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Running Head: anthropogenic nutrients alter coral-symbiont relationships

Re-wiring coral: anthropogenic nutrients shift diverse coral-symbiont nutrient and carbon interactions towards symbiotic algal dominance

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Abstract

Improving coral reef conservation requires heightened understanding of the mechanisms by which coral cope with changing environmental conditions to maintain optimal health. We used a long-term (10-month) *in situ* experiment with two phylogenetically diverse scleractinians (*Acropora palmata* and *Porites porites*) to test how coral-symbiotic algal interactions changed under real-world conditions that were *a priori* expected to be beneficial (fish-mediated nutrients) and to be harmful, but non-lethal, for coral (fish + anthropogenic nutrients). Analyzing nine response variables of nutrient stoichiometry and stable isotopes per coral fragment, we found that nutrients from fish positively affected coral growth, and moderate doses of anthropogenic nutrients had no additional effects. While growing, coral maintained homeostasis in their nutrient pools, showing tolerance to the different nutrient regimes. Nonetheless, structural equation models revealed more nuanced relationships, showing that anthropogenic nutrients reduced the diversity of coral-symbiotic algal interactions and caused nutrient and carbon flow to be dominated by the symbiont. Our findings show that nutrient and carbon pathways are fundamentally "rewired" under anthropogenic nutrient regimes in ways that could increase corals' susceptibility to further stressors. We hypothesize that our experiment captured coral in a previously unrecognized transition state between mutualism and antagonism. These findings highlight a notable parallel between how anthropogenic nutrients promote symbiont dominance with the holobiont, and how they promote macroalgal dominance at the coral-reef scale. Our findings suggest more realistic experimental conditions, including studies across gradients of anthropogenic nutrient enrichment as well as the incorporation of varied nutrient and energy pathways, may facilitate conservation efforts to mitigate coral loss.

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Introduction

Understanding processes that drive nutrient dynamics within an ecosystem is a fundamental challenge in ecology. Nutrients are often limiting resources for productivity, and thus knowledge of how nutrients cycle (i.e., via fluxes and pools) within ecosystems has important implications for theory, as well as for conservation and management of ecosystems (Chapin et al. 2011). Unlike many ecosystems where the availability of nutrients is often positively correlated with productivity, coral reefs provide a 'nutrient paradox' in that they are among the most productive

ecosystems in the world but typically thrive in highly oligotrophic environments. It is hypothesized that the high levels of coral reef productivity are due to extremely efficient nutrient recycling at both the organismal (e.g., coral-symbiotic algae) and ecosystem levels (Odum and Odum 1955, Hatcher 1988, 1990). But exogenous sources of nutrients, such as those from upwelling (e.g., Rougerie et al. 1992), plankton (e.g., Richter et al. 2001), fishes (e.g., Meyer et al. 1983), and seabirds (e.g., Graham et al. 2018), also contribute to enhanced production on coral reefs. In contrast, anthropogenic nutrient enrichment is typically associated with negative impacts to coral reefs, with some important and interesting exceptions (e.g., see Szmant 2002). Despite significant attention to this topic of nutrient enrichment (Fabricius 2005, D'Angelo and Wiedenmann 2014), our basic understanding of how altered nutrient availability changes coral nutrient dynamics remains limited.

Fundamental to coral reef nutrient dynamics and productivity are scleractinian corals that serves as the foundation species of these ecosystems. Their productivity and growth through calcification depend on internal nutrient and energy exchange between the coral host and the symbiotic algae (family: Symbiodiniaceae) within its tissues (Muscatine and Porter 1977). Through photosynthesis, symbiotic algae provide organic carbon (C) to the coral host that in turn provides the algae with re-mineralized nutrients, e.g., nitrogen (N) and phosphorus (P) (Muscatine and Porter 1977). Coral also feed heterotrophically, and thus can vacillate along a continuum between heterotrophic and autotrophic nutrient acquisition to optimize efficiency under various conditions and resource availability, such as with nutrient enrichment (Porter 1976, Anthony and Fabricius 2000, Grottoli et al. 2006, Houlbreque and Ferrier-Pages 2009). But there are costs associated with shifts from heterotrophy to autotrophy that alter organismal nutrient cycling and influence productivity (Levas et al. 2016). For example, symbiotic algae are believed to be N-limited (Falkowski et al. 1993, Yellowlees et al. 2008, Wiedenmann et al. 2013), and under increased ambient availability of N have been shown to increase in density (Muscatine et al. 1989, Falkowski et al. 1993, Ezzat et al. 2015). Increased symbiont density can stimulate competition for the intracellular pool of dissolved inorganic carbon (DIC) between the coral host and the symbiotic algae, that require DIC for calcification of the coral skeleton and photosynthesis, respectively (Marubini and Davies 1996, but see also Hoadley et al. 2016). Such scenarios that many alter C or nutrient allocation may be associated with 'harmful' effects from human nutrient inputs. Yet, depending on the coral species and the severity or duration of

changing environmental conditions, shifts in nutrient acquisition can have variable outcomes (Grottoli et al. 2006, Palardy et al. 2008, Anthony et al. 2009, Shantz et al. 2016). Understanding underlying organismal mechanisms of how corals respond to such changes remains an important challenge for coral reef ecology and conservation.

Research to understand how coral respond to different regimes of nutrient availability (e.g., anthropogenic nutrient enrichment) often isolates potential drivers through experimental manipulations in laboratory settings. Such experiments can help identify mechanistic relationships, but one concern is that the experimental environment unlikely reflects the complex setting that typifies a coral reef. Further, nutrients are often manipulated to reflect scenarios that can exceed even extreme anthropogenic enrichment conditions (reviewed by Szmant, 2002). This approach has been useful for determining thresholds of tolerance to high doses of nutrients, but the dynamic relationships that underpin the coral-symbiotic algae *in situ*, or under more realistic nutrient enrichment scenarios, have not been researched as extensively.

Here we present a long-term (10-month) experiment to test how coral-symbiont C and nutrient relationships change under altered nutrient regimes; the experiment includes a recognized beneficial scenario—fish excretion (ammonium plus phosphate enrichment; (Meyer et al. 1983, Holbrook et al. 2008, Shantz et al. 2015, Huntington et al. 2017, Shaver and Silliman 2017), and a recognized detrimental scenario—anthropogenic fertilizer (ammonium plus nitrate plus phosphate enrichment; (Dubinsky and Stambler 1996, Fabricius 2011, Thurber et al. 2014). We transplanted 128 coral fragments, from two species of scleractinian coral (*Acropora palmata* and *Porites porites*), onto 16 artificial reefs in The Bahamas, with two treatments: (*1*) varying densities of fish generated by differing artificial reef structures (n = 16 ARs, see Figure 1), and (*2*) moderate levels of nutrient enrichment from fertilizer (n = 8). For each fragment, we measured nine response variables that included: coral growth rate, symbiotic algal density, elemental nutrient content (C and N for coral and algal tissue and P for algal tissue), and natural abundance of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). Specifically, we had three objectives:

1) Test how nine response variables of coral and symbiotic algae change across the fish and anthropogenic nutrient gradient.
2) Test seven prevailing hypotheses generated from the literature of coral-symbiont nutrient and carbon relationships (see Figure 2) under the two nutrient regimes.

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3) Quantify potentially unidentified coral-symbiotic algal nutrient and carbon relationships under the two nutrient regimes.

Our study had three key strengths: (*1*) it was a long-term field experiment, (*2*) the complex, non-lethal nature of nutrient enrichment design, and (*3*) the large number of response variables measured for both coral and algae. Key findings from our study were that coral growth rate increased with fish-mediated nutrients, but anthropogenic nutrients, surprisingly, had no additional effect. Nonetheless, we found that coral-symbiont associations were different under conditions of anthropogenic nutrients, whereby diverse nutrient and C relationships under fish-mediated nutrients shifted to being dominated by the algal symbiont. These findings provide new perspectives on how anthropogenic nutrients 'rewire' coral-symbiont and coral-coral interactions, and we discuss how these might inform avenues of future research.

Methods

Experimental Design

The study was conducted in The Bight of Old Robinson, Abaco, The Bahamas (N26 20.735 W77 00.016), a semi-enclosed bay dominated by seagrass that is interspersed with sand and hard-bottom habitats (Yeager et al. 2011). We took advantage of an on-going, artificial reef nutrient enrichment study, see Allgeier et al. (2018). The study included 16 artificial reefs, constructed in December 2010 from 30 cinder blocks (~40cm x 20 cm x 20 cm) in a pyramid shape (~100 cm x 80 cm at base, 60 cm height), on sparse seagrass habitat dominated by common turtle grass, *Thalassia testudinum*, at a depth of 3-4 meters. Artificial reefs provide replicable units of discrete size from which ecological responses in the local ecosystem can be measured (Hixon and Beets 1989, Carr and Hixon 1997). Environmental conditions such as salinity, temperature (range from 29-31 C°), and irradiance are relatively consistent thought the embayment (Allgeier et al. 2010, Allgeier et al. 2011, Stoner et al. 2011), thus likely varied little from reef to reef for the duration of the experiment, and were similar to conditions on nearby coral reefs (< 1 km).

