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ARTICLE

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Fish feces reveal diverse nutrient sources for coral reefs

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Abstract

Consumers mediate nutrient cycling through excretion and egestion across most ecosystems. In nutrient-poor tropical waters such as coral reefs, nutrient cycling is critical for maintaining productivity. While the cycling of fish-derived inorganic nutrients via excretion has been extensively investigated, the role of egestion for nutrient cycling has remained poorly explored. We sampled the fecal contents of 570 individual fishes across 40 species, representing six dominant trophic guilds of coral reef fishes in Moorea, French Polynesia. We measured fecal macro- (proteins, carbohydrates, lipids) and micro- (calcium, copper, iron, magnesium, manganese, zinc) nutrients and compared the fecal nutrient quantity and quality across trophic guilds, taxa, and body size. Macro- and micronutrient concentrations in fish feces varied markedly across species. Genera and trophic guild best predicted fecal nutrient concentrations. In addition, nutrient composition in feces was unique among species within both trophic guilds (herbivores and corallivores) and genera (*Acanthurus* and *Chaetodon*). Particularly, certain coral reef fishes (e.g., *Thalassoma hardwicke*, *Chromis xanthura*, *Chaetodon pelewensis* and *Acanthurus pyroferus*) harbored relatively high concentrations of micronutrients (e.g., Mn, Mg, Zn and Fe, respectively) that are known to contribute to ocean productivity and positively impact coral physiological performances. Given the nutrient-rich profiles across reef fish feces, conserving holistic reef fish communities ensures the availability of nutritional pools on coral reefs. We therefore suggest that better integration of consumer egestion dynamics into food web models and ecosystem-scale processes will facilitate an improved understanding of coral reef functioning.

KEYWORDS
consumers, coral reefs, egestion, feces, nutrient cycling, reef fish

INTRODUCTION

Nutrient cycling is important in driving ecosystem function and sustaining biological diversity (Cherel et al., 2011; DeAngelis et al., 1989; Ratnarajah et al., 2014; Stears et al., 2018; Williams et al., 2018). Animals cycle nutrients by sequestering, transporting, transforming, and releasing nutrients as waste products by excretion (elimination of

assimilated food) and egestion (elimination of unassimilated food) (Atkinson et al., 2017; Vanni, 2002). For example, wildebeest transport nitrogen across the Serengeti, while baleen whales concentrate and deposit trace metals in pelagic waters (McNaughton et al., 1988; Ratnarajah et al., 2014). However, biodiversity loss is increasing at an alarming rate due to local and global disturbances with the potential to alter system-wide nutrient dynamics (Barnosky et al., 2011; Pereira et al., 2012). Despite the importance of animals in cycling nutrients across many ecosystems, we know remarkably little about how individual species within communities and their associated traits (e.g., taxonomy, diet) may influence their role for system-wide nutrient cycling (but see Allgeier et al., 2017; Peters et al., 2019; Wing et al., 2021). This is particularly true in highly diverse ecosystems such as coral reefs, which host a quarter of the global marine biodiversity (Carpenter et al., 2008; Plaisance et al., 2011).

Coral reefs are among the most productive ecosystems on Earth (Hatcher, 1988). In these oligotrophic systems, primary producers take up dissolved inorganic nutrients as rapidly as they are released because near-reef concentrations are typically low (Souter & Lindén, 2000). Hence, nutrient cycling by consumers is vital in maintaining high productivity (Allgeier et al., 2017; De Goeij et al., 2013). Coral reef fishes comprise some of the highest biomass of consumers on coral reefs (Jackson et al., 2001; Sorokin, 1993), and their high biodiversity (e.g., taxonomic and functional diversity) can sustain critical ecosystem processes (Brandl et al., 2019; Lefcheck et al., 2019). Fish are involved in important top-down ecosystem functions, including predation and the removal of algae and detritus (Bellwood et al., 2004; Brandl et al., 2019; Green & Bellwood, 2009; Schiettekatte et al., 2022; Tebbett et al., 2022). However, reef fishes also support coral reefs via bottom-up processes by supplying inorganic nutrients (nitrogen [N] and phosphorus [P]) to the reef ecosystem via excretion and egestion (Allgeier et al., 2017; Burkepile et al., 2013; Holbrook et al., 2008; Meyer et al., 1983). In fact, schooling fish that shelter within corals may stimulate coral growth by up to 21% through the provisioning of N and P (Meyer & Schultz., 1985), and these nutrients may enhance resistance to thermal stress in corals (Chase et al., 2018; Shantz et al., 2023).

Although much focus has been on the inorganic nutrients derived from fish excretion (Allgeier et al., 2017; Burkepile et al., 2013; Munsterman et al., 2021; Schiettekatte et al., 2022), fish feces (via egestion) also harbor key nutrients (Bray et al., 1981; Pinnegar & Polunin, 2006) that may play significant roles in coral reef ecosystem functioning (Meyer & Schultz, 1985; Rempel et al., 2022; Schiettekatte et al., 2023; Williams et al., 2018). The scarce literature available on the subject suggests that coral reef fish feces may contain macronutrients (i.e., proteins, carbohydrates, lipids) and micronutrients (e.g., zinc, iron, magnesium) that vary in concentration across species and trophic guilds, which may greatly alter the value of fecal material for other organisms (Bailey & Robertson, 1982; Crossman et al., 2005). However, this has only been investigated across a small number of reef fish species. It stands to reason that the identity and concentration of both macro- and micronutrients in feces (hereinafter referred to as the "nutrient profile") may largely depend on taxonomy, trophic guild (broadly defined here by fish diet), and life phase of coral reef fishes. As such, nutrients derived from the feces of different fishes could represent a diverse pool of resources for corals and other reef macro and microorganisms. In particular, certain minerals (Mg, Mn, Fe) appear to mitigate coral bleaching during thermal stress and may be especially important in resilience to climate change (Biscéré et al., 2018; Ferrier-Pagès et al., 2018; Houlbrèque & Ferrier-Pagès, 2009). Gaining additional insights into the diversity and abundance of nutrients supplied by reef fishes via egestion may reveal a more nuanced picture of the functional roles of fishes as nutrient recyclers.

Here, we compare fecal nutrient profiles across a diverse range of coral reef fish species. Specifically, we quantify macro- (proteins, carbohydrates, lipids) and micro- (calcium, copper, iron, magnesium, manganese, and zinc) nutrients, in addition to water content and ash, for 570 individuals across 40 species, 10 families, and six trophic guilds in Moorea, French Polynesia. We selected these nutrients because they are involved in fundamental biochemical and physiological processes (e.g., photosynthesis and cellular respiration) across many organisms and are identified as critical nutrients for many coral reef taxa (Ferrier-Pagès et al., 2018). The objectives of our study are to (1) characterize the macro- and micronutrients in the feces of a diverse reef fish community and (2) determine how fecal nutrient profiles vary across fish traits, including body size, taxonomy (family, genus, species), and trophic guild.

