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Global Change Biology (2014) **20**, 2459–2472, doi: 10.1111/gcb.12566

# Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems

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## Abstract

Corals thrive in low nutrient environments and the conservation of these globally imperiled ecosystems is largely dependent on mitigating the effects of anthropogenic nutrient enrichment. However, to better understand the implications of anthropogenic nutrients requires a heightened understanding of baseline nutrient dynamics within these ecosystems. Here, we provide a novel perspective on coral reef nutrient dynamics by examining the role of fish communities in the supply and storage of nitrogen (N) and phosphorus (P). We quantified fish-mediated nutrient storage and supply for 144 species and modeled these data onto 172 fish communities (71 729 individual fish), in four types of coral reefs, as well as seagrass and mangrove ecosystems, throughout the Northern Antilles. Fish communities supplied and stored large quantities of nutrients, with rates varying among ecosystem types. The size structure and diversity of the fish communities best predicted N and P supply and storage and N : P supply, suggesting that alterations to fish communities (e.g., overfishing) will have important implications for nutrient dynamics in these systems. The stoichiometric ratio (N : P) for storage in fish mass (~8 : 1) and supply (~20 : 1) was notably consistent across the four coral reef types (but not seagrass or mangrove ecosystems). Published nutrient enrichment studies on corals show that deviations from this N : P supply ratio may be associated with poor coral fitness, providing qualitative support for the hypothesis that corals and their symbionts may be adapted to specific ratios of nutrient supply. Consumer nutrient stoichiometry provides a baseline from which to better understand nutrient dynamics in coral reef and other coastal ecosystems, information that is greatly needed if we are to implement more effective measures to ensure the future health of the world's oceans.

*Keywords:* coastal ecosystems, consumer-mediated nutrient supply, eutrophication, fish, food web, mangroves, nitrogen, phosphorus, redfield ratio, seagrass beds

*Received 14 August 2013; revised version received 4 February 2014 and accepted 5 February 2014*

## Introduction

Scientists have long recognized the enigmatic role of nutrients in coral reef ecosystems. Although coral reef ecosystems persist in extremely nutrient poor environments, they are still among the most productive in the world, presumably due to mechanisms that maximize efficiency in nutrient and energy cycling (Odum & Odum, 1955; Johannes *et al*., 1972; Muscatine & Porter, 1977). Yet it is widely recognized that nutrient enrichment is among the greatest stressors to coral reefs globally. A common assertion is that alterations in nutrient fluxes or availability (e.g., via anthropogenic nutrient enrichment) disrupt the tight cycling, potentially leading to destabilization in ecological feedbacks and/or phase shifts (e.g., to macroalgae dominated reefs) (Deangelis, 1980; Lapointe, 1997; Scheffer *et al*., 2001; Hughes *et al*., 2010). While much research has focused on understanding nutrient dynamics within these ecosystems, this research has often overlooked potentially important biotic drivers of biogeochemical cycles, e.g., fish. Through stoichiometric processes of assimilation (storage in biomass) and regeneration (excretion or supply to the environment), fishes are among the largest pools (Maranger *et al*., 2008) and fluxes (Allgeier *et al*., 2013; Burkepile *et al*., 2013) of nutrients in oligotrophic coastal waters. Enhancing our understanding of biological controls on ecosystem-scale biogeochemical processes will provide additional insight into nutrient dynamics in coral reef ecosystems.

The Redfield Ratio has been used for decades as a theoretical basis from which to understand the coupling of N and P cycles, and the efficiency at which producers utilize these two nutrients. The 16 : 1 N : P

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ratio, describes a consistency between inorganic nutrients in deep oceanic waters and nutrients stored in planktonic biomass (Redfield, 1958), illustrating how plankton communities have evolved to maximize physiological efficiency based on availability of resources in their environment (Redfield, 1958; Sterner & Elser, 2002). While this ratio has been shown to vary across different marine and freshwater ecosystems (range: 17 : 1 to 21 : 1 in seston) (Sterner *et al*., 2008), and across biogeographic oceanic conditions (Southern Ocean 12 : 1 to Polar Ocean 20 : 1) (Weber & Deutsch, 2010), the general similarity of ratios found within a given ecosystem or biogeographic region suggests the importance of the evolutionary interplay between organisms and resources (Schindler, 1977; Howarth, 1988; Sterner & Elser, 2002). Extending these ideas to develop perspectives on nutrient stoichiometry in coral reef ecosystems, particularly with respect to the ratio of consumer nutrient supply, may provide a basis to improve our understanding of nutrient dynamics in these ecosystems.

Coral reefs are often likened to tropical rainforests because of their high species diversity (Connell, 1978), nutrient poor conditions, high levels of productivity (Odum & Odum, 1955; Hatcher, 1988), and tight nutrient cycling (Vitousek & Sanford, 1986). In these ecosystems, components of the food web that are most common, i.e. constitute a large proportion of the biomass, comprise the 'nutrient capacity' of the ecosystem (*sensu* Deangelis, 1992), essentially regulating fluxes of nutrients between pools (Hatcher, 1988; Deangelis *et al*., 1989; Deangelis, 1992). This concept is particularly relevant in tropical rainforests and coral reefs because the amount of extrinsic nutrients entering these systems is limited, and thus the amount of nutrients stored in biomass dictates the quantities of nutrients recycled within the ecosystem (Deangelis *et al*., 1989; Deangelis, 1992).

Fish historically represent one of the largest pools of biomass in coral reef and other coastal ecosystems (Sorokin, 1993; Jackson *et al*., 2001), and, for this reason, may be central in regulating fluxes and pools of nutrients (Sorokin, 1993). Consumer-mediated processes of nutrient storage and supply are largely determined by species identity, dietary resource, and body size (Vanni *et al*., 2002), and thus the structure of the fish community may influence the rate and ratios of these processes. Importantly, fish community structure can vary substantially across coral reef ecosystems due to environmental factors or anthropogenic impacts (e.g., overharvesting, habitat degradation), potentially creating highly variable nutrient dynamics across environmental gradients. As such, understanding how community structure can affect nutrient pathways may provide an important link between food web structure and ecosystem function.

We apply two extensive empirical datasets to model nutrient storage and supply by fish communities in four different types of coral reef ecosystems (*Montastraea sp.* dominated reefs, *Acropora sp.* dominated reefs, gorgonian plains, and patch reefs) of The Northern Antilles. We evaluate the degree to which fish communities regulate important nutrient pathways in coral reefs, and then compare these findings with data from two other coastal ecosystem types (mangroves and seagrass) within the same geographic region (total of 172 communities, 144 species, 71 729 individual fish). We specifically had two objectives: (i) to quantify and compare the stoichiometry of fish nutrient supply and storage (rates and ratios) across coastal marine ecosystems and (ii) to assess what aspects of fish community structure are most important for mediating nutrient supply and storage. Our findings suggest that a primary supply of nutrients to coral reef ecosystems is delivered at a relatively uniform ratio, despite broad variation in the composition of the fish communities. To provide further perspective on the potential importance of nutrient stoichiometry for coral fitness (i.e. growth, calcification, etc.), we compiled published studies from both laboratory and *in situ* settings in which corals were enriched with both N and P. Our study suggests that fish communities are important drivers of ecosystem-level biogeochemical processes, and that consumer stoichiometry may provide a useful baseline to contextualize nutrient dynamics and ecosystem function in these increasingly imperiled ecosystems.