We manipulated nutrient regimes on reefs in two ways: (*1*) altered fish-mediated nutrient supply via manipulation of the reef structure (+/- F), and (*2*) nutrient enrichment via the addition of fertilizer (+/- N; Florikan 18-6-8 NPK 8 month, type 270; the N fraction of the fertilizer is

8.3:9.7 ratio NO_3^-:NH_4^+). These two treatments were imposed on the artificial reefs in a 2x2 factorial design with a randomized block (n = 16 reefs total in 4 blocks; see map Appendix A). Fish-mediated nutrient supply was altered by reducing the physical complexity of the reefs by filling in the holes of the cinder blocks creating a smooth-sided structure. In doing so, fish biomass and community composition were substantially altered, but in a continuous manner, across reefs, i.e., even the half of the reefs with low physical structure had varying fish biomass (Allgeier et al. 2018; Figure 1A, Appendix A). Reefs were placed >150 meters apart to minimize among-reef movement of more transient fish species (Carr and Hixon 1995, 1997). Cross-reef enrichment due to fertilizer was not a concern due to the highly oligotrophic nature of the system with high rates of nutrient uptake by benthic and water column producers, and previous evidence in this system that nutrient effects do not extend beyond ~8 meters away from reefs (Layman et al. 2013, Layman et al. 2016, Allgeier et al. 2018). These conditions are consistent with previous findings on the effects of nutrient enrichment on water column nutrients from an oligotrophic embayment in Hawaii (Smith et al. 1981).

Figure 1

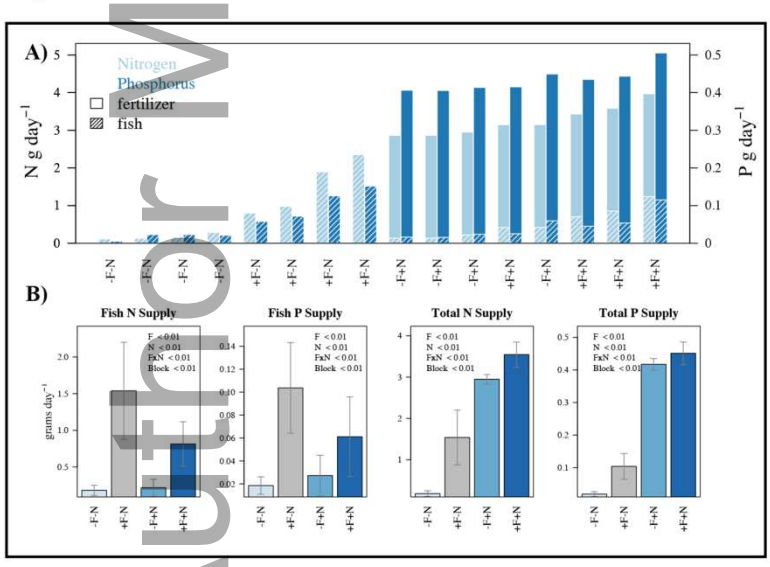

Figure 1. A) Reef-level bar plots of nutrient input (four reefs per treatment), differentiating fish-mediated and fertilizer nutrients. B) Treatment-level bar plots of nutrient input with significance tests. -/+F = low/high fish treatment, -/+N = absence/presence of fertilizer.

Fish-mediated nutrient supply was quantified by modeling species-specific nutrient supply rates onto repeated visual census data that estimated fish abundance and size. This approach has been conducted previously by the authors on these same reefs (see Allgeier et al. 2013, 2018, Layman et al. 2013), and other coral reef ecosystems in the Caribbean (e.g., Allgeier et al. 2015), and is described in greater detail in Appendix B. Importantly, because the exact density of fish could not be explicitly manipulated, the high/low fish treatment also provided a continuous gradient of fish-mediated nutrient supply across all 16 reefs used for Objectives 2 and 3 (Figure 1A).

Anthropogenic nutrient enrichment was simulated using PVC diffusers filled with slow-release fertilizer Florikan (18-6-8 NPK, type 270, 8 month; the N fraction of the fertilizer is 8.3:9.7 ratio NO_3^-:NH_4^+). Seven diffusers filled with ~500 g were suspended around each reef, on glass fritted poles, ~0.5 meters above the substrate. Diffusers have been changed every three months since December 2010 as part of an on-going enrichment study (Allgeier et al. 2018); they were changed every two months for the duration of this study to ensure more consistent enrichment effects. Because of the low ambient nutrient availability (<20 µg/L NH_4^+, <5 µg/L PO_4^-; Allgeier et al. 2010, Stoner et al. 2011) and high levels of uptake, water column nutrients are not a reliable source for estimating enrichment effects (Allgeier et al. 2013, 2018, Smith et al. 1981). Nutrient release rates from fertilizer were estimated by calculating the total mass loss of fertilizer on subset of diffusers (n=7) after deployment for 90 days (2.7 ± 0.3 SD, 0.039 ± 0.0042 SD, g $reef^{-1}$ day^{-1}, for N and P, respectively; see Appendix B and Allgeier et al. (2018) for further detail).

The likelihood that the coral fragments (located <1.5 meters from the diffusers and directly in the center of fish activity; Appendix A,B) are affected by both sources of nutrients is high because previous work on these same reefs has shown that seagrass is affected by fish nutrient supply (Allgeier et al. 2013, Layman et al. 2013) and fertilizer (Allgeier et al. 2018) at a minimum of 3, and up to 8, meters from reefs (Appendix B). We can accurately estimate the rates of nutrient supply from fishes moving within and around reefs, and from each nutrient diffuser, and thus the amount of nutrient supply at the reef-scale. But the complex nature of the environmental conditions, namely currents in a non-directional and tidal-dominated system, precludes estimation of the exact amount of nutrients that reach the coral fragments. For these reasons, we use our estimates of nutrient supply from fish and fertilizer to characterize the

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different nutrient regimes (fish only, and fish + anthropogenic nutrients) that a given coral fragment is exposed to, but we do not suggest that this precisely represents the specific nutrient supply rates or ratios that a given coral fragment experiences.

Coral Processing

Two phylogenetically diverse scleractinian species were used for this study: *Acropora palmata* and *Porites porites*. In July 2015, corals were collected on nearby reefs at a depth of 2-3 meters. Fragments were ~30-40 cm^2 in size. Before deployment to experimental reefs, the corals were photographed and weighed using the buoyant weight technique (Jokiel et al. 1978). Four individuals of each species were suspended above the reef using ~30 cm length of monofilament attached to a PVC rack (n=8 per reef; Appendix A Figure 1,2).

In May 2016, all coral fragments were removed from experimental treatments and transferred in coolers filled with seawater and processed <5 h after collection. Fragments were first weighed using the buoyant weight technique (Jokiel et al. 1978) before processing to separate coral tissue and alga cells. Coral calcification rate was calculated per day and normalized to coral surface area (mg cm^{-2} day^{-1}), which was determined using a single paraffin wax dipping at 65°C for 3 seconds (Stimson and Kinzie 1991, Veal et al. 2010).

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Host tissue was removed from the coral skeleton with an airbrush in 0.45 µm filtered seawater (Szmant and Gassman 1990). The saltwater tissue slurry was homogenized for 10 s using a Tissue Tearor (BioSpec Products, Bartlesville, OK, USA) and subsamples were taken and preserved in formalin for symbiotic algae density quantification. Cell enumerations were done via replicate hemocytometer counts (n=8) using light microscopy. Symbiotic algal densities were normalized to the skeletal surface area determined by the foil method (Marsh 1970).