METHODS

Sample collection

We collected fishes around Moorea, French Polynesia (17.5388° S, 149.8295° W) between July and August 2018 and August 2019 in two separate datasets. Dataset 1 includes fish individuals ($N = 317$) that were collected at the North Shore forereef, fringing reef, and backreef habitats across 14 sites. A subset of fishes from Dataset 1 ($N = 34$) was collected from roadside stands during this sampling time, but the precise collection sites around Moorea are unknown and these collection sites were

classified according to stand location (e.g., East or West). Dataset 2 includes fish individuals ($N = 253$) collected on the northern, eastern, and western shores of Moorea across the forereef, reef crest, backreef, and fringing reef habitats across 48 sites. In total, we collected 570 individuals across 40 species (minimum four individuals per species) of fish and 61 different sites. These species represent 70% of non-elasmobranch fish biomass on coral reefs in Moorea (Brooks, 2022). These fishes represent 10 families (Acanthuridae, Balistidae, Chaetodontidae, Cirrhitidae, Holocentridae, Labridae, Lutjanidae, Monacanthidae, Pomacentridae, Serranidae), spanning six trophic guilds (corallivores, detritivores, herbivores, invertivores, piscivores, and planktivores) as guided by the MCR LTER (Brooks, 2022), FishBase (Froese & Pauly, 2022) and Parravicini et al. (2020) (Appendix S1: Tables S1 and S2). Fishes were collected via spearfishing between 0945 and 1500 and were transported on ice back to either the University of California Gump Research Station (Dataset 1) or the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) in Moorea (Dataset 2). In the lab, fish were weighed (g) and measured for fork length (Dataset 1) or total length (Dataset 2) (cm). Feces were removed from the last 4 cm of the large intestine and were either kept in 1.5 mL Eppendorf vials at −20°C and transported back to University of California Santa Barbara in the United States (Dataset 1, $N = 317$) and freeze-dried for >36 h each to measure water content, and ground using a conical glass homogenizing pestle, or both frozen and freeze-dried for >24 h each at CRIOBE Moorea and transported to the CRIOBE in Perpignan, France, where samples were ground to a fine powder using a homogenizer (Dataset 2, $N = 253$).

Macronutrient quantification

Macronutrients (protein, lipid, carbohydrate) and ash were assessed only for Dataset 1 and full methods are described in Appendix S1: Text S1. For protein and carbohydrate analysis, we measured 10 mg of homogenized sample into 2 mL screw cap vials, diluted each sample with MilliQ water with a dilution factor of 100, and homogenized samples at 6 m/s for four 30 s cycles (Fisher Brand Bead Mill 24) with ~10 mg 0.5 mm zirconium oxide beads. These homogenates were stored in −20°C until further use. To measure total protein, we used a modified bicinchoninic (BCA) assay (Barbarino & Lourenço, 2005; Mann & Gallager, 1985). Using a thawed aliquot (50 µL) of the homogenate, we precipitated the protein from the sample or bovine albumin serum (BSA) standard with 72% trichloroacetic acid (TCA) and removed the supernatant to eliminate potential interferences, including lipids and free amino acids. We then followed a modified microplate BCA assay protocol (Thermoscientific Pierce BCA Kit) to measure absorbance at 562 nm in triplicate in a spectrophotometer multi-mode plate reader (SpectraMax id3, Molecular Devices). We measured carbohydrate using a modified version of the phenol-sulfuric acid method to determine total sugar in glucose equivalents. We extracted the carbohydrate from the samples (250 µL aliquot of the homogenate thawed, re-homogenized for 30 s at 6 m/s) and standard using cold 15% TCA, incubated samples at 4°C for 30 min, spun in a micro centrifuge (1000 rpm, 10 min), and collected the supernatant containing carbohydrates. We then estimated the carbohydrate concentration using the phenol-sulfuric acid method (DuBois et al., 1956) with a modified microplate method (Masuko et al., 2005). We measured absorbance in triplicates at 490 nm with glucose as the standard (SpectraMax id3, Molecular Devices).

To measure lipid content, we followed the methods of Mann and Gallager (1985) and Johnson et al. (2017). We measured samples in duplicates (40–50 mg; 5–10 mg when minimal sample available) into solvent-washed test tubes, added and vortexed with 100 µL water and 1.5 mL chloroform: methanol (1:2). Samples were then incubated at 4°C for 10 min and centrifuged (4000 rpm, 5 min), with the supernatant removed to a separate test tube. The remaining sample was re-extracted in 1.5 mL chloroform: methanol (2:1) and the supernatants were pooled, mixed with 950 µL NaCl (0.7%), and incubated at 4°C for 30 min. To separate the phases, samples were then centrifuged (4000 rpm, 5 min). The lower phase was measured for volume, and 1 mL was then deposited onto a pre-weighed aluminum weighing boat and dried overnight. The lipid was re-weighed, then weight was extrapolated to the entire bottom layer volume to determine lipid concentration. For ash, we pre-combusted aluminum weighing boats at 450°C for 6 h and pre-heated the samples in an oven at 100°C overnight to ensure full water loss. We combusted pre-weighed samples in a muffle furnace for 6 h at 450°C and then reweighed samples to obtain ash content.

Micronutrient quantification

Micronutrients (calcium [Ca], copper [Cu], iron [Fe], magnesium [Mg], manganese [Mn], and/or zinc [Zn]) were assessed in duplicate from Dataset 1 ($N = 157$) and a subset of Dataset 2 ($N = 65$) following modified methods of Ratnarajah et al. (2018). We chose these micronutrients because they have been identified as critical nutrients for many coral reef taxa, especially reef-building corals (Ferrier-Pagès et al., 2018). Briefly,

we manually homogenized each sample and weighed 8–40 mg subsample into metal-free acid-cleaned 50 mL polypropylene vials (Ultimate Clean Cup, Environmental Express). Samples were acid-digested (2–5 mL concentrated nitric acid; Plasma Pure Grade, Fisher Scientific and 0.125 mL of 30% hydrogen peroxide) overnight. They were then heated to 90°C for 2 h, cooled, and diluted to 5% nitric acid. Identical procedures were followed for blanks. Samples were then analyzed by inductively coupled plasma mass spectroscopy (ICP-MS) at the Bren School of Environmental Science and Management at University of California, Santa Barbara facilities. A separate subset of samples from Dataset 2 ($N = 185$) were analyzed at University of Michigan for micronutrients (Ca, Cu, Fe, Mg, Mn, and/or Zn) and prepped and measured by ICP-MS according to Rempel et al. (2022). Both procedures followed similar protocols and resulted in similar measurements; therefore, micronutrients were pooled. When measurements were returned as negatives, they contained nutrient concentrations too low to detect and were reported as 0.