## Materials and methods

Biogeochemical processes of nutrient storage and supply [for nitrogen (N) and phosphorus (P)] were quantified across a large spatial gradient of Caribbean fish communities. We focused on four coral reef ecosystem types: *Montastraea sp.* dominated reefs, i.e. coral-rich areas dominated by *Montastraea sp*; *Acropora sp.* dominated reefs, i.e. coral-dominated reefs with high relief, typically associated with reef crests and dominated by both live and dead *Acropora* species; gorgonian plains, i.e. low-relief areas dominated by gorgonians and fleshy algae; and patch reefs, i.e. discrete hard bottom coral reefs surrounded by sand or seagrass. We also included data from mangrove and seagrass ecosystems in our analysis for comparative purposes. Fish surveys were conducted in 2002 across seven islands in the Northern Antillies that experience similar, relatively low, fishing pressure (see Mumby *et al.* (2006) and Harborne *et al.* (2008) for methodological details). Surveys consisted of three types of transects (30 × 2, 30 × 4 and 50 × 4), and individuals were identified to species level and estimated for body length (nearest cm)(see Mumby *et al*., 2006 and Harborne *et al*., 2008 for further methodological details).



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### Nutrient excretion

Bayesian statistics allow parameters to be estimated based on observed distributions (the data) and prior distributions that allow knowledge from additional studies to be applied explicitly and quantitatively (Mccarthy, 2007). In this study, we used Bayesian statistics to develop models that predict excretion rate as a function of wet mass by informing empirical data (the observed data) with bioenergetics models (used to generate the priors), thus incorporating the two most widely applied methods to estimate fish excretion (Schaus *et al*., 1997; Schreck & Moyle, 1990a; Whiles *et al*., 2009) into singular models of nutrient excretion by fishes. The modeling approach was developed such that if the empirical data were robust then the final model would primarily be a reflection of these data (i.e. the priors developed from the bioenergetics model would only minimally inform the output). When the empirical data were not robust, due to lack of individual empirical measurements on rare species or high variability in the data, the final model would then be more of a reflection of the bioenergetics models (i.e. the priors would have more influence on the output). In doing so, this approach allowed us to: (i) underpin extensive empirical data to produce extremely robust models with realistic error, and (ii) fill gaps in the empirical dataset for which empirical data was incomplete.

This modeling process consisted of four steps:

1. Bioenergetics models were developed for each family in our dataset to estimate excretion rates of N and P for a given mass of an individual fish.
2. These data were run in an initial Bayesian simple linear regression analysis (using uninformative priors), to generate parameter estimates for the slope and intercept of each model ($y = mx + b$, where $y$ is excretion rate, $x$ is the wet mass of an individual, $m$ is the slope and $b$ is the intercept) (see detailed methods for bioenergetics models below and in the Supporting Information).
3. A second Bayesian simple linear regression analysis was conducted using the empirical data. In this case we used the posterior distributions [i.e. the mean and standard deviation(SD)] for the slope and intercept generated in Step 2 as the priors for the model (Mccarthy, 2007). In this way we were able to take advantage of all available data and multiple approaches to generate robust estimates of nutrient supply by fishes.
4. The posterior distributions of these final estimates for the slope and intercept were then used to calculate the excretion rate for every fish within our survey dataset – see Ecosystem Modeling section for further explanation.

### Estimating excretion rate using bioenergetics models

Bioenergetics models use a mass balance approach given *a priori* knowledge of the natural history (e.g., diet, feeding activity), physiology (e.g., stoichiometry of predator and prey, assimilation efficiency of nutrients, consumption rates, energy density of prey), and environmental conditions (temperature) (Schreck & Moyle, 1990b; Hanson *et al*., 1997). Diet data were compiled from a suite of published works including thousands of diet analyses by the authors (Munro, 1983; Layman & Silliman, 2002; Rypel & Layman, 2008; Hammerschlag-Peyer & Layman, 2010; Layman & Allgeier, 2012) and stomach content data for every fish used in this study (J.E. Allgeier unpublished). In total, bioenergetic models for 31 genus and 25 families within our surveys were developed (see Supporting Information for further detail).

### Estimating empirical excretion rates

All fish were captured using hook and line or traps on Abaco Island, The Bahamas between 2008 and 2011. Fish were captured in coral reef, mangrove, and seagrass ecosystem types representing all of the ecosystem types for which excretion rates were modeled herein. Fish were pooled across ecosystem type, such that individuals from a given species could have been caught in any one or all ecosystems. We accounted for potential differences in resource availability across ecosystem type, which would be predicted to affect recycling rates, in two ways: (i) individuals within a given species were often collected from different ecosystem types and potential variation across ecosystem type was pooled, and thus accounted for, in our empirical models, (ii) we modeled error for diet nutrient content in our bioenergetics models (see Supporting Information). Excretion rates, for nitrogen - $NH_4^+$ and phosphorus – soluble reactive phosphorus (SRP), were measured *in situ* following the methodologies of Schaus *et al*. (1997), as modified by Whiles *et al*. (2009). Values were control corrected through the use of multiple (typically $n = 6$) identical control incubation bags without fish (see Supporting Information for details on nutrient analyses). Each fish used for excretion experiments ($n = 665$ individual fish, 79 species, 46 genera and 26 families; size range: 2–107 cm) was weighed for wet mass and measured to standard length. Fish were identified, and dissected to remove stomach contents, and then frozen for transport to Odum School of Ecology and processed for elemental content (C, N and P; see Supporting Information). The University of Georgia's Institutional Animal Care and Use Committee approved protocols for the capture and handling of fish (AUP # A2009-10003-0). Water samples (filtered with 0.45 μm Whatman nylon membrane filters) were immediately placed on ice and, within 10 h, analyzed for $NH_4$ using the methodologies of Taylor *et al*. (2007), or frozen for transport to the Odum School of Ecology (UGA) for SRP analyses using the ascorbic acid method and colorimetric analyses (APHA, 1995).