Symbiotic algae and coral tissue were separated by a series of centrifugation washes. Each algal and coral fraction was microscopically verified to ensure homogeneity, and placed on pre-combusted Whatman GF/F glass microfiber filters, sealed in individual bags, and kept frozen at -20°C until analyzed. Elemental analysis for percent C and N, as well as the natural abundance of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) for coral tissue and algae were measured using a Carlo Erba CHN Elemental Analyzer (Model NA1500) coupled to Thermo Finnigan Delta V Isotope Ratio Mass Spectrometer via a Thermo Finnigan Conflo III Interface. Percent P was measured using dry oxidation-acid hydrolysis extraction followed by colorimetric analysis (Alpkem RF300). All

246 elemental laboratory analyses were conducted at the University of Georgia, Center for Applied
247 Isotope Studies.
248
249 *Statistical Analysis*
250 We used two statistical modeling approaches to accomplish our three objectives outlined
251 above.
252 • *Objective 1* tested treatment-level effects (fish-mediated and fish + anthropogenic
253 nutrients) on the nine measures of coral and algae. To do this we ran a three-way
254 ANOVA with an additional test for a block effect on all samples across all reefs
255 (response = F(+/-) * N(+/-)*species + block).
256 • *Objective 2* tested how well seven hypotheses regarding coral-symbiont relationships,
257 drawn from the literature (see Figure 2), explained the observed coral-symbiont
258 interactions under the two nutrient regimes using confirmatory structural equation
259 modelling.
260 • *Objective 3* extended the approach from *Obj. 2* to quantify potentially unidentified coral-
261 symbiont nutrient and carbon relationships under the two nutrient regimes using
262 exploratory structural equation modelling.
263 Structural equation models (SEMs) are probabilistic models specifying causal relationships
264 between predictor and response variables in a single network. SEMs can incorporate indirect
265 effects by allowing response variables to be functions of other response variables (Grace et al.
266 2012). SEMs consist of multiple individual component models (i.e., here they are linear
267 regressions) that each test for specific hypotheses. They can be used in a confirmatory manner to
268 test these specific hypotheses (used for *Objective 2*) or in an exploratory manner to identify
269 unspecified relationships and remove unimportant ones (used for *Objective 3*). Using the SEM
270 approach, we were able to move beyond conventional approaches (e.g., ANOVA used for
271 *Objective 1*) to identify and better understand the important coral-symbiont relationships as they
272 pertain to different nutrient regimes of fish and anthropogenic enrichment.
273 We generated a single SEM that consisted of seven component models – each articulating
274 specific hypothesis that were drawn from the literature (Figure 2). This same model structure
275 was used for *Objective 2* and *3* (see below). These hypotheses included relationships between
276 coral and symbiont elemental content and natural abundance of stable isotopes, as well as

277 symbiotic alga densities (cm^{-2}) and coral growth (mg cm^{-2} d^{-1}); see Figure 2 for the hypothesis-
278 based component models and appropriate citations. The hypothesized relationships outlined in
279 Figure 2 are not specified in terms of directionality (positive or negative); however, the output
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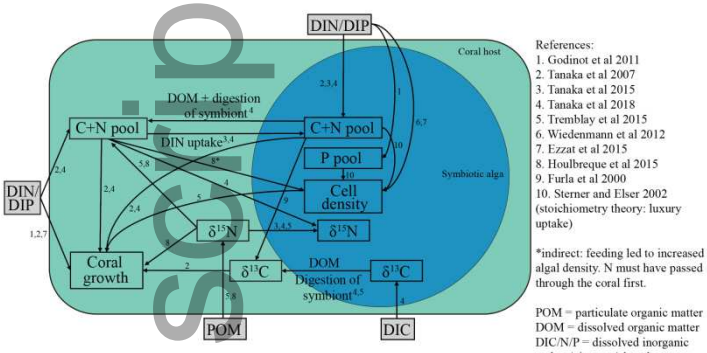

Component models that make up the complete SEM. Each model, described in text, represents a general hypothesis generated from the literature (numbers in Figure 2 correspond with citations below).

Component model	Response	Predictor(s)
1	$C{:}N_{coral}$	$Nutrients_{ambient} + \delta^{15}N_{coral}$
Coral and algae can take up N from the water column and heterotrophically feed on particulate matter with consequences for increased $\delta^{15}N$ signature of the holobiont (Tanaka et al 2018, 2015, 2007, Muscatine et al. 2005, Tremblay et al 2015)		
2	$\delta^{13}C_{coral}$	$C{:}N_{symbiont} + \delta C^{13}{}_{symbiont}$
Dissolved organic carbon produced from the photosynthetic activity of the algae ($\delta^{13}C_{algae}$) is a primary source of C to coral and thus is expected to be positively correlated with $\delta^{13}C_{coral}$. Additionally, a larger C pool in the algae means that more C is available to be transferred to the coral (Tanaka et al 2018, 2015, 2007).		
3	$C{:}N_{symbiont}$	$C{:}N_{coral} + Nutrients_{ambient}$
Ambient nutrients are expected to increase N concentrations in the algae (decreased C:N), and the recycling of nutrients via metabolic waste products are expected to influence the correlation between the coral C:N and algae C:N (Tanaka et al 2018, 2015, 2007). The SEM cannot account for recycling (called feedback loops) (Lefcheck et al 2016) and the direction of N flow therefore goes from the coral to algae. The recycling of C and N is also expressed in component model 2.		
4	$\%P_{symbiont}$	$Nutrients_{ambient}$
P concentrations in symbiotic algae tend to increase with ambient phosphate concentrations (Godinot et al 2011).		
5	$\delta^{15}N_{symbiont}$	$\delta^{15}N_{coral} + C{:}N_{coral}$
Coral heterotrophy of particulate matter from the water column, that is indicated by an increased $\delta^{15}N$ signature in the coral, can be a source of N that is mediated into the N cycling loop between the coral and algae (Muscatine et al. 2005, Tremblay et al 2015).		
6	$Density_{symbiont}$	$Nutrients_{ambient} + C{:}N_{symbiont} + \%P_{symbiont} + C{:}N_{coral}$
Algae can take up nutrients from the water column increasing the nutrient pool available for their growth (Tanaka et al 2018, 2015, 2007), which can lead to increased algal density cm^{-2} (Ezzat et al 2015, Wiedenmann et al 2012).		
7	$Growth_{coral}$	$C{:}N_{coral} + \delta^{15}N_{coral} + \delta^{13}C_{coral} + C{:}N_{coral} + \%P_{symbiont} + Density_{symbiont} + Nutrients_{ambient}$
Energy from algal photosynthates plus most other compartments will, to various degrees, have an influence on the calcification rates and growth (mg cm^{-2} d^{-1}) of the coral (Ezzat et al 2015, Houlbreque et al 2015, Tanaka et al 2007, Godinot et al 2011, Ferrier-Pagès et al 2000).		

Figure 2. Hypothesized C and nutrient relationships (or pathways) within the coral-algal symbiosis. Boxes are nutritional and physiological attributes of the coral (light blue) and the algal symbionts (dark blue). Arrows between boxes describe established pathways of nutrient and energy exchange between the coral and algae reported in the literature, as indicated by numbers and described by the component models in the table below. The hypothesized relationships outlined here are not specified in terms of directionality (positive or negative); however, output from the SEM provided directionality (Figure 4). DOM: Dissolved organic matter (i.e., photosynthates, amino acids, lipids), POM: Particulate organic matter (i.e., phytoplankton and zooplankton), DIC: Dissolved inorganic carbon (i.e., bicarbonate), DIN: Dissolved inorganic nitrogen (i.e., ammonium, nitrate), DIP: Dissolved inorganic phosphorus (i.e., phosphate).

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from the SEM provided directionality, an important benefit of using SEMs because past findings have found both negative and positive effects of, for example, nutrient supply on coral growth.

The seven component models were run using the *piecewiseSEM* package in R following Lefcheck (2016) to generate two outcomes (one for each objective). For *Objective 2*, we conducted a confirmatory analysis to test for support for the specified hypotheses, herein referred to as the '*Confirmatory model'*. For *Objective 3*, using the same initial SEM with the seven component models, we incorporated a stepwise process to explore important unspecified relationships and eliminate specified relationships that were not significant from *Objective 2* (Figure 2). By considering alternative models, we identified the best candidate model according to AICc (corrected for sample size) and Fisher's C statistic (Grace et al. 2012), herein referred to as the '*Exploratory model'*.

The stepwise process was conducted as follows: (*1*) Shipley's test of directional separation (Shipley 2009) was run across the component models to determine missing significant relationships between variables present in the SEM; (*2*) the missing relationships were added, and this alternative model was run to determine the significance of model relationships, whereby those with *p*-value>0.1 were removed – this step was conducted because some models with marginally significant relationships had lower AICc (Burnham and Anderson 2002); and (*3*) we then tested a series of candidate models by removing any non-significant relationships (*p*-value>0.05). The goodness-of-fit (Fisher's C statistic) and AICc were used to assess the best model. To assess model validity, we plotted residuals against fitted values for each component model. The data were hierarchically structured and thus each component model included random effects for block, reef, and species. Although understanding the species-level effects is of interest, we used species as a random effect for two reasons: (*1*) despite being significant in our treatment-level analyses, there were no significant interactions between the species term and either nutrient treatment, suggesting that although there was a different mean effect by species, the magnitude of change across treatments was similar (i.e., different intercept but not slope), and (*2*) given the number of parameters of interest we had insufficient data to run separate models for each species and for each nutrient regime, as the ratio of sample size to variables should not be less than five (Grace et al. 2015). Variables that did not follow a normal distribution were either log- or square root-transformed.