Data analyses

All statistical analyses were performed in R (version 2022.02.0) using the packages vegan (Oksanen et al., 2022), pairwiseAdonis (Martinez Arbizu, 2020) and lme4 (Bates et al., 2014). We assessed relationships between macro-/micronutrients and reef fish trophic guilds or species by using non-metric multidimensional scaling (NMDS) ordinations on log-transformed nutrients, based on a Bray–Curtis dissimilarity index (Bray & Curtis, 1957), using the "envfit" function to visualize patterns and identify correlations between nutrients and trophic guilds or species. We then conducted separate NMDS analyses within specific trophic guilds (corallivores and herbivores) and genera (*Chaetodon* and *Acanthurus*) because these groups had large sample sizes, are abundant around Moorea, and play key roles in coral reef ecosystem functioning (Brooks, 2022; Tebbett et al., 2022). To test the effects of trophic guilds and species on nutrient contents, we computed permutational analyses of variance (PERMANOVAs) based on Bray–Curtis dissimilarity index and 999 permutations with "site" included as a random effect. Pairwise differences were tested using the function "pairwiseAdonis," and *p*-values were adjusted according to a Bonferroni–Holm correction to account for multiple comparisons.

Next, to determine which variables best predicted nutrient content, we ran a series of mixed effects models with fixed effects (family, genus, species, body mass, and trophic guild) tested independently, additively, and interactively for each macro- and micronutrient. There were 61 unique collection sites, classified by distinct GPS coordinates or distinct roadside stand spots, so we included "site" as a random effect. Collinear variables (family, genus, and species) were not tested additively or interactively with each other. Complementary models were compared using the Bayesian Information Criterion (BIC), where the lowest BIC score was accepted as the best fit; however, only models with ΔBIC <7 were considered in the analyses (Jerde et al., 2019).

Data residuals were tested for normality, homogeneity, and moderate correlation, and data were log transformed when they did not fit normality assumptions. Outliers ($N = 15$) were removed if values were outside 1.5× interquartile range across all individuals and within a species. If values for one individual were determined to be outliers for more than two macro- or micronutrients, this suggests that samples were contaminated or not processed correctly, so all nutrients of that type (either macro- or micro-) were removed for that individual (Grubbs, 1950; Wing et al., 2021). We standardized the length metrics across the two datasets, converting all lengths to total lengths using published species-specific scaling parameters (Brooks & Adam, 2019). We sampled 570 individuals across 40 species to capture the coral reef fish community; however, some of our sampled species were underrepresented for certain fecal nutrients. We therefore present sample sizes with mean ± SD values (Appendix S1: Tables S1 and S2) and graphically present results from species with ≥ four individuals for major macronutrients (carbohydrate, lipid, protein) or micronutrients (Ca, Cu, Fe, Mg, Mn, Zn), resulting in 26 species for macro- and 39 species for micronutrients. For NMDS ordinations, we include species with ≥ four individuals each measured for all major macro- or micronutrients.

RESULTS

Feces macronutrient composition

The concentration of fecal macronutrients varied substantially across 26 coral reef fish species (Figure 1, Appendix S1: Table S1). Ash and water were the primary components of fish feces across all species (Figure 1A, Appendix S1: Table S1). However, the mean protein concentration of feces varied 33-fold, from 1.4% dry weight (DW) in *Acanthurus olivaceus* to 45.7% DW in *Naso lituratus* (Appendix S1: Table S1). The mean carbohydrate concentration varied 13-fold, from 0.5% DW in *Scarus psittacus* to 6.3% DW in *Acanthurus nigrofuscus* (Appendix S1). For lipids, *Amanses scopas* contained the lowest concentration at 1% mean DW, compared to

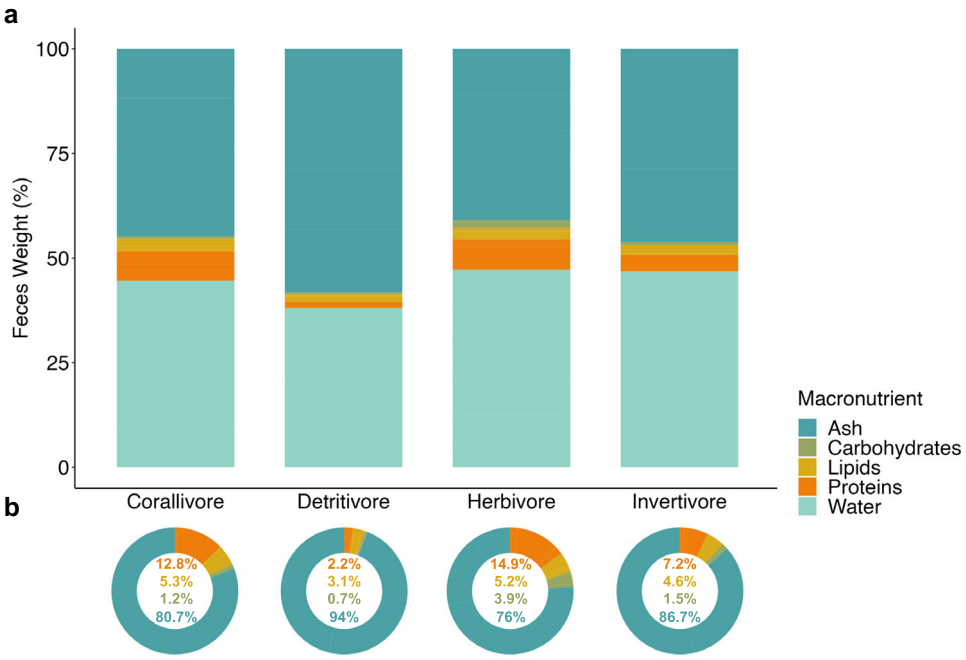

FIGURE 1 Mean macronutrient content across trophic guilds normalized to (a) 100% feces weight and (b) 100% feces dry weight (excludes water). Data represent species with $N \geq 4$ individuals per species and depicts normalized means for three corallivore species, four detritivore species, six herbivore species, and three invertivore species.

Odonus niger at 9% mean DW, a 9-fold difference (Appendix S1: Table S1). Meanwhile, *N. lituratus* had the lowest mean ash content at 31.5% DW compared to *A. scopas* at 89.5% DW (Appendix S1: Table S1).

Variation in macronutrients across trophic guilds

Macronutrient concentrations (protein, carbohydrate, lipid) varied by trophic guild (Figure 1a,b). For instance, we found that invertivores and detritivores egested the highest relative proportion of ash. Corallivore and herbivore feces contained relatively high proportions of protein. We did not have an adequate sample size to measure macronutrients in planktivores or piscivores.