### Bayesian regressions for excretion estimates

Previous research on fish nutrient stoichiometry has shown that variation within families is relatively constrained (Vanni *et al*., 2002). As such, we used genus- or family-level bioenergetics models to inform empirical data in a Bayesian framework (i.e. bioenergetics models were employed to constrain excess variance in empirical excretion models when present). To further illustrate this approach, we follow each step taken to generate the final equation (excretion rate = wet mass × slope + intercept) (provided above) with an example



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species: gray snapper (*Lutjanus griseus*). Step 1: A genus-level bioenergetics model for *Lutjanus* was developed. Step 2: A Bayesian simple linear analyses was run using the size-specific data generated from the bioenergetics model. Step 3: A second Bayesian simple linear analysis was run using the empirical excretion data (i.e. collected from individual gray snapper; $n = 70$), whereby the priors for this model were determined by the estimates for the slope and intercept calculated from the bioenergetics data in Step 2. Step 4: The estimates (and SD) for the slope and intercept from this final model were applied to calculate the excretion rate for all gray snapper found within the dataset using Monte Carlo simulations (see section 'Ecosystem Modeling' below).

In the case of the gray snapper models, the empirical data were robust and thus the priors generated from the bioenergetics model had little influence on the final model (e.g., the slope from the empirical data alone, the bioenergetics model, and the final model were: $m_{\text{emprical}} = 0.000018$, $m_{\text{bioenergetic}} = 0.0001$, $m_{\text{final}} = 0.000022$). In cases where the empirical data was less robust, the bioenergetics model would have more influence on the final slope estimate. In all cases, the prior estimates influenced the variance associated with each parameter estimate. To account for all potential sources of error we used Monte Carlo simulations to perpetuate uncertainty into our final estimates of excretion for each individual fish (see section 'Ecosystem modeling' below).

All models were constructed at the level of taxonomic resolution for which we had optimal data. For example, if there were not sufficient empirical data at the species level to generate significant linear models of wet mass vs. excretion (at $\alpha = 0.1$, typically >8 individuals), data would be pooled among species within the same genus and informed with the appropriate genus-level bioenergetics model. Using this approach, we developed 27 species-, 25 genus-, and 16 family level models. With these models nutrient supply and storage could be estimated for 144 of the 158 species. Using this approach we accounted for 99.4% of the biomass of fishes within the field surveys.

All models were run with three chains for 50 000 iterations with a burn-in period of 1000. Data for excretion models were not transformed and assumptions of normality were met. Bayesian analysis was run using the 'rjags' package in R (R Development Core Team, 2008).

## *Ecosystem modeling*

Excretion estimates were modeled onto each individual fish ($n = 71{,}729$) using the equations generated from the Bayesian models, within all communities ($n = 172$, within 82 independent sites), to quantify species-level and then aggregate community-level rates of N and P and N : P supply and storage. Fish nutrient supply is a function of body size, organism identity, and diet (Schreck & Moyle, 1990b; Vanni *et al.*, 2002). As such, we used Monte Carlo simulations to model uncertainty into our estimates of fish nutrient supply for individual fish within the dataset. For each fish, we sampled from the posterior distribution of both the slope and intercept from our Bayesian excretion models to calculate 1000 mass-based, species-specific excretion estimates (Robert & Casella, 2010). These values were summed to provide a distribution of community-level aggregate estimates ($n = 1000$) of N, P, N : P supply. We applied the same methodology to calculate nutrient storage, whereas in this case we sampled 1000 times from the normal distribution (mean ± SD) associated with our stoichiometric estimates for body nutrient content at each taxonomic level (typically genus or species). In doing so, we modeled realistic estimates of error into each step of our analysis to create a range of values that represent a realistic distribution of nutrient supply and storage for every fish and the entire community (Supporting Information). Because we sampled from a normal distribution for each estimate, this error propagation approach should not inherently alter the mean value of the aggregate community-level excretion, but instead provide information as to how much variability there may be in this mean as a result of potential error or natural variability. Aggregate values for all supply and storage processes were averaged at the site-level (82 total sites) within each ecosystem type and analyzed using ANOVA and Tukey's HSD *post-hoc* tests.

## *Hierarchical mixed effects models*

To explore aspects of fish communities that most affect each process, we averaged all communities to the site-level ($n = 82$) and applied hierarchical linear mixed effects models and information theory (Akaike information criterion, $AIC_c$) (Burnham & Anderson, 2002), with each process of storage or supply (N supply, P supply, N : P supply, N storage, P storage, N : P storage) as a dependent variable. All models included the independent variables: Species Richness (Richness), a measure of the number of species within a community; Species Diversity (Sp Div) and Trophic Group Diversity (TG Div), measured by the reciprocal Simpsons' Diversity Index (Simpson, 1949) at the species level and trophic group level, respectively; mean Trophic Level (mean TL) as calculated following Mumby *et al.* (2006), mean Maximum Size of each species within the community (Max Size) calculated following Nicholson & Jennings (2004); and skewness of the size frequency distribution of the community ($S_{size}$) calculated by determining the skewness of the size frequency distribution of the community (Joanes & Gill, 1998), whereby the further the value deviates from zero, either positive or negative, the more small or large individuals dominate the community, respectively. Trophic group classifications were based on discrete trophic delineations following Newman *et al.* (2006) (i.e. piscivore, piscivore-invertivore, macroinvertivore, microinvertivore, herbivore, omnivore, planktivore). All models included 'ecosystem type' as a random variable (intercept only; Supporting Information) to account for variability among ecosystems. In all cases, model assumptions of normality and heterogeneity were met. We additionally calculated the percent contribution of each trophic group classification and each species for biomass, N and P for each ecosystem type. All analyses were performed using R software (R Development Core Team, 2008).

Given the consistency in the stoichiometry of nutrient supply and storage from fishes across coral reef ecosystem types



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(see Results), we explored the generality of our findings by reviewing published experiments on nutrient enrichment of coral. To date, much coral research has been conducted on the effects of nutrient enrichment on coral fitness (herein defined as growth, calcification or fertility); however, the vast majority of these studies have only been concerned with the effects of a single nutrient on coral (N or P). We were interested in how different ratios of N : P may affect coral fitness across field and laboratory experiments. To do so we searched the Web of Science database using various combinations of the words: coral, nutrient, nitrogen, phosphorus, and enrichment. Sources were also pulled from relevant literature reviews, including Szmant (2002), Fabricius (2011)and Ferrier-Pages *et al.* (2000). In total, we identified 11 studies (>2 experiments per study with up to 13 replicates) in which N and P were added simultaneously, and some form of coral fitness was measured.

## Results

Rates of nutrient supply via fish excretion (N range: 0.0003 g $m^{-2}$ $day^{-1}$–0.02 g $m^{-2}$ $day^{-1}$; P range: 6.9 × $10^{-5}$ g $m^{-2}$ $day^{-1}$–2.3 × $10^{-3}$ g $m^{-2}$ $day^{-1}$; see Supporting Information Figure S3 for comparisons with other studies) and storage of nutrients in fish body tissue (N range: 0.05 g $m^{-2}$ – 4.12 g $m^{-2}$; P range: 0.014 g $m^{-2}$ –1.4 g $m^{-2}$) significantly differed among ecosystem types. Patch reefs had the greatest supply and storage of N and P per unit area, and seagrass beds had the lowest storage and supply (Fig. 1). Ratios of N : P supply did not statistically differ among the four coral reef ecosystem types. Ratios of N : P storage were also similar among coral reef types - seagrass beds differed from gorgonian plains, patch reefs and mangroves, but not from *Montastraea*- or *Acropora*-dominated reefs (Fig. 1).

