).

3.3.1. Unique biogeochemical niche of mangrove lagoon corals

Complementary density plots for PC1 and PC2 revealed some overlap in predicted biogeochemical niche (BN) between coral species from both habitats, for both the host and Symbiodiniaceae fractions in 2018 and 2019 (Fig. 5a & c). Greatest overlap in BN was observed in PC1 for the host tissue of the two coral species in the mangroves in 2018 (Fig. 5b, overlap of 94.56 %). Smallest overlap occurred in the Symbiodiniaceae fraction of *P. lutea* from the mangroves and *A. millepora* in the reef in 2018 (Fig. 5a, overlap of 0.004 %, Table S13). For both coral species, in general (*P. lutea* tissue in 2018 being the exception) least overlap occurred in PC1 between reef and mangrove corals, with at least 25 % difference in predicted BN space, and an average of 79.5 % difference in predicted BN space, for both the host and Symbiodiniaceae fractions, suggesting variance in the multidimensional space occupied by the characteristic concentrations of elements of each species between the reef and mangrove habitats.

3.3.2. Coral elementome data were not proportional to the seawater elementome

At each timepoint, discrete water samples were collected to provide a snapshot of the mean dissolved seawater elementome of each habitat, noting that elemental forms were not assessed (e.g., bioavailable versus non-bioavailable) as per Moore et al. (2013). The ratio of each element in reef relative to mangrove waters was determined (Fig. 6a) and were compared to the corresponding ratio of each element in reef relative to mangrove for either coral tissue or Symbiodiniaceae cellular fractions. The largest difference between reef and mangrove elemental content was typically in the symbiont fraction, with Symbiodiniaceae of mangrove corals often exhibiting higher elemental content (as illustrated by being on the right-hand side of the black dotted line in Fig. 6b-e); this higher content was typically greater than the proportional difference in the seawater between the mangrove and reef suggesting several elements such as Sn, Pb, Co, Cd, Sr were likely bioaccumulated in mangrove corals. For other elements such as Mn and Fe, the higher cellular content in mangrove relative to reef waters, could reflect the higher abundance of the elements in the mangrove waters, albeit proportionally different (Fig. 6a).