The *Confirmatory model* and *Exploratory model* approach were both applied to each nutrient regime scenario in our experiment, e.g., using the continuous gradient of fish-mediated nutrient supply with no fertilizer (+F-N or –F-N), and fish-mediated nutrient supply with fertilizer (+F+N or –F+N). This resulted in four separate SEMs (two each for *Objective 2* and *3*), each represented by path diagrams, allowing simple visualization of important relationships (or pathways) in the model (e.g., Figure 4). Standardized regression coefficients for each relationship and conditional r^2 values for each component model were used to compare differences among models.

Results

The experimental design created significantly different nutrient regimes across treatments (Figure 1B), consistent with previous research on these reefs (Allgeier et al. 2018). Of the 128 individual coral fragments 13 died (3, 5, 3, and 2, from -F-N, +F-N, -F+N, and +F+N treatments, respectively), only one of which was *P. porites*. An additional eight were excluded due to large tissue lesions that likely affected fragment growth (half of which were from fertilized reefs), leaving 47 and 60 live coral fragments of *A. palmata*, and *P. porites*, respectively.

Objective 1) Coral growth (mg cm^{-2} day^{-1}) and coral C:N increased significantly in the presence of high fish-mediated nutrient supply, but anthropogenic nutrients had no additional negative or positive effect (Figure 3). There were no significant effects due to anthropogenic nutrient enrichment (Figure 3). The interaction term between fish and anthropogenic nutrients was never significant. Species differed in the magnitude of their response to treatments in all cases, with the exception of symbiotic algal $\delta^{15}N$ in which there was no significant difference. In no case did species differ in the direction of the response, i.e., there were no significant treatment-species interactions. A significant block effect was found for algal C:N (p-value = 0.05), algal $\delta^{13}C$, and algal $\delta^{15}N$.

Objective 2) Our '*Confirmatory model'* allowed us to test seven hypotheses of coral-symbiotic algal nutrient and carbon interactions drawn from the literature (Figure 2), and found limited support for most under either nutrient regime scenario (Figure 4). These hypotheses were characterized by specific coral-symbiotic algae nutrient relationships, called 'pathways' following Grace et al. 2012, and are indicated by black and red arrows (positive and negative, respectively) of which only a few were significant (p<0.05, solid arrows; Figure 4). Key findings from these models were: (*1*) the overall hypothesis support was similar across the two nutrient regimes, largely because most pathways were not significant in either (p>0.05, dashed arrows;

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Results:

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How are the species differences accounted for? There are many differences, but the conclusions don't seem to address this. What this actually mean for the physiology of the coral ?

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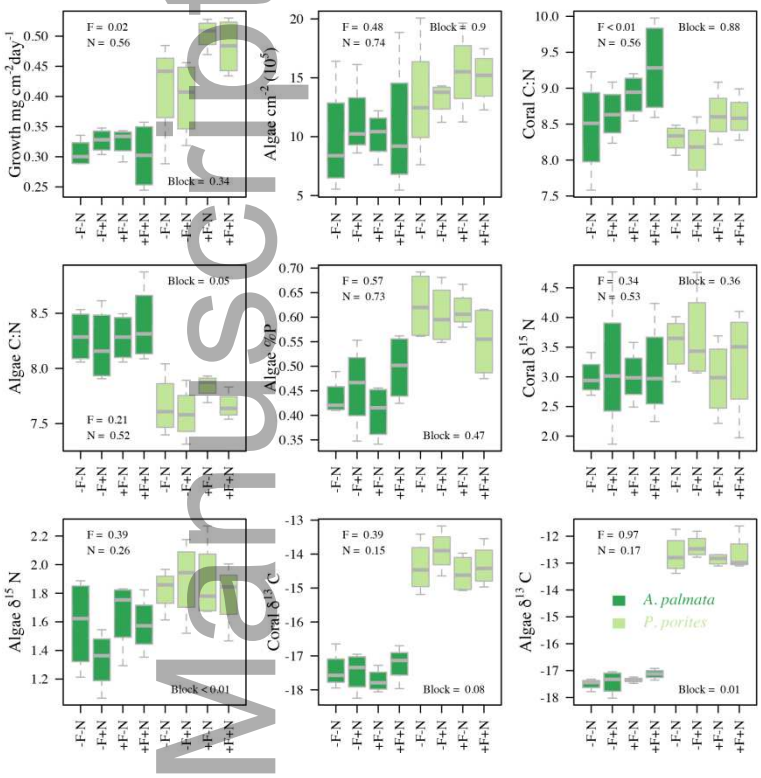

Figure 3. Treatment-level means for each of the nine variables, measured for each coral fragment, with associated significance for a three-way ANOVA, including a test for a block effect. -/+F = low/high fish treatment, -/+N = absence/presence of fertilizer. There were no significant F*N interactions. Species differed in the magnitude of their response to treatments in all cases, with the exception of symbiotic algal $\delta^{15}N$ in which there was no significant difference. In no case did species differ in the direction of the response, i.e., there were no significant treatment-species interactions. *P. porites* and *A. palmata* are light green and dark green respectively.

Figure 4a and b); (*2*) algal %P positively affected algal density ($p<0.05$) in the fish-only treatments (Figure 4a; Figure 2, component model 6); (*3*) coral $\delta^{13}C$ was positively correlated with coral growth ($p<0.05$) only under the fish only regime (Figure 4c: Figure 2, component model 7); (*4*) under the anthropogenic nutrient regime, coral $\delta^{15}N$ was negatively correlated with coral C:N ($p<0.05$; Figure 4b; Figure 2, component model 1); (*5*) Component model 2 was partially confirmed by the correlation between algal and coral $\delta^{13}C$; and (*6*) Component model 3 was partially confirmed in that algal C:N is correlated to coral C:N. In summary, the

Confirmatory models did not provide an overall good fit to the data in either nutrient regime scenario; Fisher's C *p*-value = 0, and a model is interpreted as being consistent with the data if the Fisher's C statistic is small and its *p*-value is large, i.e., alpha > 0.05 (Grace et al 2012).

Objective 3) Our goal was not to belabor confirmation or rejection of the literature-generated hypotheses, particularly because they were all generated under different conditions and with various coral species. Instead, a primary motivation was to use previous findings to frame our *Exploratory models* with the objective to identify novel pathways and generate new hypotheses from which to motivate future research (Grace 2012, Lefcheck 2016). The *Exploratory models* were generated using the *Confirmatory model* as the initial model structure to begin the stepwise model selection process. For both nutrient regimes, the Shipley's test of directed separation indicated that many significant, and reasonably plausible, pathways were missing. The *Exploratory models* allowed us to identify the pathways that most accurately represent coral-symbiont interactions by including previously missing, and excluding non-significant, relationships to generate the best-fit model (see Figure 4 for differences in AICc scores between *Confirmatory models* and *Exploratory models*).

A key finding from the *Exploratory models* was that under the fish only regime, coral-symbiotic algal interactions were more diverse in terms the number of significant pathways between variables (Figure 4c); under elevated anthropogenic nutrient enrichment, these pathways became strongly mediated through the algal symbiont (Figure 4d). A useful aspect of SEMs is that they identify which variables could not be explained by any other parameter in our model, called exogenous variables. Under the fish only regime there were three exogenous variables, coral $\delta^{15}N$, algal $\delta^{13}C$, and coral C:N. In contrast, under the anthropogenic nutrient regime, there was only one exogenous variable, algal $\delta^{13}C$, highlighting the dominance of this variable for all pathways.