Given that our estimates are accounting for potential error in each calculation used to model these data to the ecosystem-level (as accounted for using Bayesian posterior distributions and thousands of Monte Carlo draws), the ranges and SD associated with our estimates are also of considerable interest as they indicate a realistic range at which nutrients could be supplied or stored at the ecosystem scale (Fig. 2). The SD and range

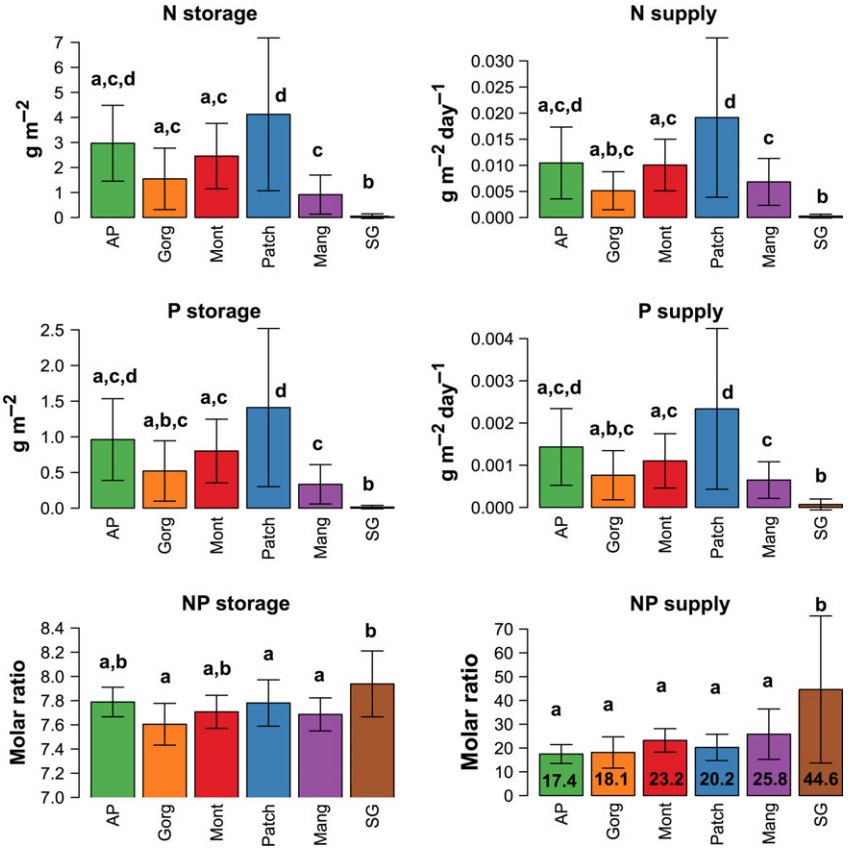


**Fig. 1** Barplots of nitrogen (N) and phosphorus (P) storage and supply, and their ratios in molar units. Error bars indicate ±1 SD. Each ecosystem is represented by abbreviations as follows: AP = Acropora sp. dominated reefs, Gorg = gorgonian plains, reorder these please to "Mont = Montastaea sp. dominated reefs, Patch = patch reefs, Mang = mangroves" and SG = seagrass beds. Letters above each column indicate significance based on Tukey HSD post hoc tests. Bars within each plot with the same letter do not significantly differ (*P*-value > 0.05). Note, SG and Patch differ only at *P*-value = 0.053 for N supply, and SG and Gorg differ at *P*-value = 0.059 for P storage.



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of values associated with the N : P supply ratios of the four coral reef ecosystems were small (gorgonian reefs: range = 7.4–27.7, SD = 6.6, *Montastraea* reefs: range = 13–48.2, SD = 4.9, Patch reefs: range = 10.1–32.9, SD = 5.5, *Acropora* reefs: range = 9.1–23.3, SD = 3.9) relative to those in seagrass (range = 4.9–262.1, SD = 30.9) and mangrove (range = 16.2–70.4, SD = 10.6) ecosystems (Fig. 2). The mean ratio of nutrient supply for the four coral ecosystems was 19.6 ± 2.6 SD.

To explore aspects of fish communities that most affect each process, we averaged all communities to the site-level ($n$ = 82) and applied hierarchical linear mixed effects models and information theory (Akaike information criterion, $AIC_c$) (Burnham & Anderson, 2002), with each process of storage or supply (N supply, P supply, N : P supply, N storage, P storage, N : P storage) as an independent response with six predictor variables (see Supporting Information for model and parameter details). We found strong support for species richness (Richness), species diversity (Sp. Div) (Simpson, 1949), and mean maximum size of the community (Max Size) for all processes with the exception of NP storage (Table 1). Trophic group diversity (TG Div) only received marginal support across models and was not significant for NP storage. The mean trophic level of the community (Mean TL) was an important predictor of NP supply (negative relationship), and moderately so for NP storage (positive), suggesting that the amount of N relative to P decreases for nutrient supply and increases for nutrients storage, although weakly, with increased average trophic level. There was a significant effect of ecosystem (random intercept only) in all models, suggesting interecosystem variability in the mean ecosystem response, but not the direction or magnitude of change (i.e. slope) associated with this relationship.

The role of species and trophic levels had strong support across ecosystem types, so we illustrated these relationships by plotting the proportion of N and P that each species and trophic group contributes to aggregate supply or storage (Fig. 3, for nutrient supply) (see Supporting Information Figure S1, S2 for nutrient storage). Notable differences can be seen between processes of storage and supply, namely that storage of N and P mirror that of biomass, whereas supply rates do not. For example, piscivores (Pisc) excrete large amounts of P relative to their biomass due to the high relative P content of their diet. Herbivores (Herb) typically contribute disproportionately small amount of P relative to their biomass. For example, *Kyphosus sectatrix* (Bermuda chub), an herbivore feeding on low quality dietary resources, has the largest proportion of biomass (14.1% of total; Rank 1) in fish communities associated with *Gorgonian* reefs, but contribute only 1.3% of the total P (Fig. 3).

We compiled published studies to assess how different ratios of N : P may affect coral fitness across field and laboratory experiments. Positive effects of nutrients on coral were found when the ratio of experimental enrichment was within a range of 11–29 N : P (Table 2), whereas very high (750 : 1) or very low (<5 : 1) N : P ratios were typically associated with no or decreased growth. This provides qualitative support for the hypothesis that coral thrive at certain ratios of nutrient supply, and is consistent with the range at which we found fish communities to supply nutrients to the four coral reef types (~20 : 1). Of particular note are experiments by Stambler *et al.* (1991), whereby coral that was supplied with a nutrient ratio of ~20 : 1 grew significantly faster than those exposed to ratios of 150 : 1, 30 : 1, and 7.5 : 1, with 45%, 65% and 62% decreased growth rates respectively (Table 2).