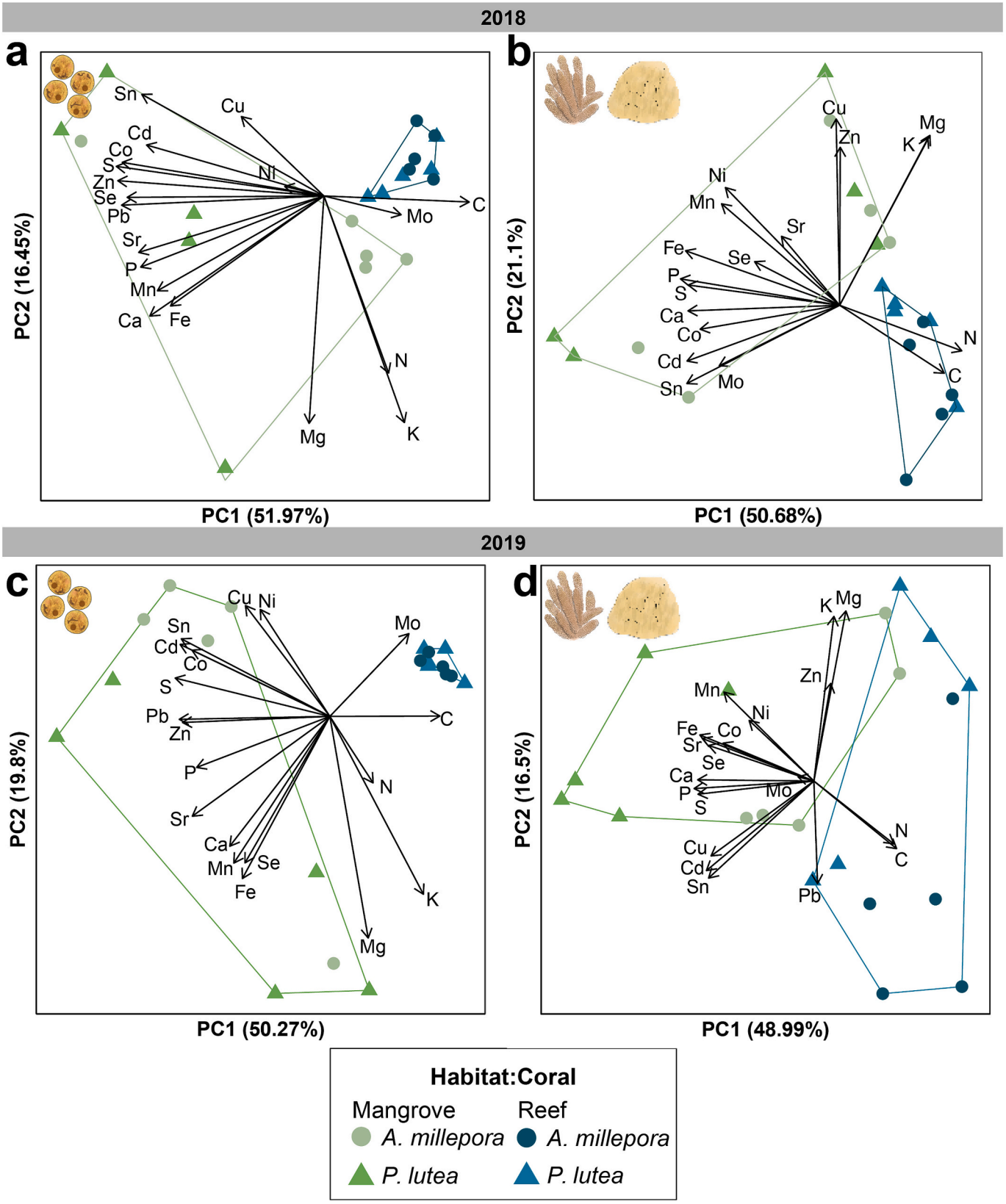

Fig. 2. Principal component analysis (PCA) of macronutrients and trace elements (ng/cm^2), for (**a**) Symbiodiniaceae and (**b**) host tissue of coral species *Acropora millepora* and *Porites lutea* collected from the Woody Isles mangrove lagoon and Low Isles reef habitat in 2018 and (**c**) Symbiodiniaceae and (**d**) host tissue of coral species *Acropora millepora* and *Porites lutea* collected from the Woody Isles mangrove lagoon and Low Isles reef habitat in in 2019.