Our NMDS ordination analyses according to macronutrients revealed clustering by the five trophic guilds (Figure 2a) and the trophic guild had a significant effect on macronutrient concentration (PERMANOVA, $F_4 = 9.59$, $R^2 = 0.20$, $p < 0.001$). Detritivores were distinct from all trophic groups in their fecal macronutrients (pairwiseAdonis, $p < 0.05$ for all comparisons), as well as herbivores, corallivores, and invertivores from one another (pairwiseAdonis, $p < 0.05$ for all comparisons), while other trophic groups did not statistically differ from one another.

The concentration of macronutrients egested by fishes was best predicted by genus or trophic guild, and/or in conjunction with mass (Appendix S1: Table S3). Trophic guild was the best predictor for lipid concentration ($\chi^2 = 39.57$, df = 5, $p < 0.001$) as well as for carbohydrate concentration in conjunction with body mass (log[mass]: $\chi^2 = 13.86$, df = 1, $p < 0.001$; trophic guild: $\chi^2 = 46.03$, df = 5, $p < 0.0001$) (Appendix S1: Table S3). In contrast, genus was the best predictor of ash content ($\chi^2 = 164.94$, df = 17, $p < 0.0001$) as well as for protein concentration either alone (genus: $\chi^2 = 666.89$, df = 18, $p < 0.0001$), or in conjunction with body mass (log[mass]: $\chi^2 = 14.68$, df = 1, $p < 0.0001$; genus: $\chi^2 = 677.85$, df = 18, $p < 0.0001$) (Appendix S1: Table S3).

Feces micronutrient composition

Fecal micronutrients varied extensively across 39 coral reef fish species (Figures 2 and 3, Appendix S1: Table S2). Mean copper concentrations in feces ranged from 0 ppm in *Chlorurus spilurus*, *Ctenochaetus flavicauda* and *Scarus psittacus* to 163 ppm in *Thalassoma hardwicke* feces (Figure 3, Appendix S1: Table S2). A ~1800-fold difference was measured in mean Fe concentrations, from 24 ppm in *Amanses scopas* to 43,015 ppm in *Acanthurus pyroferus* feces (Appendix S1: Table S2). For Mg, *A. scopas* had the lowest fecal concentration with a mean of 3116 ppm while *Chromis xanthura* had a mean of 65,863 ppm Mg, a 21-fold difference (Figure 3, Appendix S1: Table S2). Species such as *T. hardwicke* had no measurable fecal Ca, whereas *A. scopas* contained a mean of 398,207 ppm of fecal Ca

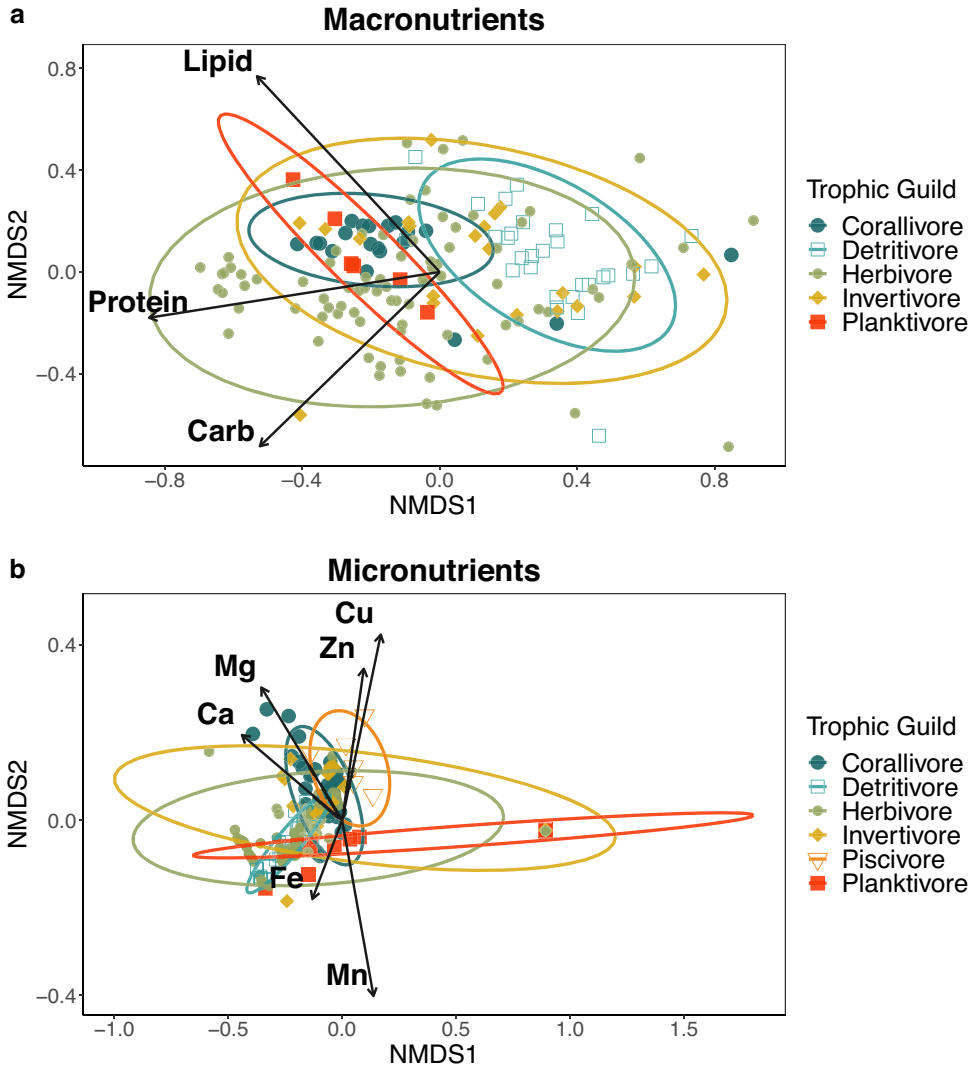

FIGURE 2 Non-metric multidimensional scaling (NMDS) ordinations of fecal (a) macronutrients (carb [carbohydrates], protein, lipid) ($k = 2$, stress = 0.119, $N = 159$) and (b) micronutrients (calcium [Ca], copper [Cu], iron [Fe], magnesium [Mg], manganese [Mn], and zinc [Zn]) across individuals ($k = 2$, stress = 0.041, $N = 249$) by trophic guild. Plots are based on the Bray–Curtis dissimilarity index and nutrients are shown as vectors, scaled down by 50% in (b). Ellipses depict 95% confidence interval. Each data point represents an individual. The macronutrient plot excludes piscivores due to a small sample size.

(Figure 3, Appendix S1: Table S2). On the other hand, *A. scopas* showed the lowest mean concentration of Mn at 0.6 ppm while *T. hardwicke* had the highest mean concentration of fecal Mn at 167 ppm (Figure 3, Appendix S1: Table S2). The mean Zn concentration varied ~1800-fold, from 0.4 ppm in *Scarus psittacus* feces to 784 ppm in *Chaetodon pelewensis* feces (Figure 3, Appendix S1: Table S2).