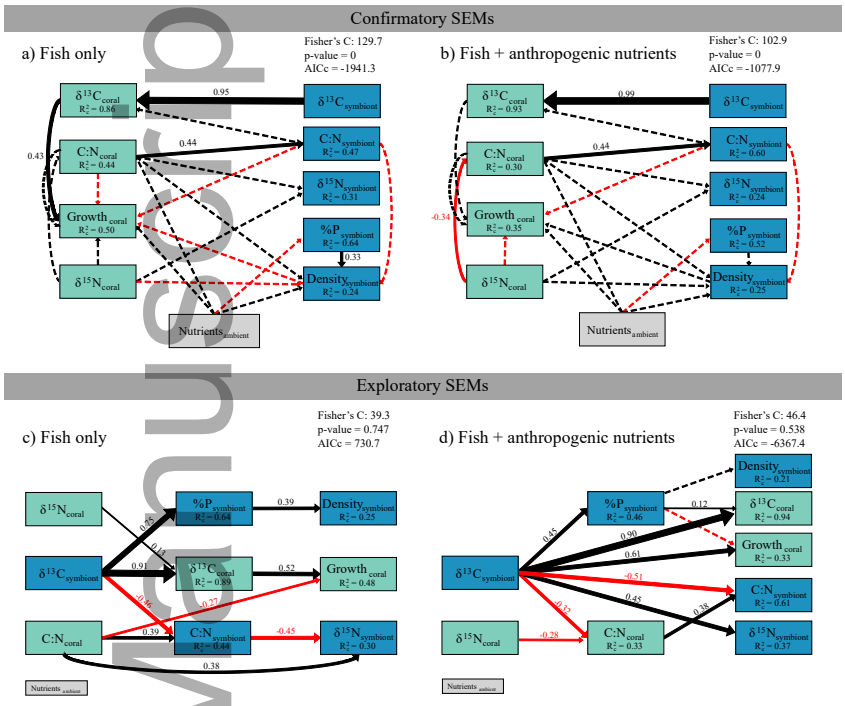

Figure 4. Path diagrams of the *Confirmatory* and *Exploratory* SEMs that depict the significant (solid arrows) and non-significant (dashed arrows) relationships between coral (light blue) and algal (dark blue) variables in a single SEM. Arrow thickness corresponds to the standardized regression coefficient (-1 to 1), and arrow color refers to the direction of the relationship (black: positive, red: negative). The Confirmatory models include all of the tested hypotheses. The exploratory models are the best-fit models generated through a stepwise process for each nutrient enrichment scenario. Excluded variables (those that were not important for the model) are shown in smaller boxes (ambient nutrients in c and d). Model statistics include conditional R^2 (R^2_c) for the response variable of each component model, Fisher's C (a lower score indicating a better fit), *p*-value (alpha = 0.05), and AICc for each complete SEM.

The *Exploratory model* for the fish only nutrient regime showed that coral growth was directly affected by coral $\delta^{13}C$ (positively) and coral C:N (negatively)(Figure 4c; Figure 2, component model 7). Under the fish-only nutrient regime, coral growth was indirectly mediated through coral $\delta^{13}C$ by two factors: symbiotic algal $\delta^{13}C$ (positive) – this strong correlation confirmed that corals derive most of their C via algal produced photosynthate (Figure 2;

component model 2); and coral $\delta^{15}N$ (positive) - showing that heterotrophic feeding also positively contributes C flow to the coral. Symbiotic algal density had no direct or indirect effect on coral growth. Ambient nutrients were excluded from the best-fit model, as they did not significantly affect any other variable and did not improve the model fit – an expected finding because the random effect on reef in our model largely accounted for the variation in nutrient input. When this random effect was removed, ambient nutrients positively affected coral C:N and coral growth.

The best-fit *Exploratory model* under the anthropogenic nutrient scenario showed that coral growth was only influenced by symbiotic algal $\delta^{13}C$ (Figure 4d). Despite being non-significant, effects of algal %P on coral growth (negative) and on symbiont density (positive) were retained in the model because of an improved fit relative to the model without these pathways (ΔAICc 7209.3). An additional difference associated with the presence of anthropogenic nutrients was the decoupling of coral-coral C or nutrient pathways, e.g., under the fish-alone nutrient regimes there were three direct and one indirect, coral-coral C or nutrient pathways, whereas under the anthropogenic regime there was only one. Environmental nutrients were excluded from the best-fit model as it was not significantly affected by any other variable and did not contribute substantially to the model fit.

Discussion

The mechanisms that underpin how coral respond to anthropogenic nutrient enrichment and the degree to which this relates to global declines in coral reef health remain poorly understood (Szmant 2002, D'Angelo and Wiedenmann 2014). Central to this problem is identifying how nutrient enrichment can alter the interaction between the coral host and its symbiotic algae. Previous work has been dominated by experiments that expose coral to high levels of nutrients that often exceed those found on eutrophied reefs, with the expectation of negative effects on coral. The goal of our study was to shift perspectives by exploring the effect of *in situ* enrichment from 'beneficial' nutrients (fish excretion only), and the combination of 'beneficial' and 'harmful' (anthropogenic nutrients), where all treatments were *a priori* anticipated to be non-lethal. Whereas findings from our treatment-level analyses corroborate previous research showing beneficial effects of fish-mediated nutrients for coral growth (Meyer et al. 1983, Holbrook et al. 2008, Shantz et al. 2015, Huntington et al. 2017, Shaver and Silliman 2017),

Commented [JEA7]: R2:
Discussion: Many statements are made without any confirmation of the data that was collected. For example, line 392: needs refs, why is fish poop beneficial, it isn't always? There are no refs to check this statement. Additionally, it would help to put this in context of the results that you actually measured.

I think that overall there is great information in this paper, but it needs to be rewritten with better context and explanation of why and what was done. Additionally, please check for sweeping statements that are not supported by your data.

Commented [JEA8]: Secondly, while it is novel that nutrients had an impact of the symbiotic nutrient metabolism without any adverse affects for coral health, I don't think it is suprising. A very similar "transitional" state of the nutrient metabolism from symbiont mutualism to symbiont parasitism has been shown before in relation to thermal stress. Gibbin et al 2018 showed that short-term termperature acclimation resulted in reconfiguration of carbon and nitrogen metabolism when the coral-algal symbiosis, and without any physiological impact. In this instance, it was not known whether this change was a result of host acclimation or symbiont parasitism. Other experiments have shown positive (e.g. Krueger et al. 2017) or negative (e.g. Baker et al. 2018) responses of corals to sub-bleaching thermal stress associated with changes to carbon and nitrogen metabolism. It seems to me that a transition from a cooperative to uncooperative nutrient metabolism may well be pre-cursor to many stress responses in corals, regardless of the environmental driver (reviewed in Morris et al. 2019 for coral bleaching). I think this would be worth mentioning as well.

anthropogenic nutrients were found to be relatively benign. These findings contrast general expectations of negative effects of nutrient enrichment, but support findings that moderate enrichment may positively affect coral growth (D'Angelo and Wiedenmann 2014, Shantz et al. 2016). Despite this, a more comprehensive analysis of all coral and symbiotic algae relationships revealed that anthropogenic nutrients highly altered internal nutrient and carbon relationships such that they were dominated by the algal symbiont. These findings highlight a striking parallel between how anthropogenic nutrients promote symbiont dominance with the holobiont, and how they promote macroalgal dominance at the coral-reef scale (Fabricius 2005, D'Angelo and Wiedenmann 2014). We hypothesize that our experiment captured coral in a transition state, from a mutualistic symbiosis to a potentially antagonistic interaction (D'Angelo and Wiedenmann 2014, Shantz et al. 2016) , and provide a new perspective on the mechanisms by which a single stressor—nutrient enrichment—can compromise coral such that they are more susceptible to additional stressors such as overfishing or climate change.

Our experimental design allowed us to analyze results categorically at the treatment-level (ANOVAs), and in a continuous regression framework (SEMs). From the treatment-level perspective, findings revealed that fish-mediated nutrients enhanced coral growth rates – corroborating previous findings (Meyer et al. 1983, Holbrook et al. 2008, Shantz et al. 2015, Huntington et al. 2017). Addition of anthropogenic nutrients did not change the overall positive effect of fish-mediated nutrients, demonstrating that we achieved our goal of non-lethal enrichment, which was supported by a ~90% survivorship of transplanted coral – a high success rate for coral transplantation (Okubo et al. 2005). At face value, this finding contrasts previous findings that anthropogenic nutrients are detrimental for coral growth and survival (Marubini and Davies 1996, Fabricius 2005), particularly because the fertilizer treatment did not significantly alter any response variable. However, this is an important finding in light of the results from our more comprehensive SEM analysis, as it demonstrates coral were able to maintain net positive growth and homeostasis in internal nutrient pools despite changes in the way in which the coral mediates nutrients between these pools. One hypothesis supporting these findings is that coral have likely evolved relatively high levels of flexibility in coping with variable nutrient inputs at the reef-scale from sources, such as upwelling (Rougerie et al. 1992) and great variation in consumer-mediated nutrient supply (Allgeier et al. 2014), but also spatially within reefs at more localized scales (Meyer et al. 1983, Holbrook et al. 2008, Shantz et al. 2015, Graham et al. 2018,

Savage 2019). In a more general sense, these findings suggest the outward appearance of coral at the individual- or reef-scale may be an insufficient measure of stress, and that additional assessment of nutrient and energy pathways may be needed to assess reef health.