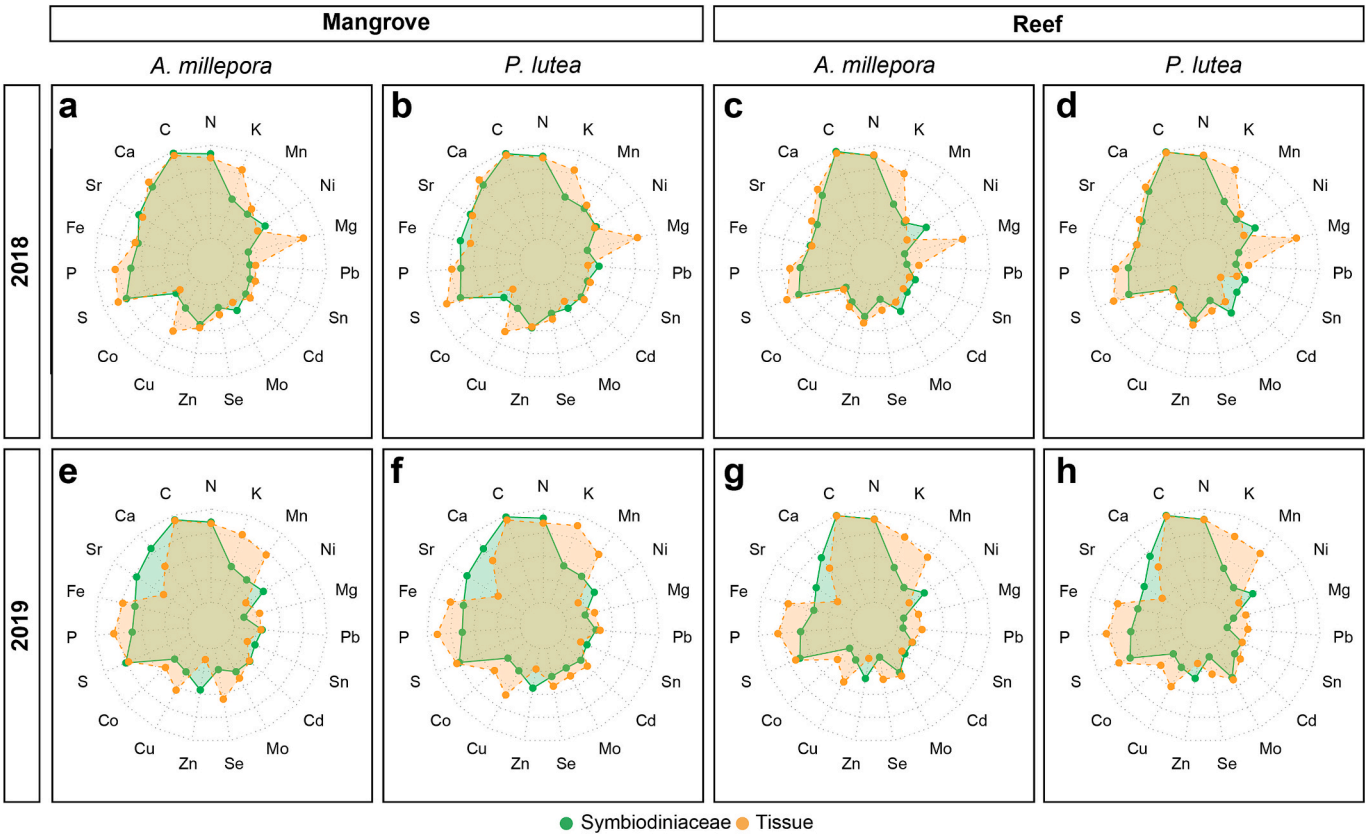

Fig. 3. Radar plots of the elementome profiles of the host tissue and Symbiodiniaceae components of (**a**) *Acropora millepora* and (**b**) *Porites lutea* from the Woody Isles mangrove lagoon in 2018 and 2019 (**e-f**) and (**c**) *A. millepora* and (**d**) *P. lutea* from the Low Isles reef habitat in 2018, and 2019 (**g-h**). Macronutrients and trace elements expressed as ug/cm^2 or ng/cm^2 respectively.

4. Discussion

Vegetative islands are well documented to provide essential nutrients such as nitrates and phosphates to adjacent coral reefs (Benkwitt et al., 2022; De Falco et al., 2022; Doty and Oguri, 1956; Raapoto et al., 2019). Our data here reveals that such islands, notably those with mangrove dominated lagoons, also provide a supply of POC and essential macro- and micronutrients that are available to resident corals. While many mangrove systems are considered uninhabitable for corals due to low light and a lack of suitable substrate, some mangrove lagoons have conditions conducive to coral survival, including systems in the Caribbean (Stewart et al., 2022; Yates et al., 2014), New Caledonia (Camp et al., 2017; Maggioni et al., 2021), and on the Great Barrier Reef (Camp et al., 2019). The highly variable and often extreme conditions found in these vegetative mangrove lagoons has seen resident coral populations described as highly resilient to certain stressors, such as low pH, low oxygen, and highly variable temperatures (e.g. Camp et al., 2018). Work by Haydon et al. (2023) found corals from the Woody Isles mangrove lagoon did not bleach during a transient laboratory heat stress experiment exposing them to an average of 32.7 °C (and daytime peak of 35 °C for 7 days), when their reef counterparts did. Further work by Tanvet et al. (2023) found that mangrove corals from New Caledonia under experimental conditions maintained higher rates of coral calcification under low pH than their reef counterparts. While not immune to stress (Alessi et al., 2024; Bartels et al., 2023), and with noted trade-offs to survival in these hostile conditions sometimes reported (Scucchia et al., 2023), physiological plasticity to diversify energy acquisition has been proposed as a driver supporting coral survival in these systems and their superior performance under periods of stress (Camp et al., 2018; Denis et al., 2024). For example, enhanced heterotrophic potential due to elevated levels of organic carbon was postulated to support corals surviving in the hostile environmental conditions of the Bouraké mangrove lagoon in New Caledonia (Camp et al., 2017). Our data here supports the notion of higher heterotrophic potential due to the elevated POC measured in the Woody Isles lagoon, however, future work directly measuring rates of heterotrophy is recommended. Furthermore, our results demonstrate greater resource availability for resident corals in terms of NOx, PO_4^{3-} and many essential and non-essential micronutrients.

4.1. Nutrient enriched waters of the Woody Isles vegetative mangrove lagoon

Mangrove waters can be high in nutrients due to ground water input, leaf litter decomposition and from faeces of local animal populations (Kristensen et al., 2008). However, whether mangrove waters act as a net source or sink of nutrients depends on factors including the input of terrestrial or oceanic nutrients, changes in redox conditions, anthropogenic inputs, local environmental conditions such as weather, tidal conditions, and the mangrove community composition (Adame et al., 2010; Adame and Lovelock, 2011; Kristensen et al., 2017; Matos et al., 2022). Our observations suggest that the water of Woody Isles are typically nutrient rich compared to the neighbouring Low Isles reef, despite local tidal forcings likely to exchange nutrients between the Woody Isles mangrove lagoon and Low Isles reef (Hamylton et al., 2019). Dissolved organic carbon levels were only slightly elevated in the mangrove lagoon relative to Low Isles reef, supporting the likely outflow of mangrove derived nutrients to the reef. Notably however, POC was a lot higher in the mangrove lagoon, suggesting greater retention of particulate matter within the mangrove system. Woody Isles has an estimated 25,000 migrating pied imperial pigeons between November and March, which along with the normal resident bird populations are likely