Variation in micronutrients across trophic guilds

Examining fecal micronutrients across trophic guilds (Figure 3) revealed trends that also emerged on the NMDS ordinations (Figure 2b). We observed limited clustering among trophic guilds (Figure 2b). The ordination showed a tight clustering among piscivores, detritivores, and corallivores compared to the other trophic guilds (Figure 2b). Trophic guilds significantly differed in micronutrient concentrations (PERMANOVA, $F_5 = 8.52$ $R^2 = 0.17$, $p < 0.001$), including differences in detritivore fecal nutrients compared to all trophic guilds (pairwiseAdonis, $p < 0.05$ for all comparisons) and differences in corallivore and planktivore, corallivore and invertivore, and herbivore and planktivore fecal nutrients (pairwiseAdonis, $p < 0.05$ for above comparisons) (Appendix S1: Table S5).

There was no single best variable (species, genus, family, mass, or trophic guild) that consistently predicted the

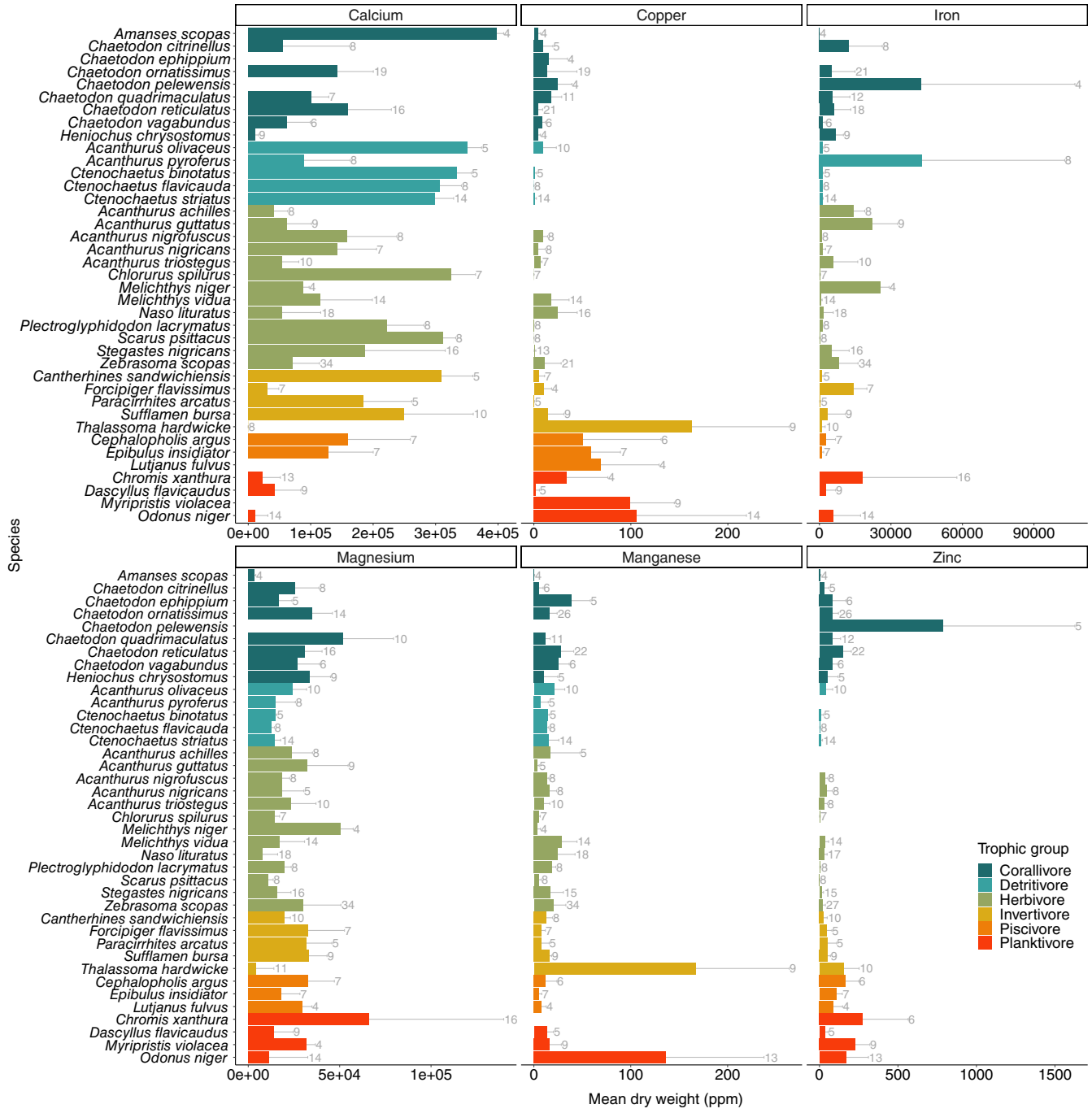

FIGURE 3 Mean dry weight (ppm) of calcium, copper, iron, magnesium, manganese, and zinc measured in feces of 39 reef fish species across six trophic guilds in descending order (corallivore, detritivore, herbivore, invertivore, piscivore, planktivore). Error bars represent SD. Data represents species with $N \geq 4$ individuals per species per nutrient and numbers in gray represent sample size and for cases where the nutrient was not measured for the species, no number or bar is shown. See Appendix S1: Table S2 for full dataset.

concentration of micronutrients egested by fishes (Appendix S1: Table S6). Trophic guild was the best predictor for Ca ($\chi^2 = 75.92$, df = 5, $p < 0.0001$) and Cu ($\chi^2 = 96.54$, df = 5, $p < 0.0001$) concentrations (Appendix S1: Table S6). In contrast, genus was the best predictor for Fe ($\chi^2 = 173.06$, df = 22, $p < 0.0001$), Mn ($\chi^2 = 249.04$, df = 22, $p < 0.0001$), and Zn ($\chi^2 = 277.96$, df = 23, $p < 0.0001$) concentrations, whereas family was the best predictor for Mg concentration ($\chi^2 = 66.89$, df = 10, $p < 0.0001$) (Appendix S1: Table S6). Body mass was a common (though non-significant) additive predictor for nutrients; Cu concentrations increased with body mass whereas Fe, Ca, Mn, and Zn concentrations decreased with body mass (Appendix S1: Table S6).