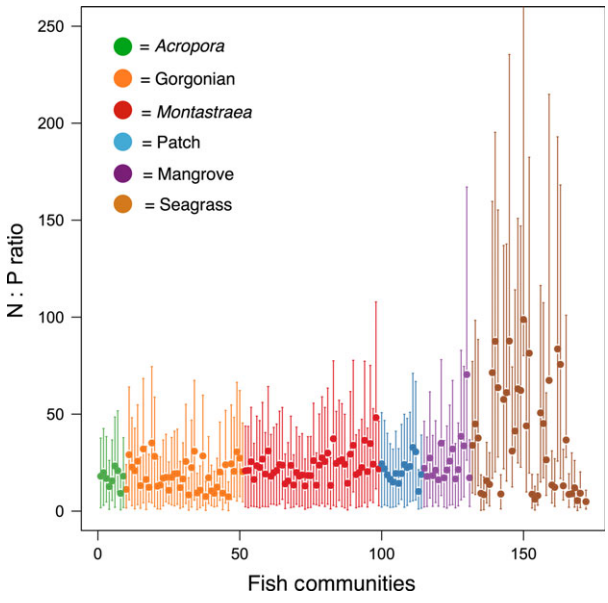


**Fig. 2** Mean (points) and standard deviation (SD) (bars) of N : P supply for 172 fish communities across six ecosystem types. Each mean and standard deviation is calculated using 1000 Monte Carlo permutations to account for potential sources of error associated with variability in nutrient excretion by all individuals within each community.

## Discussion

In coastal ecosystems, the traditional model of inputs of nitrogen (N) and phosphorus (P) is based on advective (e.g., riverine, oceanic, and atmospheric sources)(Howarth, 1988) and geologic processes (e.g., siliciclastic vs. carbonate dominated systems)(Lapointe *et al.*, 1992). In this study, we demonstrate that supply rates and



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**Table 1** Results from hierarchical mixed effects models showing relationships between aggregate nitrogen (N), phosphorous (P) and NP ratio of supply (g $m^{-2}$ $day^{-1}$), and N, P and NP ratio storage (g $m^{-2}$) of nutrients and six independent variables of community assembly: Species Richness (Richness), the number of species within a community; Species Diversity (Sp Div), and Trophic Group Diversity (TG Div); mean trophic level (mean TL) and mean maximum size per species within the community (Max Size); skewness of the size frequency distribution of the community (Ssize) acting as another metric of the size of individuals in the community. The darkness of color indicates relative amount of support for that given parameter within the model. The values associated with each parameter are the parameter coefficients of log-transformed data, whereby all data were transformed the same way for each model. The sign indicates positive or negative relationships

| | Richness | Sp Div | TG Div | Mean TL | Size Structure | Max Size |
|---|---|---|---|---|---|---|
| P supply | 1.58 | -1.00 | 0.73 | 0.67 | 0.13 | 3.15 |
| N supply | 1.82 | -0.94 | 0.22 | 0.37 | | 1.79 |
| NP supply | 0.27 | 0.12 | -0.42 | -0.36 | -0.14 | -1.07 |
| P storage | 1.76 | -0.80 | 0.47 | 0.26 | 0.15 | 3.69 |
| N storage | 1.93 | -0.91 | 0.53 | 0.31 | 0.14 | 3.56 |
| C storage | 1.92 | -0.91 | 0.48 | 0.33 | 0.13 | 3.58 |
| NP storage | | | | 0.04 | -0.01 | |

=Not significant.
=Significant, not within top 2 models.
=Significant, within top 2 but not all models.
=Strong support.

ratios provided by fish communities are substantial and warrant inclusion among the most important sources of nutrients in coastal ecosystems. We show that the quantity of individual nutrients supplied and stored by fish communities can vary markedly among coastal ecosystem types, and that these processes are strongly driven by the body size, and identity of species and trophic groups within a community. Moreover, the stoichiometric ratio at which these nutrients are supplied and stored is relatively consistent across coral reef ecosystem types despite substantial variability in the quantity of either nutrient (N or P) supplied by the fish community. Supply of nutrients by fishes, and consumers in general, may provide an alternative perspective through which to understand nutrient dynamics in coastal ecosystems.

The role of consumers in mediating ecosystem-scale biogeochemical processes has been previously described in terrestrial (Mcnaughton *et al.*, 1988; Frank *et al.*, 1994; Augustine & Mcnaughton, 2006), freshwater (Kitchell *et al.*, 1979; Evans-White & Lamberti, 2006; Mcintyre *et al.*, 2007; Small & Pringle, 2009), and marine (Pomeroy *et al.*, 1963; Haertel-Borer *et al.*, 2004; Wilson *et al.*, 2009; Allgeier *et al.*, 2013) environments. In context of marine environments, these biogeochemical pathway has been shown to affect localized rates of production for primary producers (Layman *et al.*, 2011; Allgeier *et al.*, 2013), and coral (Meyer & Schultz, 1985a, b; Grover *et al.*, 2002), as well as inorganic carbon budgets at the scale of entire oceans (Wilson *et al.*, 2009). In this study, we demonstrate that at the ecosystem-scale, fish communities contribute substantially to both nutrient storage and supply (see Supporting Information Figure S3 for other nutrient supply comparisons). The quantity of nutrients varied dramatically, with the most nutrients being supplied (per unit area) on patch and *Acropora sp.*-dominated reefs, and the least in seagrass beds. Yet, in the context of other nutrient sources, quantities provided by fish communities were found to be substantial. For example, nitrogen supplied by an average fish community in *Montastraea* dominated reefs (0.01 g N $m^{-2}$ $day^{-1}$), represent ~ 2.5 times the net N supplied from consumers in terrestrial systems (e.g., the entire bison and elk herd in Yellowstone National Park; 0.007 g N $m^{-2}$ $day^{-1}$) (Frank *et al.*, 1994)(see Supporting Information Figure S3 for other nutrient loading rate comparisons).