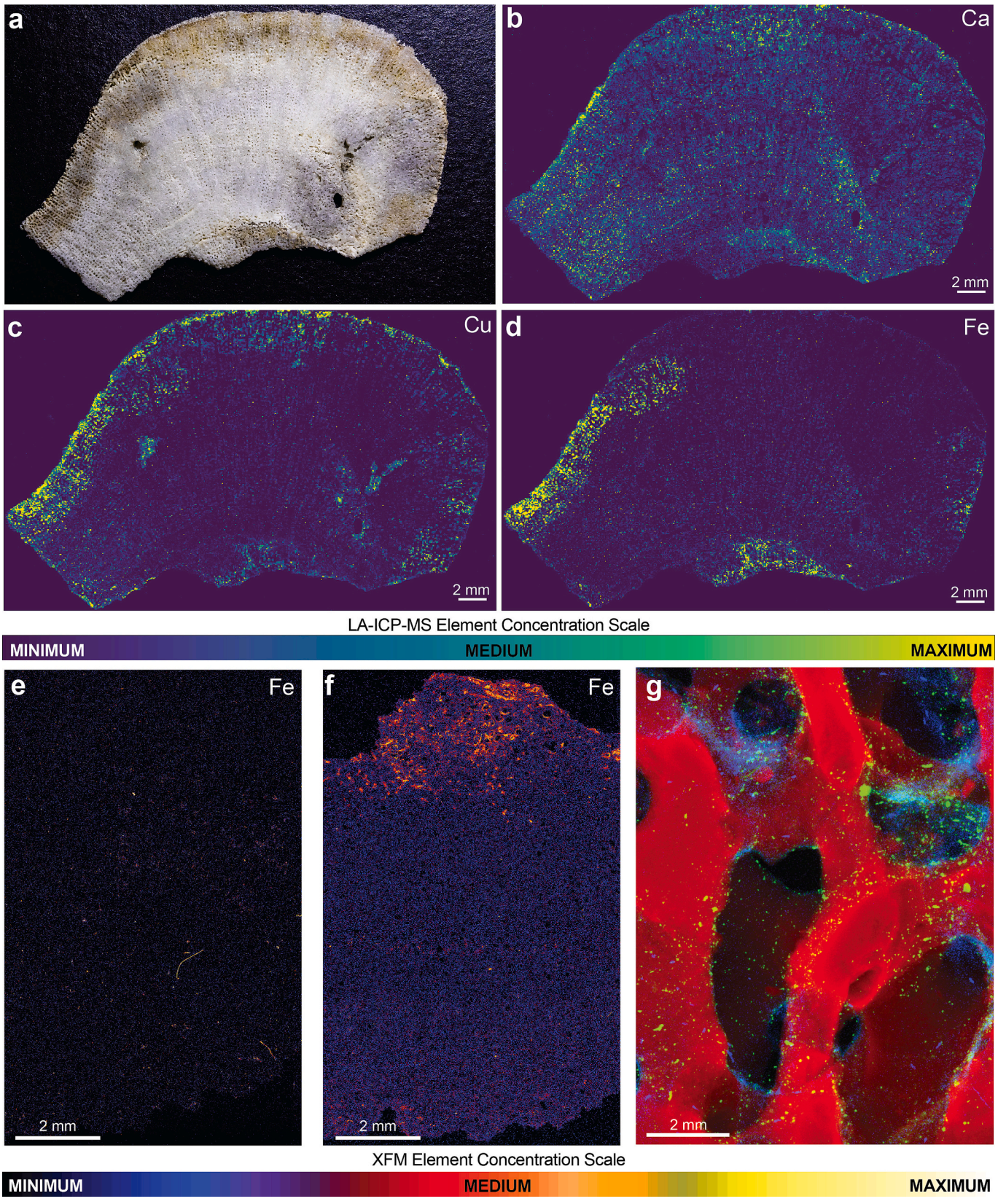

Fig. 4. Elemental maps of *Porites lutea* (a) shows the light image prior to analysis, (b) a map of Ca in *P. lutea* from Low Isles reef, produced using LA-ICP-MS (c) a map of Cu in *P. lutea* from Low Isles reef, produced using LA-ICP-MS (d) a map of Fe in *P. lutea* from Low Isles reef, produced using LA-ICP-MS. The image units are in counts for b-d. (e) a map of Fe distribution in *P. lutea* from the Low Isles reef produced using XFM, (f) a map of Fe distribution in *P. lutea* from vegetative mangrove lagoon produced using XFM, (g) a map of Calcium (red); Copper (green); Bromine (blue) overlaid for *P. lutea* from the Low Isles reef produced using XFM.