Variation in micronutrient quantities within trophic guilds and within genera

In addition to the differences in nutrient profiles across trophic guilds, differences in fecal micronutrient profiles also are apparent within trophic guilds (i.e., herbivore Figure 4a, corallivore Figure 4b). The NMDS ordination for fecal micronutrient concentrations of herbivore species revealed clustering (Figure 4a), and micronutrient concentrations significantly differed across herbivore species (PERMANOVA $F_9 = 8.99$, $R^2 = 0.50$, $p < 0.001$). Distinct clusters separated *N. lituratus* from *C. spilurus*, *P. lacrymatus*, *S. psittacus*, and *S. nigricans*, as well as *S. psittacus* from *A. nigrofuscus*, *A. triostegus*, *N. lituratus*, *P. lacrymatus* and *Z. scopas* for example (pairwiseAdonis, $p < 0.05$ for above comparisons) (Figure 4a; Appendix S1: Table S5). *A. nigrofuscus* also differed from *A. triostegus* and *C. spilurus*, as well as *S. nigricans* from *Z. scopas* (pairwiseAdonis, $p < 0.05$ for above comparisons) (Figure 4a; Appendix S1: Table S5). When investigating patterns of micronutrient concentrations within the herbivorous genus *Acanthurus*, we observed that the four species formed distinct clusters (Figure 4c; PERMANOVA $F_3 = 11.17$, $R^2 = 0.61$, $p < 0.001$) and all four *Acanthurus* species significantly differed in micronutrient concentrations (pairwiseAdonis, $p < 0.05$ for all comparisons) (Appendix S1: Table S5).

For corallivores, the NMDS ordination for fecal micronutrient concentrations across seven species also revealed clustering (Figure 4b), and these species differed significantly in their micronutrient concentrations (PERMANOVA, $F_6 = 22.45$, $R^2 = 0.80$, $p < 0.001$). *Chaetodon quadrimaculatus* differed significantly in micronutrient concentrations from *C. reticulatus*, and *C. vagabundus* (pariwiseAdonis, $p < 0.05$ for above comparisons) (Figure 4b; Appendix S1: Table S5). Additionally, *A. scopas* significantly differed from *C. ornatissimus* and *C. reticulatus*, and *H. chrysostomus* differed from *C. ornatissimus* (pairwiseAdonis, $p < 0.05$ for above comparisons) for example. When we investigated ordination patterns of micronutrient concentrations within the genus *Chaetodon*, there was tight clustering, and these micronutrient profiles differed significantly across species differed significantly (PERMANOVA,

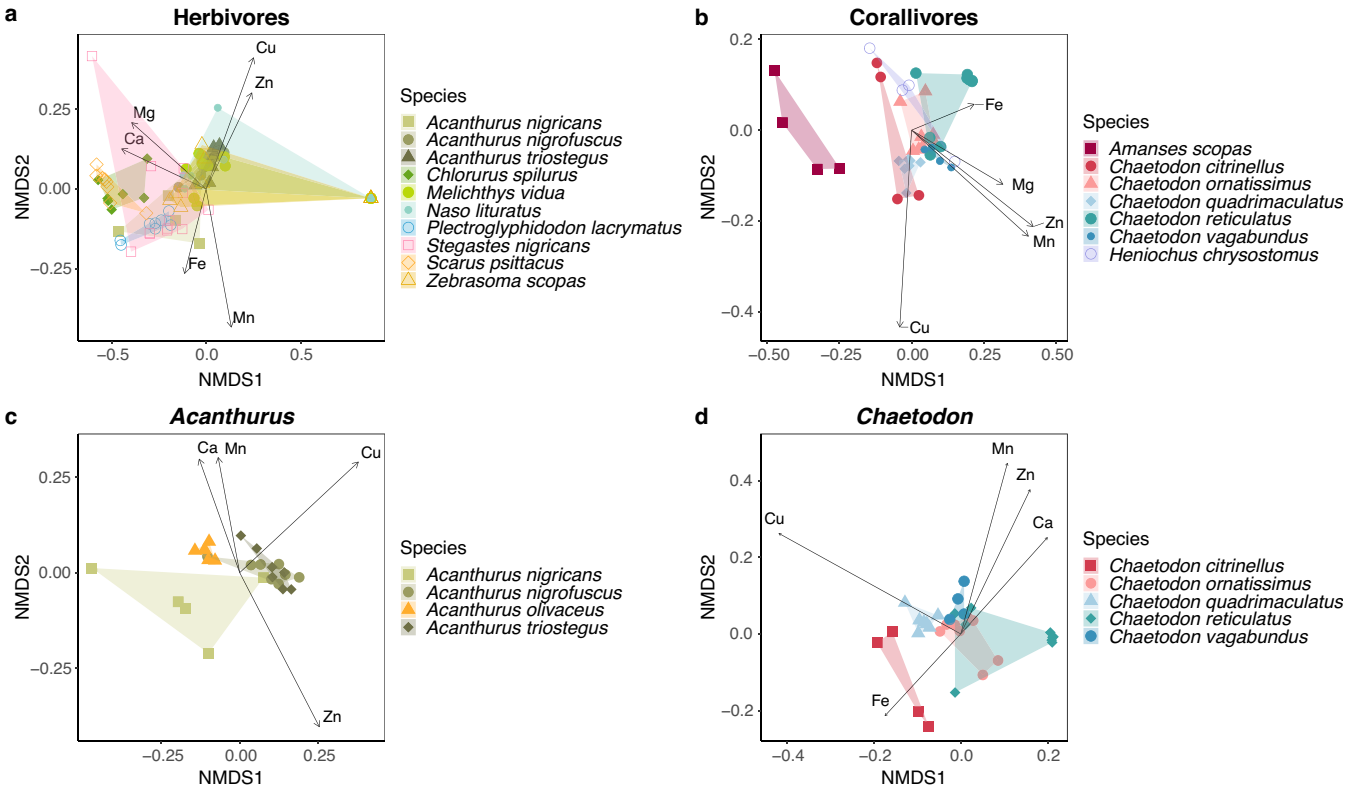

FIGURE 4 NMDS ordinations based on significant ($p < 0.05$, based on a permutation test) fecal micronutrients (calcium [Ca], copper [Cu], iron [Fe], magnesium [Mg], manganese [Mn], and zinc [Zn]) in species within the (a) herbivore trophic guild ($k = 2$, stress = 0.025), (b) corallivore trophic guild ($k = 2$, stress = 0.118), (c) genus *Acanthurus* ($k = 2$, stress = 0.041), and (d) genus *Chaetodon* ($k = 2$, stress = 0.078). Each polygon represents the nutrient profile of a single fish species, with each point corresponding to an individual. Colors represent each species. Plots are based on the Bray–Curtis dissimilarity index and nutrients are shown as vectors, scaled down by 50%. See Appendix S1: Table S2 for full dataset.

$F_4 = 8.19, R^2 = 0.55, p < 0.001$) (Figure 4d). The micronutrient profile of *C. quadrimaculatus* differed from *C. citrinellus*, *C. reticulatus*, and *C. vagabundus*, in addition to *C. citrinellus* differing from *C. ornatissimus* and *C. reticulatus* (pariwiseAdonis, $p < 0.05$ for above comparisons) (Figure 4d; Appendix S1: Table S5).