Extending our analysis by using SEMs to fit more complex models revealed a more nuanced understanding of the dynamics of the coral-symbiont system. Our *Confirmatory model* approach allowed us to simultaneously test seven hypotheses of coral-symbiont inorganic nutrient and carbon interactions drawn from the literature in a single SEM that was applied independently to the fish-only (F+N- and F-N-), and the fish + anthropogenic nutrient regimes (F+N+, F-N+; Figure 2 and 4a and b). These models confirmed an essential energy pathway of C transfer between coral and algae with the directional positive relationship between coral and algal $\delta^{13}C$ (Figure 4a and b) – a hallmark relationship of all animal-algal mutualisms that indicates algae are providing their host with fixed C through photosynthesis (Venn et al. 2008). Whereas other hypothesized relationships were confirmed (e.g., coral $\delta^{13}C$ – coral growth, coral C:N – algal C:N, coral $\delta^{15}N$ – coral C:N, algal %P – algal density) the overall poor model fit for both *Confirmatory models* suggests that coral growth is more likely mediated through additional pathways.

Building on our *Confirmatory models* and the hypotheses provided by past work (e.g., cited studies in Figure 2), a key outcome of our *Exploratory models* was that the anthropogenic nutrient regimes fundamentally restructured nutrient and C coral-symbiont interactions (Figure 4). Under conditions of fish-only nutrients, coral growth was supported directly by two pathways: (*1*) increased availability of N in coral tissue (negative relationship with coral C:N), and (*2*) higher availability of photosynthate (positive relationship with coral $\delta^{13}C$; Tremblay et al. 2014, Tremblay et al. 2015, Tanaka et al. 2018). Coral growth was additionally supported by two indirect pathways: (*1*) the positive relationship between algal $\delta^{13}C$ and coral $\delta^{13}C$ showing a positive relationship between algal photosynthesis and coral growth, and (*2*) the positive relationship with coral $\delta^{15}N$ suggesting that coral were also feeding heterotrophically (Muscatine et al. 2005) and that this positively influenced growth.

In contrast to the more diverse pathways that underpinned coral growth under fish-only nutrient enrichment, coral growth was likely only supported by photosynthate from the algae in the anthropogenic nutrient regime as indicated by a direct positive pathway from algal $\delta^{13}C$ (Muscatine et al. 2005). In fact, a key finding from the *Exploratory* anthropogenic nutrient model

was overall algal dominance of all nutrient and C pathways (Figure 4d). For example, algal $\delta^{13}C$ was linked to every other variable in the model, with the exception of coral $\delta^{15}N$, via six direct and two indirect pathways, whereas in the fish only model algal $\delta^{13}C$ was associated with only three direct and three indirect pathways. These findings are consistent with past work that shows that moderate nutrient levels can increase algal dominance in the holobiont without necessarily having an effect on coral growth (Tanaka et al. 2007). However, algal proliferation may lead to stress and increasingly antagonistic interactions for the coral - the primary mechanism for this being that increased algal densities create a greater demand of resources on the coral, shifting the mutualism toward antagonism with negative consequences for growth or calcification (Marubini and Davies 1996), and/or increased susceptibility to bleaching (Baker and Cunning 2012, Wiedenmann et al. 2013). Yet, we found no evidence that algal cell density increased in response to the anthropogenic nutrient enrichment regime. Instead, we found that algal cell density was no longer significantly predicted by any coral or algal variables (Figure 4D), as was the case under the fish-only conditions (e.g., $\%P_{algae}$ was positively related to algal density; Figure 4C). It is possible, however, that the increased ambient availability of nutrients from our fertilizer disrupted internal nutrient dynamics such that the algal density was more strongly governed by extrinsic nutrient availability. Further, previous research has shown that the presence of nitrate from anthropogenic nutrients (that includes NO_3^- and NH_4^+, whereas fish excretion is exclusively NH_4^+) would in of itself encourage algal proliferation within the host (Ezzat et al. 2015, Shantz et al. 2016). As such, it is possible that other metrics of symbiont growth would have supported this expectation (e.g., increased cell size, or density per host protein or lipid content). Nonetheless, we hypothesize we did not find increases in algal density because of the moderate level of our enrichment regime. We suggest this provides further support that our experiment captured coral at a transition state whereby further increases in ambient nutrient availability would result in increased algal densities with potentially harmful implications for the coral host.

Our findings help identify new, and hone existing, hypotheses that we hope can inform future research to understand coral-symbiotic algal interactions and how they respond to changing environmental conditions. Resulting Hypothesis 1: *Considering interactions between the coral host and the algal symbiont in a traditional food web context may be a useful framework through which to quantitatively understand coral health*. The successful application of SEMs in our analysis highlights the potential utility of framing the complex coral-algal symbiont relationships

Commented [JEA9]: Lines 468-479: Although symbiont cell density did not increase per surface area under anthropogenic nutrients, maybe other metrics of symbiont growth changed. For example, maybe they increased in density per host protein instead. Maybe they invested in increasing chlorophyll production, cell size and nutrient storage. While perhaps the nutrient content/isotope evidence presented suggests this is not the case, I don't think it can be ruled out and it should be mentioned.

in a food web context whereby food web networks (e.g., Dunne et al. 2002), or interaction strengths (e.g., McCann et al. 1998), could directly quantify the diversity and stability of these interactions under changing environmental conditions. The use of isotopes, either natural abundance, or tracers, could also complement this approach by providing means to quantify interaction strengths. Resulting Hypothesis 2: *Coral-symbiotic algal interactions exist along a continuum between mutualism and antagonism that is highly dynamic.* Our findings provide new evidence in support of this long-standing hypothesis by showing that anthropogenic nutrients can to some extent appear benign (e.g., no effect on growth), but also fundamentally shift internal processes. This strongly suggests that corals can persist under highly variable relationships with their symbiont. Similar evidence suggest that coral subjected to short-term temperature shift can exhibit substantial reconfiguration of their coral-symbiont interactions that appear 'benign' in that they do show pronounced external changes (Morris et al. 2019). Therefore it appears that the transition state that we hypothesize captured in our study, may also occur from additional stressors. A key challenge is to extend experiments to include an even greater range of nutrients (or other stressors) such that species interaction dynamics can be more rigorously captured. Resulting Hypothesis 3: *The ratio (N:P) of nutrient supply may be more important than supply rate for understanding nutrient enrichment for coral.* This hypothesis is rooted in the resource ratio hypothesis (Tilman 1982), ecological stoichiometry (Sterner and Elser 2002), and more contemporary work with corals (e.g., Wiedenmann et al. 2013). It is also supported by this study in that the N:P ratio across the two nutrient regimes differed more than the nutrient supply rates (Allgeier et al. 2018). Previous work has supported the hypothesis that fishes supply nutrients at an optimal ratio for coral, and this may be disrupted by the low N:P ratio of anthropogenic nutrients (Allgeier et al. 2014). However, testing this requires overcoming the fundamental challenge for any field-based study where water movement and/or fish movement are present – i.e., knowing the exact amount of nutrients coral are subjected to, a key limitation in this study.

Substantial debate remains over the role of anthropogenic nutrient enrichment for coral health (see discussion in Bruno et al. 2019). A key challenge is that nutrient enrichment often does not result in drastic changes in ambient nutrient avialability, making it difficult to quantify net effects to ecosystems. For example, in a long-term study over the course of nearly four decades in the Floriday Keys, Lapointe et al. (2019) found a marginal increase in dissolved inorganic nitrogen over time, and negligible increases in NH_4^+, NO_3^-, or PO_4^{3-}, despite the

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Secondly, while it is novel that nutrients had an impact of the symbiotic nutrient metabolism without any adverse affects for coral health, I don't think it is suprising. A very similar "transitional" state of the nutrient metabolism from symbiont mutualism to symbiont parasitism has been shown before in relation to thermal stress. Gibbin et al 2018 showed that short-term termperature acclimation resulted in reconfiguration of carbon and nitrogen metabolism when the coral-algal symbiosis, and without any physiological impact. In this instance, it was not known whether this change was a result of host acclimation or symbiont parasitism. Other experiments have shown positive (e.g. Krueger et al. 2017) or negative (e.g. Baker et al. 2018) responses of corals to sub-bleaching thermal stress associated with changes to carbon and nitrogen metabolism. It seems to me that a transition from a cooperative to uncooperative nutrient metabolism may well be pre-cursor to many stress responses in corals, regardless of the environmental driver (reviewed in Morris et al. 2019 for coral bleaching). I think this would be worth mentioning as well.

tremendous amount of nutrients entering the system from the Florida Everglades. While Lapointe et al. (2019) claimed that these increases in DIN led to reduced coral cover, research in the same region reported that that live coral cover was positively correlated to the proximity to shore on 84 patch reefs, indicating that increased land-based nutrients may actually be promoting coral health (Lirman and Fong 2007). The fact that outcomes to nutrient enrichment on coral reefs are so variable, plus findings from our study, provide a strong case that nutrient enrichment effects on coral reefs maybe in fact common, but simply highly cryptic. The significance of this for conservation is that improved monitoring of coral reefs to understand the degree to which they are stressed, may require additionally sampling coral and algal tissue to characterize nutrient and energy pathways.