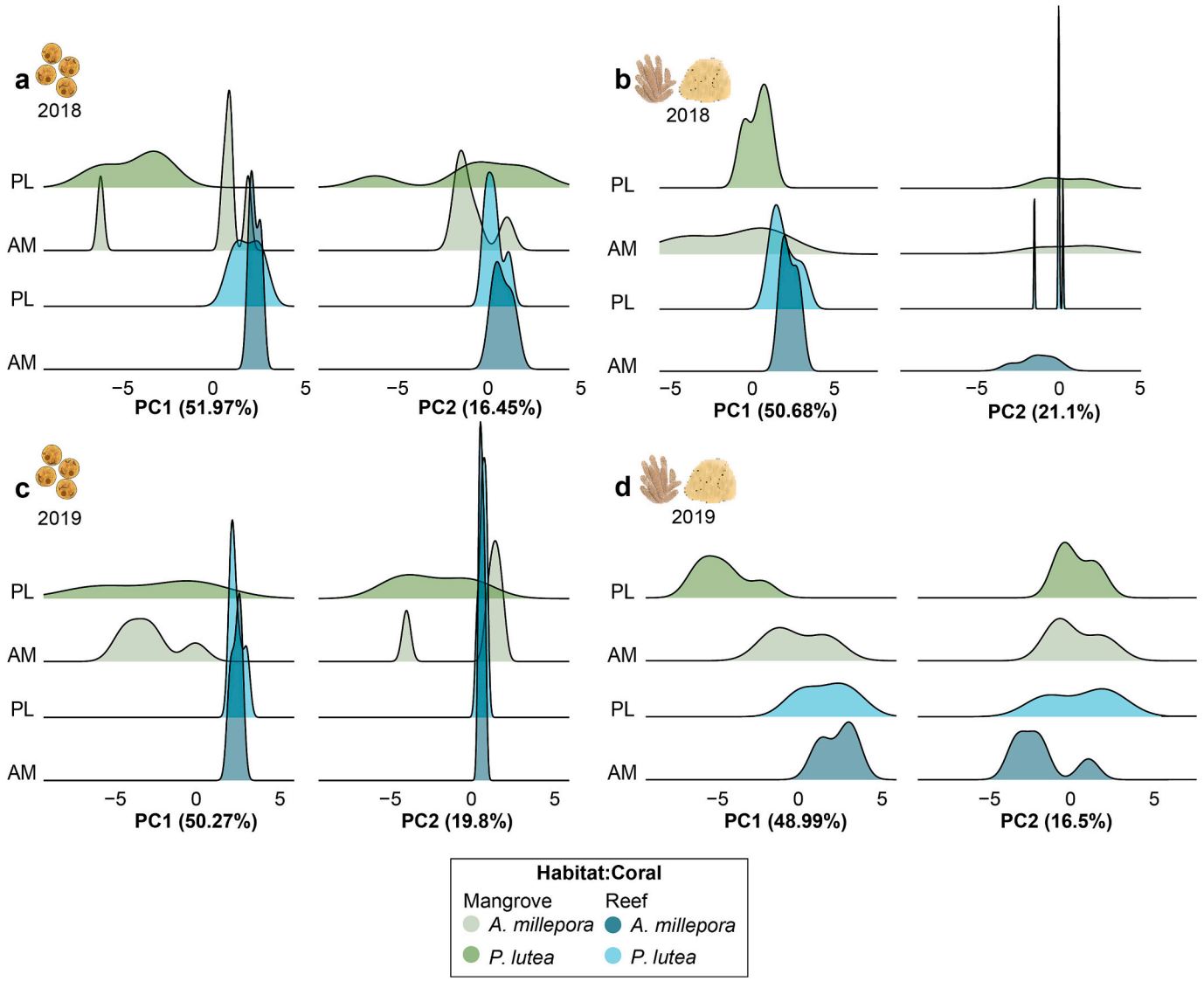

Fig. 5. Elementome data presented as density plots for PC1 and PC2 to display the theoretical biogeochemical niche for each coral species' (*Porites lutea* and *Acropora millepora*) algal symbiont and host fractions in both habitats (Low Isles reef and Woody Isles mangrove lagoon). The overlapping coefficient of the PC1 and PC2 density plots for each coral species' algal symbiont and host fractions in both habitats was calculated with the overlap function of the overlapping package (version 2.1, (Pastore, 2018)) and are presented in Table S13.

to contribute significant nutrients into the system. Water samples collected in June (outside of the migratory pigeon period) had lower NOx and PO_4^{3-} for both the mangrove and reef sites than the samples collected between December and February (inside the migratory pigeon period). Notably, the mangrove lagoon waters still had higher NOx and PO_4^{3-} than the reef waters in June, supporting the notion of elevated nutrients within the lagoonal system. Other island systems have documented the important role birds play as local nutrient sources (Benkwitt et al., 2022; Graham et al., 2018; Savage, 2019), with stable nitrogen isotopic data suggesting corals can assimilate guano-derived nitrogen on a local scale (Lorrain et al., 2017). In the study by Lorrain et al. (2017) high NOx concentrations were found at sites close to seabird populations which is concurrent with our data – and in combination with stable nitrogen isotopic data – these authors concluded that bird guano likely nitrogen enriched the base of the marine ecosystem.