DISCUSSION

High productivity on coral reefs is facilitated by the efficient internal cycling of energy and nutrients. Reef fishes are a dominant consumer group on reefs, but how they recycle different types of nutrients in their feces has not been studied in detail. We measured the fecal nutrient composition from 570 coral reef fish individuals spanning 40 species and representing 70% of non-elasmobranch fish biomass around Moorea, French Polynesia (Brooks, 2022). We found that feces are diverse in nutrient quantity and quality across fish species. The best predictor variable (body size, taxonomy, and trophic guild) for macro- and micronutrient concentrations varied for each nutrient, highlighting the complexity of interactions in nutrient recycling in coral reef ecosystems. We measured biologically important minerals for corals (Cu, Fe, and/or Zn) (Ferrier-Pagès et al., 2018) in the feces of corallivores, planktivores, invertivores, and piscivores, and we demonstrate significant variability in concentrations in herbivores and corallivores. The composition of fecal nutrients varied substantially across trophic guilds as well as across species within the same trophic guilds, especially for herbivores and corallivores, and across species within the genera *Acanthurus* and *Chaetodon*. Thus, when considering the nutrients that fishes recycle in their feces, some trophic guilds and even species within these trophic guilds contribute unique nutrient profiles (Figures 4 and 5). The variation in fecal nutrient concentrations across fish species underscores the diversity of reef fish functional roles and reinforces their importance for nutrient supply and ecosystem functioning on coral reefs.

Compared to the breadth of knowledge in terrestrial systems (Beard et al., 2002; Leslie et al., 2008; Pastor et al., 1993; Veldhuis et al., 2018), our understanding of how aquatic consumers recycle nutrients via their feces is surprisingly small. Although the egestion of nitrogen, phosphorous, and carbon is increasingly incorporated into bioenergetic models for aquatic consumers (Atkinson et al., 2017; Schiettekatte et al., 2020, 2023; Williams et al., 2018), fecal micronutrient composition has remained largely unexplored, especially for reef fishes where only a limited set of species and trophic groups have been investigated (Bailey & Robertson, 1982; Crossman et al., 2005). Our findings align with previous results, as we found similar concentrations of ash, protein, carbohydrate, and lipid concentrations in the feces of the few overlapping species, including *Acanthurus olivaceus* and *Ctenochaetus striatus* (Appendix S1; Bailey & Robertson, 1982). However, we found higher protein concentrations in species such as

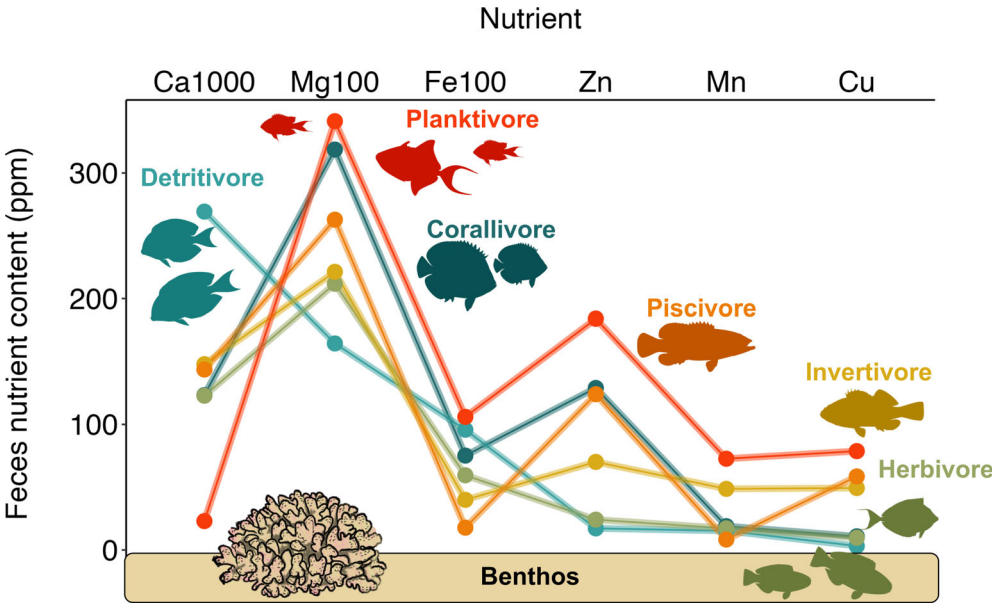

FIGURE 5 Summary schematic demonstrating mean micronutrient (Ca, Mg, Fe, Zn, Mn, Cu) contribution by primary trophic guilds of coral reef fishes in ppm. To maintain the *y*-axis scale Ca, Mg, and Fe are represented as fractions of original values by 1000 (Ca) and 100 (Mg and Fe). The benthos is included below to contextualize the approximate quantity of nutrients that may disperse into the water column and land on benthos. Trophic guilds are represented by species within each guild (fishualize: Schiettekatte et al., 2019).

Naso lituratus. Herbivores show highly variable amino acid absorption efficiencies (Crossman et al., 2005), which may explain the high and variable protein values reported here. Similar to Schiettekatte et al. (2023), which compares CNP across reef fish feces, we found that the quality of fish feces varied strongly across and within trophic guilds. The consistency of fecal nutrient concentrations in the same species across different studies, despite relatively different locations (Moorea, Palau, and the Great Barrier Reef), reflects the shared nutritional requirements and broad feeding behaviors across these species (Bailey & Robertson, 1982; Crossman et al., 2005).

Fecal nutrient content represents components from unassimilated food. Thus, we can directly link species' diets to their fecal nutrient content. Given that fine-scale partitioning has been demonstrated in coral reef fish diets (Casey et al., 2019), we would expect this to translate to differences in fecal nutrient profiles. Corallivores, for example, feed on coral polyps, which are rich in lipids (8%–40% DW) (Stimson, 1987) and proteins (15%–23% DW) but are characterized by lower concentrations in carbohydrates (0.62% DW) (Ben-David-Zaslow & Benayahu, 1999). Moreover, coral tissue can contain relatively high levels of trace metals such as Zn (467 ppm DW) and Mg (533 ppm DW) (Hanna & Muir, 1990), and dead coral skeleton consist of 3.20% Mg (32,000 ppm) (Goldberg et al., 2019). Consistent with their trophic guild, we found that obligate corallivores, such as *Chaetodon pelewensis* and *C. reticulatus*, harbored higher fecal concentrations of Zn and Mg than the facultative corallivore *C. vagabundus* that has a more generalized diet including algae (Froese & Pauly, 2022), which is generally lower in these elemental concentrations (Rempel et al., 2022). Dietary content also mirrored fecal nutrients of *Chromis xanthura*, which consume planktonic diets that are generally rich in Fe and Zn and exhibited high fecal concentrations of these nutrients (Twining et al., 2004).