The fish-derived nutrient dynamic has important characteristics that distinguish it from other sources of nutrient supply in coastal ecosystems. First, estimates for fish excretion likely occur at much smaller spatial scales (e.g., in our study; tens to hundreds of square meters) than other extrinsic sources (e.g., riverine exports; tens to hundreds of square kilometers). Second, because many fish acquired their food resources within the ecosystem, some proportion of community-level nutrient supply represent recycled nutrients as opposed to 'novel' nutrients entering the system via extrinsic sources (e.g., rivers, upwelling, etc.). However, the role of translocation of nutrients across ecosystem boundaries does function as an important nutrient subsidy (or loss) between adjacent systems; for example, Haemulid fishes (grunts) often forage in seagrass by night and school on coral reefs by day



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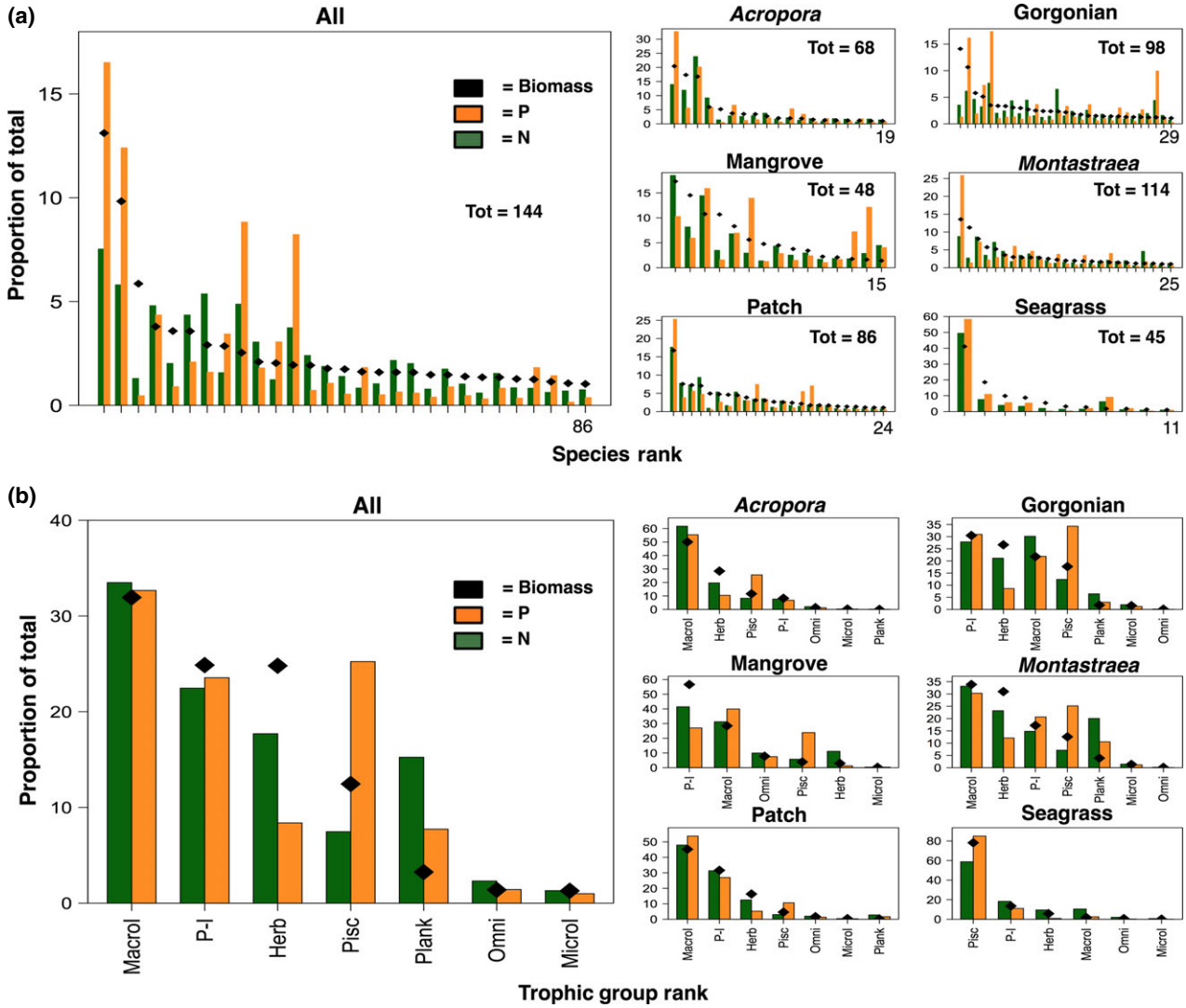


**Fig. 3** Percentage of nitrogen (N) or phosphorus (P) that individual species (a) and trophic groups (b) contribute to the total aggregate supply, relative to their biomass (black diamonds), for all ecosystems combined and each ecosystem independently. *X*-axis is the ranking of species (here only species that represent >1% of total biomass are represented (all bars per panel do not sum to 100%). Tot indicates the total number of species within each ecosystem) or trophic group by biomass. See Supporting Information Table S2 for the rank of species biomass across ecosystem types.

(Ogden & Ehrlich, 1977). The critical point is that any factor that influences availability of nutrients for primary producers and microbes, has consequences relevant at the ecosystem-scale. Like tropical rainforests, the high rates of production in coral reefs are dependent on extremely high turnover rates of biological material and energy (Vitousek & Sanford, 1986; Hatcher, 1988). Our study highlights the role of fish communities, through either translocation or internal recycling, as an important source of limiting nutrients that may be critical in fueling the high rates of production found on coral reefs (Odum & Odum, 1955; Sorokin, 1993).

Understanding how community structure influences nutrient storage and supply helps link biotic drivers to large-scale biogeochemical pathways. The mean maximum size of each species within a community (Max Size) (positive relationships), as well as species richness (positive relationships) and species diversity (negative relationships), were found to be the three most important predictors of N or P nutrient supply and storage across all ecosystem types. These results strongly implicate the role of biodiversity and species-level traits, but also basic measures of community structure, in driving biogeochemical processes (parameters such as mean trophic level were also important predictors in our



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**Table 2** Results from experimental coral enrichment studies given relative to the individual study control values. Ratios in bold indicate values within range of supply ratios found in our study