In our current study C:N was lower for mangrove corals, primarily due to higher carbon content in the reef corals. While POC was higher in the mangrove system and could contribute to the resident corals energetic needs, it did not translate to elevated carbon content of the coral. Mangrove corals in Woody Isles (Camp et al., 2019) have been documented to have higher respiration rates which could in part explain their lower carbon content. Furthermore, previous studies on *Pocillopora acuta* from Woody Isles mangrove lagoon found their Symbiodiniaceae fix and translocate less carbon (29.88 % less) than their reef counterparts, corresponding with reduced rates of gross photosynthesis per cell. Under suboptimal environmental conditions, such as those experienced in Woody Isles mangroves, reduced carbon availability could increase the relative availability of nitrogen in the holobiont, thereby supporting higher symbiont densities which compete with the host for available environmental ammonium (Rädecker et al., 2023), as well as other key resources (Tansik et al., 2017).Whether the reduced carbon in mangrove corals limits access to available ammonium would require further investigation, but the high Symbiodiniaceae densities reported in our current study, and our previous work (Camp et al., 2019; Ros et al., 2021), supports the hypothesis from Rädecker et al. (2023).

Beyond enrichment of macronutrients, the mangrove waters were also enriched in several essential trace elements, including Fe, Mn, Co and Zn and non-essential elements such as Pb and Cd. Bird guano can be high in metals, including potentially toxic metals such as Cd, which could explain the enrichment of these metals within the Woody Isles