Insights from our research may also benefit the study of coral survivorship, and development beyond early recruitment - processes that are considered to be essential for maintaining reef reslience (Gleason and Hofmann 2011, Doropoulos et al. 2016). Immediately following settlement, coral are particularly susceptible to stressors (Graham et al. 2008), and further understanding of the nutrient and energy pathways that underpin the early colonization of the coral by symbiotic algae may provide important insights into this critical life history stage (Harii et al. 2009, Graham et al. 2013, Humanes et al. 2017). Further, this approach may help identify individuals or species that may be most resilient to stress associated with tranplantation. Our findings suggest that utilization of more realistic experimental conditions, including studies across gradients of anthropogenic nutrient enrichment as well as the incorporation of quantifying nutrient and energy pathways, may facilitate conservation efforts to mitigate coral loss.

Our study brings to light new perspectives and hypotheses about the effects of nutrient enrichment for coral. We provided additional support for the important role that consumers play in mediating nutrients in near-shore environments (Allgeier et al. 2017) and highlighted the cryptic effects anthropogenic nutrients can have in these systems. Interestingly, the patterns that emerge in our findings also parallel our understanding of the impacts of nutrient enrichment on coral reefs at the ecosystem scale – anthropogenic nutrients shunt energy away from coral pathways and through algal pathways. This pattern can only be speculated on at this point, but is suggestive of the consistent manner in which human activity tends to rewire ecological interactions at different scales of biological organization.

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Figure 1

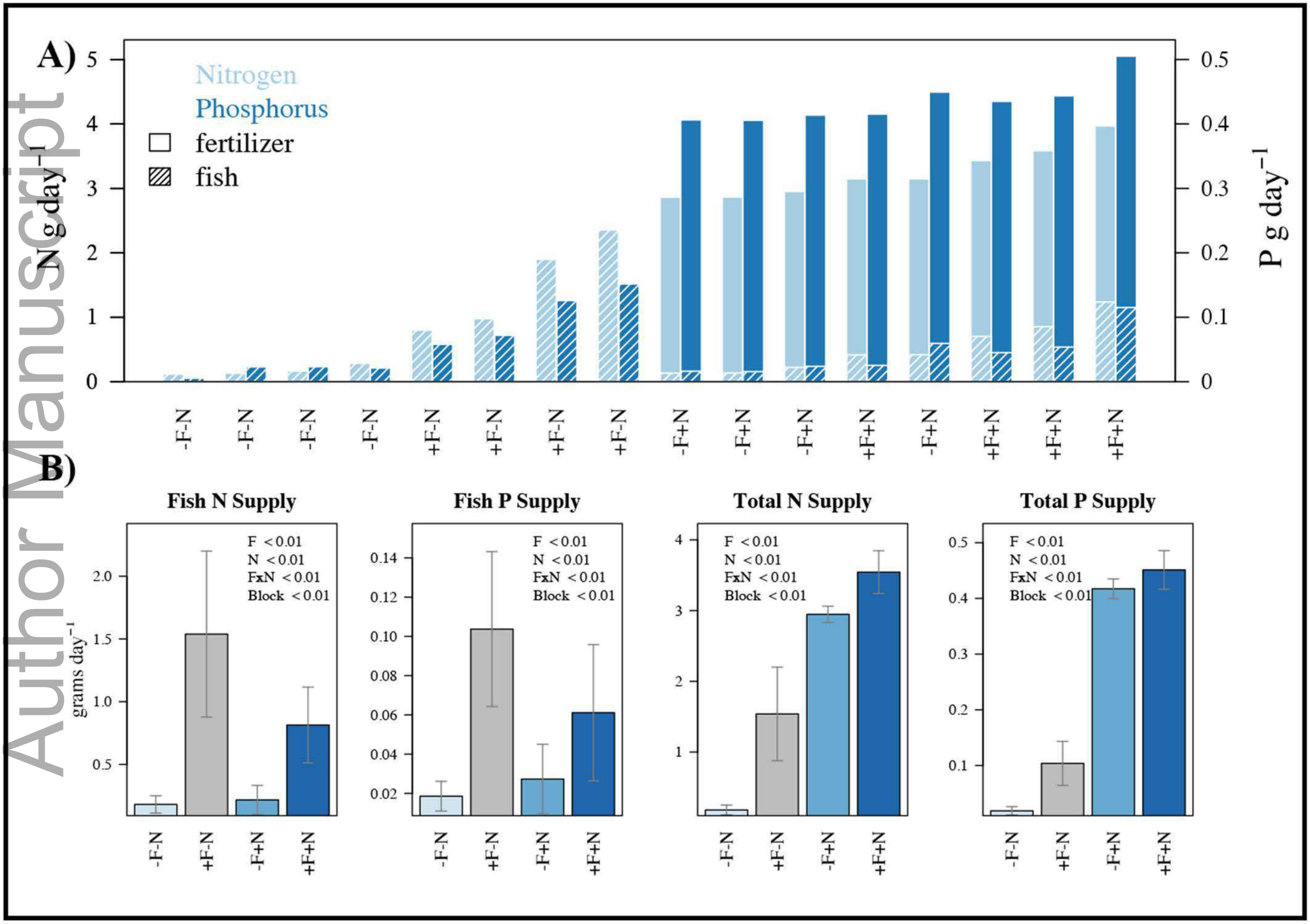
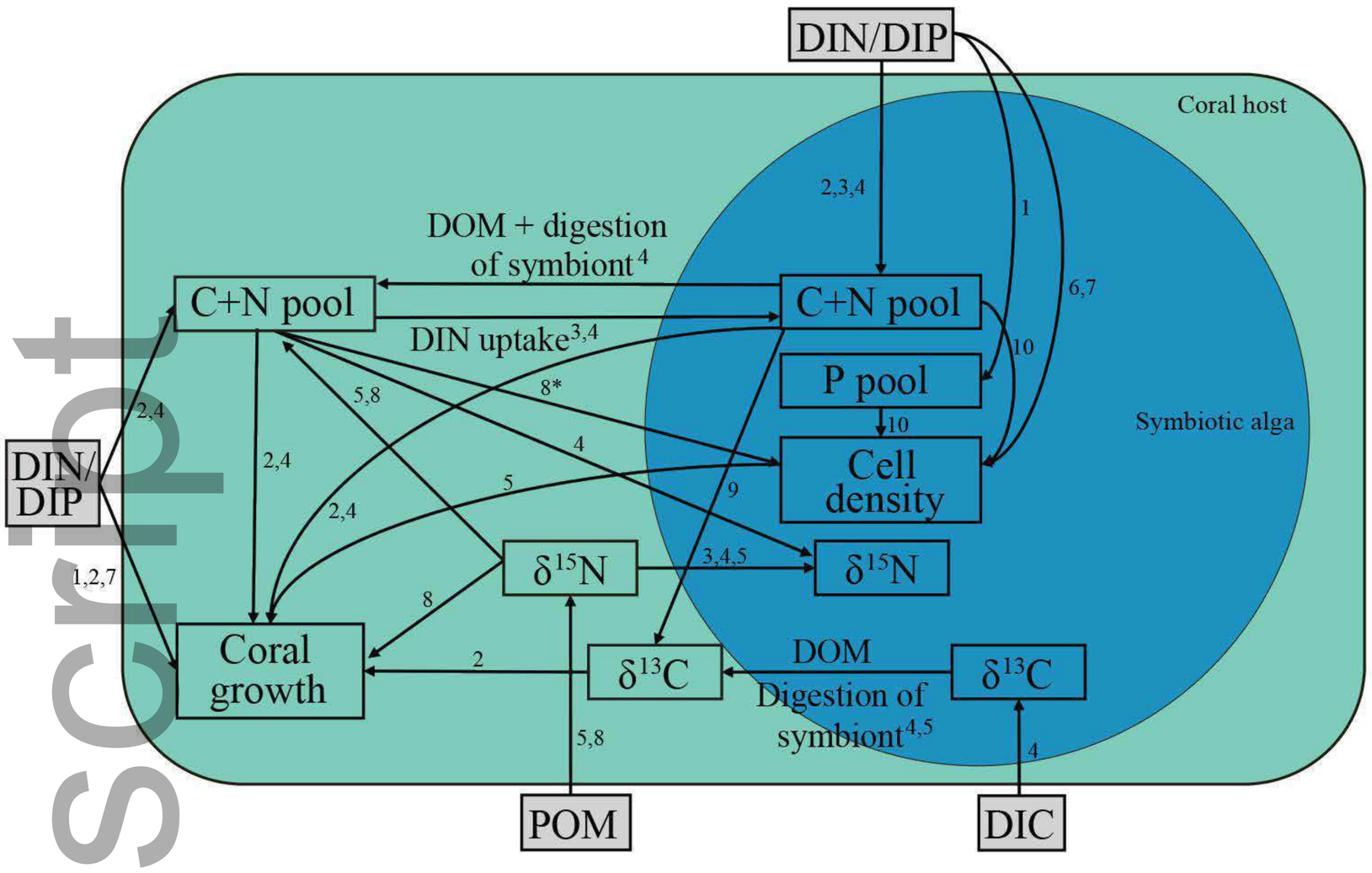