| Citation | Exp. Cond | Coral species | Time (days) | Treatment | N form | N amt (μM) | P form | P amt (μM) | Ratio (molar) | Result - relative to control | Notes |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Wiedenmann et al. 2012 | lab | 7 sp of sleractinian coral | NA | Ambient | $NH_4$ | 6.5 | $PO_4$ | 0.3 | ***21.7*** | 7.6 zoo per mg protein<br>1.6 pg algae per cell | |
| | lab | 7 sp of sleractinian coral | NA | Enriched | $NH_4$ | 4.5 | $PO_4$ | 0.006 | 750.0 | 52% decrease in zoo<br>63% decrease in algae | |
| Atkinson et al. 1995 | lab | 57 sp of hermatypic coral | NA | Enriched with upwelled ocean water | $NH_4 + NO_3$ | 5.2 | $PO_4$ | 0.6 | ***11.7*** | Increased growth | Low pH possible confounding factor |
| Ferrier-Pages et al. 2000 | lab | Stylophora pistillata | 28 | Enriched | $NH_4$ | 8–10 | $PO_4$ | 2–3.5 | 2.7–5 | Decreased growth | 13 independent ratios used |
| | lab | Stylophora pistillata | 35 | Enriched | $NH_4$ | 15–20 | $PO_4$ | 1.5–2.75 | 5.8–10.7 | Decreased growth | 10 independent ratio used |
| Meyer et al. 1983 | in situ | Acropora palmata | 365 | Enriched With Fish Excretion | $NH_4$ | 4 | $PO_4$ | 0.2 | ***20.0*** | 37%, 38% increase in tissue N and P, respectively | |
| | in situ | Porites furcata | 365 | Enriched with fish excretion | $NH_4$ | 9.6 | $PO_4$ | 0.62 | ***15.5*** | 42% increase in growth | |
| Stambler et al. 1991 | lab | Pocillopora damicornis | 44 | Enriched | $NH_4$ | 2 | $PO_4$ | 0.1 | ***20.0*** | 0.12 mm $day^{-1}$ | |
| | lab | Pocillopora damicornis | 44 | Enriched | $NH_4$ | 15 | $PO_4$ | 0.1 | 150.0 | 45% decrease | |
| | lab | Pocillopora damicornis | 44 | Enriched | $NH_4$ | 15 | $PO_4$ | 0.5 | 30.0 | 65% decrease | |
| | lab | Pocillopora damicornis | 44 | Enriched | $NH_4$ | 15 | $PO_4$ | 2 | 7.5 | 62% decrease | |
| Harrison & Ward 2001 | lab | Acropora longicyanthus | NA | Ambient | $NH_4$ | 0.65 | $PO_4$ | 0.2 | 3.3 | 90% survivorship | |
| | lab | Acropora longicyanthus | NA | Enriched | $NH_4$ | 1.65 | $PO_4$ | 1.02 | 1.6 | 68% decrease in fertility | |
| | lab | Acropora longicyanthus | NA | Enriched | $NH_4$ | 10.65 | $PO_4$ | 10.02 | 1.1 | 70% decrease in fertility | |
| | lab | Acropora longicyanthus | NA | Enriched | $NH_4$ | 100.65 | $PO_4$ | 100.02 | 1.0 | 74% decrease in fertility | |
| Koop et al . 2001 | in situ | Entire community | 450 | Enriched | $NH_4$ | 10 | $PO_4$ | 2 | 5.0 | No effect for suite of measurements | Largely no effect, but when present typically negative |
| | in situ | Entire community | 390 | Enriched | $NH_4$ | 20 | $PO_4$ | 4 | 5.0 | No effect for suite of measurements | Largely no effect, but when present typically negative |
| Reneger & Reigl 2005 | lab | Acropora cervicornis | >14 | Enriched | $NO_3$ | 4.98 | $PO_4$ | 2.09 | 2.4 | 67% decrease in growth | |
| | lab | Acropora cervicornis | >14 | Enriched | $NO_3$ | 10.01 | $PO_4$ | 4.06 | 2.5 | 86% decrease in growth | |
| Minimally detailed studies | | | | | | | | | | | |

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**Table 2** (Continued)

| Citation | Exp. Cond | Coral species | Time (days) | Treatment | N form | N amt (μM) | P form | P amt (μM) | Ratio (molar) | Result - relative to control | Notes |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Kinsey and Davies 1979 | in situ | NA | NA | Enriched | $CH_4N2O$ (urea) | 20 | $PO_4$ | 2 | 10.0 | 50% decrease in growth | |
| Tomascik and Sander 1985 | in situ | NA | NA | Enriched | $NH_4$ + $NO_3$ | Up to 3 /up to 4.5 | $PO_4$ | Up to 2 | NA | 50–90% decrease in growth | |
| Bell and Tomascik 1993 | in situ | NA | NA | Enriched | $NH_4$ + $NO_3$ | 2–8, 2–8 | $PO_4$ | 1–2 | NA | Decrease in growth | |

see Supporting Information Table S3 for detailed record of experiments.

models). Diversity, a measure of richness and evenness, had a negative relationship with all nutrient processes, such that communities that supply or store the most nutrients (and those with the highest species richness) tend to be dominated by a few species with disproportionate ecosystem effects (Fig. 3).

Diversity effects are further revealed when comparing the proportion of each nutrient contributed by a given species or trophic group relative to their biomass (Fig. 3, Supporting Information Table S2). Our models reveal that certain species and trophic groups have strong effects on the supply of particular nutrients, e.g., predators for P, herbivores for N. For example, in seagrass ecosystems, the predatory fish species, *Tylosurus crocodilus* (i.e. houndfish, species rank number 1), represented ~41% of the community biomass, but ~58% of the P supply. Consistent with our statistical models, disproportionate species effects are clearly important in influencing the net differences in nutrient storage (Figure S1, S2), and moreso supply, across ecosystems. Yet, while species effects are evident to some degree in all ecosystems, model results are largely driven by the disproportionate biomass of a few species in seagrass beds (Fig. 3). Conversely, species richness, size structure, and community composition appear to be more important predictors of fish mediated biogeochemical process in coral reef and mangrove ecosystems.

When considering the ratio at which nutrients are supplied, diversity measures were substantially less important in our models relative to community structure, e.g., mean trophic level, size distribution of the community and the Max Size. These predictors were all negatively related to N : P supply, suggesting that the larger the average size of individuals within a community (and the larger proportion of higher trophic levels within the community), the lower the N : P supply ratio. This result is corroborated by the fact that predators, which are often among the largest fish within a community, typically excrete nutrients at low N : P ratios (Schindler & Eby, 1997; Allgeier *et al*., 2013). Previous research has demonstrated that overfishing reduces the rate at which nutrients are supplied to coastal marine ecosystems (Layman *et al*., 2011) and inland waters (Mcintyre *et al*., 2007); our study extends these findings and suggests that fishing pressure, by targeting larger individuals and predators (Myers & Worm, 2003; Mumby *et al*., 2006), may also alter the ratios at which nutrients are supplied in marine ecosystems. The strong selectivity of fishers for large predators in coastal marine ecosystems, suggests overfishing should increase the NP supply ratio. Interestingly, this contrasts previous findings in freshwater ecosystems, where fishers target species with high biomass, which



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in this case were not predators, thus decreasing the supply ratio (Mcintyre *et al*., 2007).

Despite strong differences in nutrient supply rates and storage of N and P among ecosystems, there was an intriguing similarity in the stoichiometric ratios at which these two nutrients were stored (range: 7.6–7.8) and supplied (range: 17.4–23.2) among the four coral reef ecosystem types. Accordingly, the SD associated with N : P supply (as calculated by propagating uncertainty in every level of our calculations) is small across the coral reef ecosystem types (range: 3.9–6.6 SD) relative to seagrass and mangrove ecosystems (30.9 and 10.6 SD, respectively)(Fig. 2), suggesting that supply rates from coral reef fish communities do not deviate substantially from a relatively consistent ratio. The importance of consumers in regulating the nutrient stoichiometry of their environment has been a focal aspect of study in benthic (Vanni, 2002; Evans-White & Lamberti, 2006), and pelagic environments, particularly within the zooplankton-phytoplankton model system (Elser & Urabe, 1999) and fish (Kitchell *et al*., 1979; Vanni, 2002). This research dates back to Redfield (1958) and is strongly rooted in resource ratio competition theory, following the premise that a supply ratio can dictate which primary producer species will be competitively dominant (Tilman, 1982). This theory, while typically associated with short-term community dynamics, has obvious evolutionary underpinnings (Falkowski *et al*., 1998; Quigg *et al*., 2003). In resource poor environments, there is strong selective pressure for adaptations that maximize utilization of resources that are most critical for growth and fitness (Elser *et al*., 2000; Sterner & Elser, 2002; Branco *et al*., 2010). As such, there may be important evolutionary consequences for the structure and function of coral reef ecosystems if fishes, as a dominant source of nutrients, are supplying those nutrients at relatively consistent ratios (at the level of the entire community).