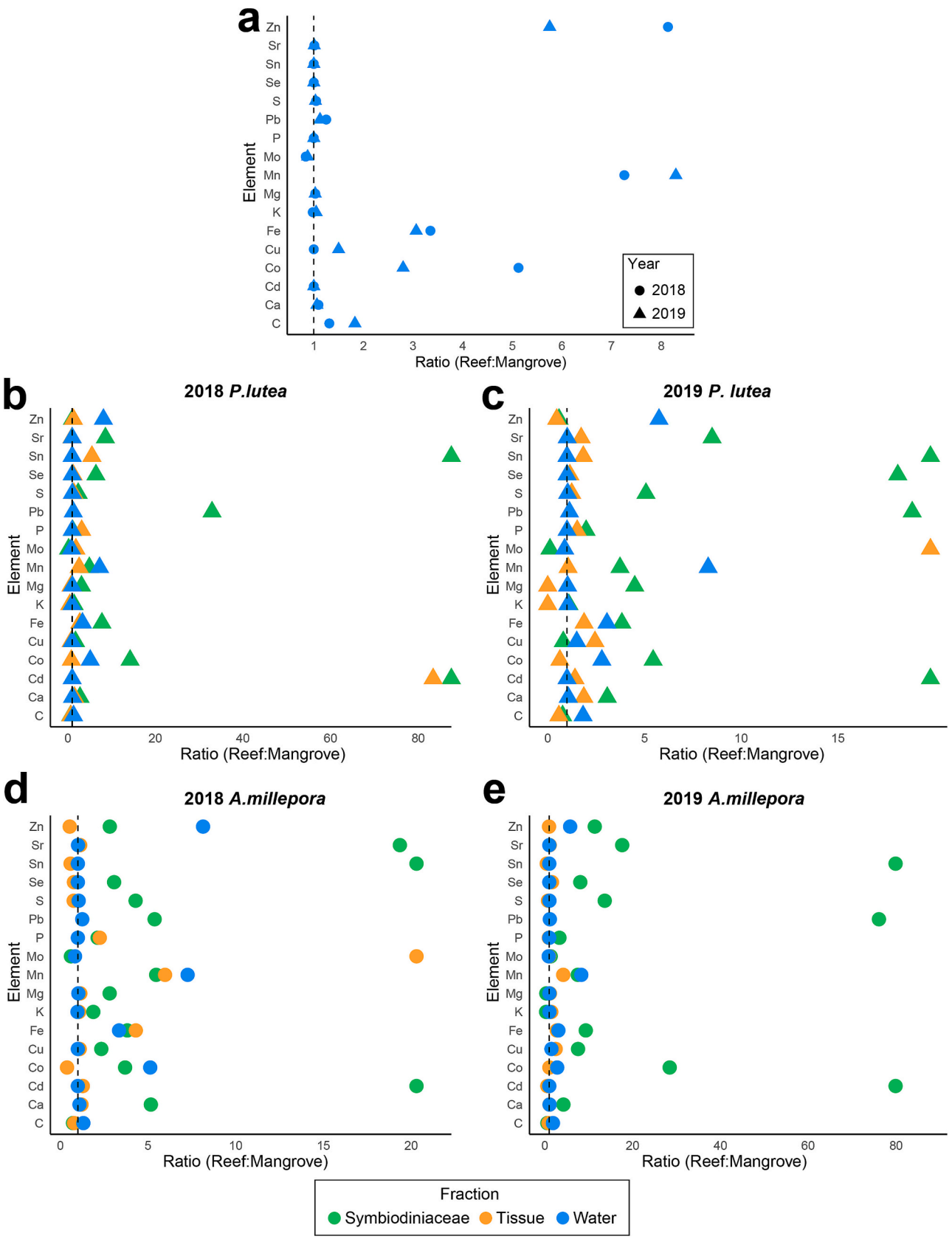

Fig. 6. Proportion plots for elemental content in the reef versus mangrove lagoon corals (host tissue and Symbiodiniaceae fractions) and seawater. The black dotted line represents a 1:1 ratio of elements in both the reef and mangrove lagoon. Any dots on the righthand side of the plot indicate higher elemental content in the mangrove lagoon than the reef. (a) ratio of reef-to-mangrove seawater elemental content, (b) ratio of reef-to-mangrove seawater and coral elemental content for *P. lutea* in 2018 and (c) 2019, (d) ratio of reef-to-mangrove seawater and coral elemental content for *A. millepora* in 2018, and (e) 2019.

mangrove waters (De La Peña-Lastra et al., 2022). Mangrove lagoons can also be enriched in metals due to early diagenetic processes (Berner, 1980), environmental contamination (Alderton, 1985), and vegetation acting as sediment traps that can settle and suspend associated metals (Ca Çador et al., 1996). Furthermore, mangrove roots can uptake mineral nutrients and other cations and anions (Ernst, 1990). To minimise toxicity, particularly to metals, mangroves have developed detoxification strategies which include preferential metal fixation within root tissues, metal exclusion through rhizosphere oxidation, and the formation of metal-rich mineral deposits commonly referred to as iron plaques (Chai et al., 2022; Machado et al., 2005). A study of iron plaques in Brazil found the plaques were high in Fe, Mn and Zn, with an estimated average concentration of 12,370, 500, and 59 μg g^{-1} respectively (Machado et al., 2005); notably these were three metals enriched in the Woody Isles mangrove lagoon waters and resident corals. Iron plaques have been documented to influence the bioavailability of nutrients (including impacting C, N and P cycles) and metals in mangroves and surrounding waters (Fan et al., 2023). Future work examining mangrove iron plaques would further our understanding of their specific contribution to coral nutritional ecology in these extreme systems.

4.2. Mangrove corals had a distinctive elementome

Across both years and for both coral species, distinctive habitat-specific coral elementomes were evident. Reef corals had higher carbon content in both their tissue and algal symbionts and a higher C:N. Ratios of C-to-N are indicative of cellular storage, where higher C:N indicates greater storage capacity for reef than mangrove corals in our study (Szmant et al., 1990). Many trace elements were elevated in the mangrove corals in line with elevated values in mangrove waters, supporting the proposal that vegetative mangrove lagoons supply essential elements to resident coral taxa. While mangrove coral elementomes did not proportionally match the mangrove lagoon seawater elementome this is to be expected given that seawater elementome analysis did not account for elemental bioavailability, particulate matter, and coral homeostasis (Reich et al., 2023). Yet, there were some notable similarities between the mangrove coral and the mangrove seawater elementomes, with enrichment in Mn and Fe observed relative to the reef coral and reef water elementomes. In laboratory testing, the coral *Stylophora pistillata* supplemented with non-toxic concentrations of Mn (4.1 μg L^{-1}) maintained photosynthesis and did not bleach under thermal stress compared to control colonies without Mn additions (Biscéré et al., 2018). The same outcome was observed when both Mn and Fe (at 3.0 μg L^{-1}) were supplemented together, but not when Fe was supplemented alone (Biscéré et al., 2018). We hypothesise therefore that the elevated Mn found in the mangrove waters contributes to coral survival in the harsh conditions due to its essential role in cellular respiration, cell stress responses (e.g. superoxide dismutase) and photosynthesis (Biscéré et al., 2018; Ferrier-Pagès et al., 2018; Montalbetti et al., 2021; Reich et al., 2023).