Although we show significant effects of taxonomy, body size, and trophic guild on fecal nutrient recycling, we found high intra-specific variability in nutrient concentrations for some species (e.g., *Acanthurus pyroferus*, *Thalassoma hardwicke*, *Odonus niger*) and could not account for all extrinsic and intrinsic factors that influence diet and metabolism (Ben-David-Zaslow & Benayahu, 1999; Lowman et al., 2021; Stimson, 1987). For example, some fishes may switch their diet across seasons and physio-chemical water conditions (Clements & Choat, 1993; Johnson et al., 2017). In addition, local stressors such as marine pollution (e.g., nearshore reefs exposed to pollution in Moorea, see Adam et al., 2021) can lead to significant changes in benthic composition on coral reefs (Adam et al., 2021; Bonanno & Orlando-Bonaca, 2018; Hanna & Muir, 1990), ultimately affecting diet and muscle tissue nutrient content (Robinson et al., 2022). These environmental factors likely influence some taxa, life stages, or trophic guilds to shape patterns of nutrient recycling. Our finding that feces nutrient composition was generally not well predicted by broader taxonomy (family) and instead often showed high inter- and intra-specific variability in composition, contrasts with the finding that family is the best predictor of excretion rates in fish (Allgeier et al., 2021; Vanni et al., 2002). Thus, studying egestion as a form of fish-mediated nutrient supply demonstrates that each fish may contribute to nutrient recycling in distinct ways.

We identify diverse nutrient profiles, demonstrating that a suite of critical nutrients is recycled and potentially provided to benthic organisms such as corals, algae, and microorganisms via fish feces. Corals in particular, require an array of micro- and macronutrients (e.g., N, P, Mg, Mn, Fe, Cu, and Zn) to sustain their metabolism (Ferrier-Pagès et al., 2018). For instance, nutrients produced by fishes can have positive effects on coral growth and were shown to increase coral thermal tolerance (Meyer et al., 1983; Shantz et al., 2023). In addition, Mg, Mn, and Fe are known to ensure proper photo-physiological performance of coral symbiotic dinoflagellates, especially during periods of thermal stress (Ferrier-Pagès et al., 2018). Heterotrophic feeding supplies coral dinoflagellate symbionts with Mg, Mn, and Fe, which comprise antioxidant enzyme structures that scavenge reactive oxygen species (ROS) produced in excess during thermal stress (Ferrier-Pagès et al., 2018; Weis, 2008). Mn and Fe are also critical for photosynthesis because of their implication in chlorophyll production and amino acid synthesis, and elements such as Cu and Zn are cofactors to critical enzymes involved in metabolism (Morel et al., 1994; Twining & Baines, 2013). The organic nutrients released from egestion as particulate matter may serve as food for heterotrophs including corals (Hatcher, 1988; Robertson, 1982). These nutrients may also provide a substrate for bacterial decomposition (Turner, 2002) that may make some of these nutrients more bioavailable to other organisms. However, the bioavailability of nutrients will largely determine their contribution to nutrient recycling on coral reefs. Future research needs to assess the bioavailability of fish-derived nutrients through feces to corals, algae, and other macro- and micro-organisms.

Compared to other marine species, coral reef fish feces are rich in certain nutrients. We found that some coral reef fish species contained one to two orders of magnitude greater fecal Fe concentrations (e.g., *Acanthurus pyroferus* 43,015 mg kg^{-1}) than found in sperm whales (757 mg kg^{-1}) and predatory seabirds, like the south polar skua (3928 mg kg^{-1}). We further found that a small-bodied wrasse, *Thalassoma hardwicke*, had a four-fold greater fecal Mn concentration than multiple species of whales, seabirds, and seals (167 mg kg^{-1} vs. 22–43 mg kg^{-1}) (Ratnarajah et al., 2014; Wing et al., 2021). Despite their small size

compared to the above marine animals, coral reef fishes represent a high proportion of biomass within their ecosystem; thus, their total fecal output represents a large nutrient contribution. Thus, the loss of species or trophic guilds has the potential to shift food webs and further alter nutrient recycling (Allgeier et al., 2017; Halvorson & Atkinson, 2019; Peters et al., 2019). Overfishing often removes larger and/or higher trophic level fish (piscivores, herbivores, detritivores) on coral reefs, and the loss of these individuals could cascade down to benthic communities and impact nutrient recycling (Allgeier et al., 2016; Micheli et al., 2014; Mumby et al., 2006; Zaneveld et al., 2016). Species that are targeted by small-scale fisheries around Moorea (Nassiri et al., 2021) tend to have nutrient-rich fecal profiles. For instance, fisheries-targeted piscivores (e.g., *Epibulus insidiator* and *Cephalopholis argus*) showed relatively high fecal Zn concentrations in our study while targeted detritivores (e.g., *Acanthurus olivaceus*) typically contained relatively high fecal Ca concentrations. Species like *Chlorurus spilurus* and *Naso lituratus* are also commonly targeted by recreational fishing (Nassiri et al., 2021), and while they are both herbivores, these species supply distinct fecal micronutrient profiles. The loss of any of these species could directly translate to the loss of certain key nutrient recycling pathways, with negative consequences for coral reef community structure and functioning.

CONCLUSION

Here, we highlight a missing functional link of nutrient recycling in a key group of consumers, coral reef fishes, and reveal the diversity of nutrients cycled by reef fishes through egestion. Many closely related coral reef fish species have minimal overlap in their trophic niches (Brandl et al., 2020; Casey et al., 2019; Eurich et al., 2019; Pozas-Schacre et al., 2021). Similarly, our results show that reef fish feces differ in nutrient profiles at the level of trophic guilds as well as, in some cases, at the species-level. By enabling the recycling of a diversity of macro- and micronutrients, fish communities may confer benefits to many other species that inhabit coral reefs. However, global and local stressors (e.g., pollution, overfishing) are changing reef landscapes and fish assemblages, threatening the nutrient recycling pathway provided by reef fishes. Thus, it is important for both terrestrial and marine environments to continue to reveal the underappreciated functional roles that many groups of animals play in nutrient cycling.

AUTHOR CONTRIBUTIONS

Erika J. Eliason and Deron E. Burkepile conceived the ideas and designed methodology; all authors contributed to sample collection; Jacey C. Van Wert conducted laboratory analyses; Jacey C. Van Wert, Leïla Ezzat, and Katrina S. Munsterman analyzed the data; Jacey C. Van Wert led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Van Wert et al., 2023a) are available from Dryad: https://doi.org/10.25349/D9Q036. Code (Van Wert et al., 2023b) is available from Zenodo: https://doi.org/10.5281/zenodo.7898136.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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