Nutrient supply ratios differed markedly between coral (~20 ± 2.6 SD) and seagrass (~45 ± 30.9 SD) and mangrove ecosystems (~26 ± 10.6 SD). Various ecosystem and community attributes may contribute to these differences. An initial assumption might be that, given the relatively consistent ratio at which nutrients are stored across communities (Fig. 1), differences in dietary nutrient ratios may be driving differences in supply ratios. Yet, while there are certainly differences in food availability across the ecosystem types, our statistical models suggest that community characteristics (namely size structure) may account for these trends. For example, mangrove ecosystems are widely regarded for their function as nursery habitat for coral reef fishes, and are expected to have fish communities with relatively small average body size (Adams *et al*., 2006). Small fish in theory, should excrete nutrients at a higher stoichiometric N : P ratios than larger fish, due to higher metabolic rates. Because N excretion is directly correlated to metabolism (unlike P), smaller fish are expected to excrete high quantities of N relative to their body size (Schreck & Moyle, 1990a,b; Hall *et al*., 2007), thus potentially increasing the net N : P supply ratio (but see Mcintyre *et al*., 2007). Seagrass beds often have large herbivore populations, fishes which excrete nutrients at high ratios of N : P owing to low quantity of P in dietary items. For example, *Sparisoma chrysopterum*, i.e. redtail parrotfish, the fifth most dominant species (in terms of biomass) in seagrass ecosystems accounts for 5.5% of the fish biomass, but only 0.4% of the P supply.

Coral reef, seagrass, and mangrove ecosystem types also differ substantially with respect to their capacity for nutrient uptake, processing and retention. A dominant pathway of nutrient uptake in seagrass and mangrove ecosystems is via plants and macroalgae that have the capacity to store excess nutrients in vacuoles, and are thus relatively plastic in their nutrient requirements (Sterner & Elser, 2002). In contrast, a large proportion of nutrient uptake on coral-dominated reefs is by the coral-zooxanthellae complex (i.e. the holobiont), which acquire nutrients and energy through both ambient environmental resource availability and complex host-symbiont interactions (Muscatine & Porter, 1977). One proposed mechanism for nutrient uptake by the coral holobiont is through algal symbiont-mediated nutrient uptake, whereby the *in hospite* zooxanthellae mediates nutrients from seawater through the coral tissue via passive diffusion. Thus, the relative availability of ambient nutrients can determine the rate of nutrient uptake by coral (Muller-Parker & D'elia, 1997). However, when nutrient availability in the ambient environment increases, zooxanthellae tend to enhance cell division, increasing their density and biomass within the coral host (Hoegh-Guldberg & Smith, 1989; Muscatine *et al*., 1989), as opposed to increasing nutrient content in vacuoles, as is common in other producers (e.g., seagrasses). In turn, increased zooxanthellae density may be associated with reduced coral calcification or growth (Marubini & Davies, 1996; Fabricius, 2011), suggesting a negative consequence to excess nutrient availability.

The potential ecological significance of the supply ratio found across our study sites is suggested by nutrient enrichment studies on coral. Reviewing experiments in which coral were enriched simultaneously with N and P, we found studies within the range of 11–29 N : P, demonstrated positive effects of nutrients on coral. This range of N : P enrichment is notably similar to the range at which our study



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reports nutrient supply ratios from fish communities (17.4, 18.1, 20.2, 23.2), providing qualitative support for the hypothesis that coral best thrive at certain N:P ratios. We propose that nutrient supply from fish communities may be a stabilizing factor for nutrient availability within coral reef ecosystems. In this context, alterations in the fish community, or enhanced nutrient input from allochthonous sources, could alter the ratio of nutrient supply to reefs and have a negative impact on coral health. For example, human-derived nutrients typically have much higher (e.g., N-rich fertilizer and riverine water, > 40 : 1) or lower (e.g., sewage and industrially derived sources, ~5–8 : 1) N : P ratios (Justic *et al.*, 1995a,b; Heck *et al.*, 2000; Sterner & Elser, 2002; Armitage *et al.*, 2005), relative to fish excretion. Therefore, human-derived nutrient enrichment to a coral reef environment, even at relatively low rates, may fundamentally alter the ratios of nutrient supply to coral.

Recent work has shown that fishes may be critical drivers of ocean scale inorganic carbon cycles, a role that was traditionally attributed to marine plankton and physical processes (Wilson *et al.*, 2009). Our research extends this work by providing robust estimates of N and P cycling and storage across a large region of coastal ecosystems in the Caribbean. The consistent ratio (~20 : 1) at which N and P are supplied by fishes may offer insight into the enigmatic role of nutrients within these ecosystems, and may thus provide a useful foundation from which to generate new hypotheses about the role of nutrients for coral reef ecosystem function. The implications for conservation efforts (e.g., mitigation of anthropogenic nutrients and regulations on overharvesting of fishes) may be significant, as it provides a complementary approach to understand how anthropogenic impacts are affecting these imperiled ecosystems. Developing a more holistic understanding of the regulating factors for biogeochemical processes is critical if we are to implement effective measures to ensure the future health of these important ecosystems.

## Acknowledgements

We thank K. Rennirt, D. Haynes, F. DeRosa, R. Appaldo, J. Richard, and Friends of the Environment for logistic and field support. M. Vanni and P. McIntyre were helpful in discussions about excretion methods and T. Maddox provided invaluable support for nutrient analyses. We thank D. Burkepile, the Rosemond lab and four reviewers for providing important feedback that substantially improved the manuscript. Funding was provided by an EPA STAR Fellowship, National Science Foundation DDIG to J.E. Allgeier, National Science Foundation OCE #0746164 and #1405198 to C.A. Layman, and Pew and ARC Laureate Fellowships to P.J. Mumby.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Complete model results for hierarchical mixed effects models. Parameter acronyms are as described in the text.
**Table S2.** Species biomass rank (associated with Figs 2, 3, Figure S1, S2) for each ecosystem type and all ecosystems together
**Figure S1.** Proportion of nitrogen (N) or phosphorus (P), that individual species contribute to the total aggregate storage, relative to their biomass, for all ecosystems combined and each ecosystem independently. *X*-axis is the ranking of species by biomass. See supplemental information for specific rank of species.
**Figure S2.** Proportion of nitrogen (N) or phosphorus (P), that individual trophic group contribute to the total aggregate storage, relative to their biomass, for all ecosystems combined and each ecosystem independently.
**Figure S3.** Comparisons among various sources of nutrients to coastal ecosystems.



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