Mangrove corals also had elevated concentrations of Pb, Cd and Sn in their Symbiodiniaceae compared to reef corals in both 2018 (note the elevated Sn was not significant in 2018) and 2019. Symbiodiniaceae have previously been documented to bioaccumulate both essential and non-essential metals in the holobiont (Ranjbar Jafarabadi et al., 2018; Reichelt-Brushett and McOrist, 2003) and are postulated to have a higher tolerance for metal bioaccumulation than the animal host (Peters et al., 1997). Prior studies have hypothesised that variability in holobiont trace metal concentrations may be a result of Symbiodiniaceae densities (Esslemont, 1999). The mangrove corals in our study had greater Symbiodiniaceae cell density which could explain the higher elemental content reported. The higher bioaccumulation of non-essential and potentially toxic elements in the mangrove corals poses a potential risk to the resident corals, highlighting that along with the harsh abiotic environmental conditions previously documented for resident corals (e.g. elevated temperature variability, low pH and low oxygen levels), the corals also have more extreme nutrient conditions to contend with. The distinct elementome of mangrove corals irrespective of coral species therefore supports the notion that coral phenotypes exist in extreme environments like those occurring in terrestrial systems (Jeyasingh et al., 2014).

4.3. Elementome heterogeneity within the coral holobiont

Data presented here revealed elementome heterogeneity between and within components of the coral holobiont. Increased abundance of elements within the host or symbiont fraction was not consistent between coral species or years, with some exceptions. For example, K was always elevated in the host regardless of any experimental factor. When ratios of elements were considered, C:P and N:P were higher in the Symbiodinaceae than the host fractions, a finding also observed by Blanckaert et al. (2020) and Grima et al. (2022). High N:P and C:N in Symbiodiniaceae suggests they are likely P limited (Blanckaert et al., 2020). The C:N:P values for the host fractions were comparable to those found in previous coral studies, however the C:N:P values for Symbiodiniaceae fractions were higher (Blanckaert et al., 2020; Grima et al., 2022), but still within ranges previously reported for other taxa (see Table 1 in Fernández-Martínez (2022)).

The elemental LA-ICP-MS and XFM mapping for *P. lutea* revealed heterogeneity in how resources were distributed across the coral holobiont, including within the host tissue layer. For the trace metals, the heterogeneity across the host tissue layer likely reflects different distribution densities of Symbiodiniaceae. While this study was not designed to ascertain the cause of this heterogeneity it would be a logical area for future study and highlights the importance of considering sample collection location within sampling design. Prior work on *Pocillopora* has revealed differences in elemental content between colony branches (Esslemont et al., 2000), supporting the data found here.

4.4. The biogeochemical niche of corals in vegetative islands

The biogeochemical niche is characterised by the multivariate space generated by a species elementome (Peñuelas et al., 2008). How plastic a species biogeochemical niche is across environments is predicted to impact how that species can respond to disturbances (Peñuelas et al., 2008, 2019). Our data suggested that both coral species have plasticity in their biogeochemical niche, supporting their survival in the altered abiotic conditions of extreme vegetative mangrove lagoons. Concurrent with prior work (Grima et al., 2022), the coral host tissue versus Symbiodiniaceae fractions had greater differences in their biogeochemical niche space than the coral species. A notable observation for both the host and Symbiodiniaceae fractions of both coral species, was the greater variance in the occupied biogeochemical niche space when originating from the mangrove lagoon (illustrated in both Figs. 2 and 5). Such a trend reflects the more heterogenous elementomes of corals originating from the mangroves; whilst many trace elements were elevated in the mangrove corals, not all trace elements were typically elevated in all mangrove replicates. Further work is therefore required to understand the implications of this heterogeneity at the community level and the role elementome plasticity may play in supporting coral survival in extreme environments.

5. Conclusions

While previous studies have documented corals persisting in extreme systems such as vegetative mangrove lagoons, data here shows coral survival in vegetative mangrove lagoons is concurrent with altered nutritional supply (POC, macro and micro nutrients) that results in a unique coral elemental phenotype and biogeochemical niche. Our data sheds new light on the plasticity of the coral elementome, and further highlights the crucial role of vegetative island systems in the survival of coral reefs, underscoring the need for conservation efforts to include cross-ecosystem protection strategies.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179455.

CRediT authorship contribution statement

Emma F. Camp: Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David Clases:** Writing – review & editing, Methodology, Formal analysis. **David Bishop:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Annette Dowd:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation. **Samantha Goyen:** Writing – review & editing, Formal analysis, Data curation. **Raquel Gonzalez de Vega:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Paige Strudwick:** Writing – review & editing, Visualization, Formal analysis, Data curation, Statistical Analysis. **David J. Suggett:** Writing – review & editing, Validation, Supervision.

Declaration of competing interest

All authors declare no competing interests.

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Data availability

All raw data can be found here: https://tinyurl.com/elementomedata

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