Figure 2



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8. Houlbreque et al 2015
9. Furla et al 2000
10. Sterner and Elser 2002 (stoichiometry theory: luxury uptake)

*indirect: feeding led to increased algal density. N must have passed through the coral first.

POM = particulate organic matter
DOM = dissolved organic matter
DIC/N/P = dissolved inorganic carbon/nitrogen/phosphorus

Component models that make up the complete SEM. Each model, described in text, represents a general hypothesis generated from the literature (numbers in Figure 2 correspond with citations below).

Component model	Response	Predictor(s)
1	$C:N_{coral}$	$Nutrients_{ambient} + \delta^{15}N_{coral}$

Coral and algae can take up N from the water column and heterotrophically feed on particulate matter with consequences for increased $\delta^{15}N$ signature of the holobiont (Tanaka et al 2018, 2015, 2007, Muscatine et al. 2005, Tremblay et al 2015)

2	$\delta^{13}C_{coral}$	$C:N_{symbiont} + \delta C^{13}_{symbiont}$

Dissolved organic carbon produced from the photosynthetic activity of the algae ($\delta^{13}C_{algae}$) is a primary source of C to coral and thus is expected to be positively correlated with $\delta^{13}C_{coral}$. Additionally, a larger C pool in the algae means that more C is available to be transferred to the coral (Tanaka et al 2018, 2015, 2007).

3	$C:N_{symbiont}$	$C:N_{coral} + Nutrients_{ambient}$

Ambient nutrients are expected to increase N concentrations in the algae (decreased C:N), and the recycling of nutrients via metabolic waste products are expected to influence the correlation between the coral C:N and algae C:N (Tanaka et al 2018, 2015, 2007). The SEM cannot account for recycling (called feedback loops) (Lefcheck et al 2016) and the direction of N flow therefore goes from the coral to algae. The recycling of C and N is also expressed in component model 2.

4	$\%P_{symbiont}$	$Nutrients_{ambient}$

P concentrations in symbiotic algae tend to increase with ambient phosphate concentrations (Godinot et al 2011).

5	$\delta^{15}N_{symbiont}$	$\delta^{15}N_{coral} + C:N_{coral}$

Coral heterotrophy of particulate matter from the water column, that is indicated by an increased $\delta^{15}N$ signature in the coral, can be a source of N that is mediated into the N cycling loop between the coral and algae (Muscatine et al. 2005, Tremblay et al 2015).

6	$Density_{symbiont}$	$Nutrients_{ambient} + C:N_{symbiont} + \%P_{symbiont} + C:N_{coral}$

Algae can take up nutrients from the water column increasing the nutrient pool available for their growth (Tanaka et al 2018, 2015, 2007), which can lead to increased algal density cm^{-2} (Ezzat et al 2015, Wiedenmann et al 2012).

7	$Growth_{coral}$	$C:N_{coral} + \delta^{15}N_{coral} + \delta^{13}C_{coral} + C:N_{coral} + \%P_{symbiont} + Density_{symbiont} + Nutrients_{ambient}$

Energy from algal photosynthates plus most other compartments will, to various degrees, have an influence on the calcification rates and growth (mg cm^{-2} d^{-1}) of the coral (Ezzat et al 2015, Houlbreque et al 2015, Tanaka et al 2007, Godinot et al 2011, Ferrier-Pagès et al 2000).

Figure 3

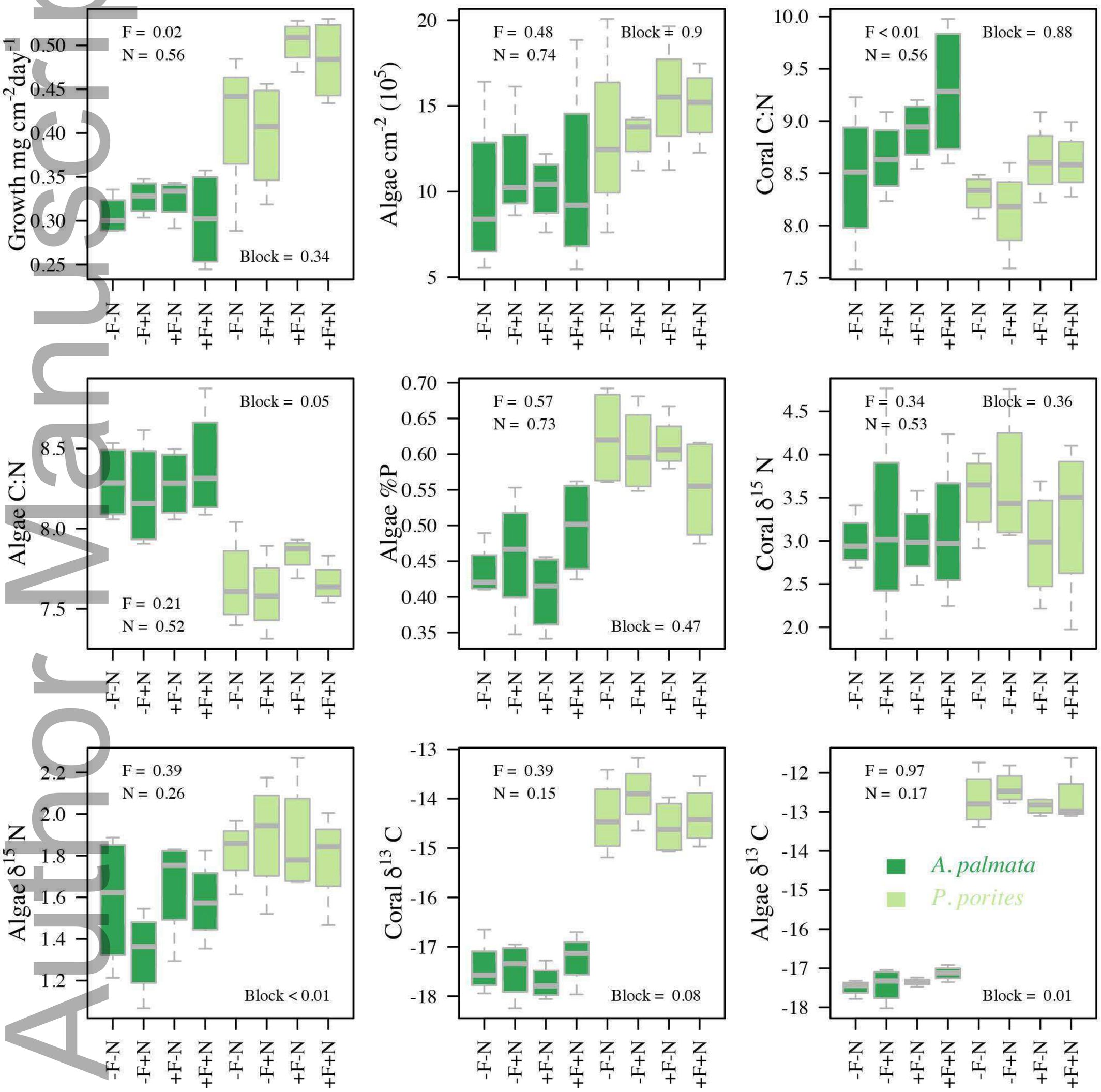

Figure 4

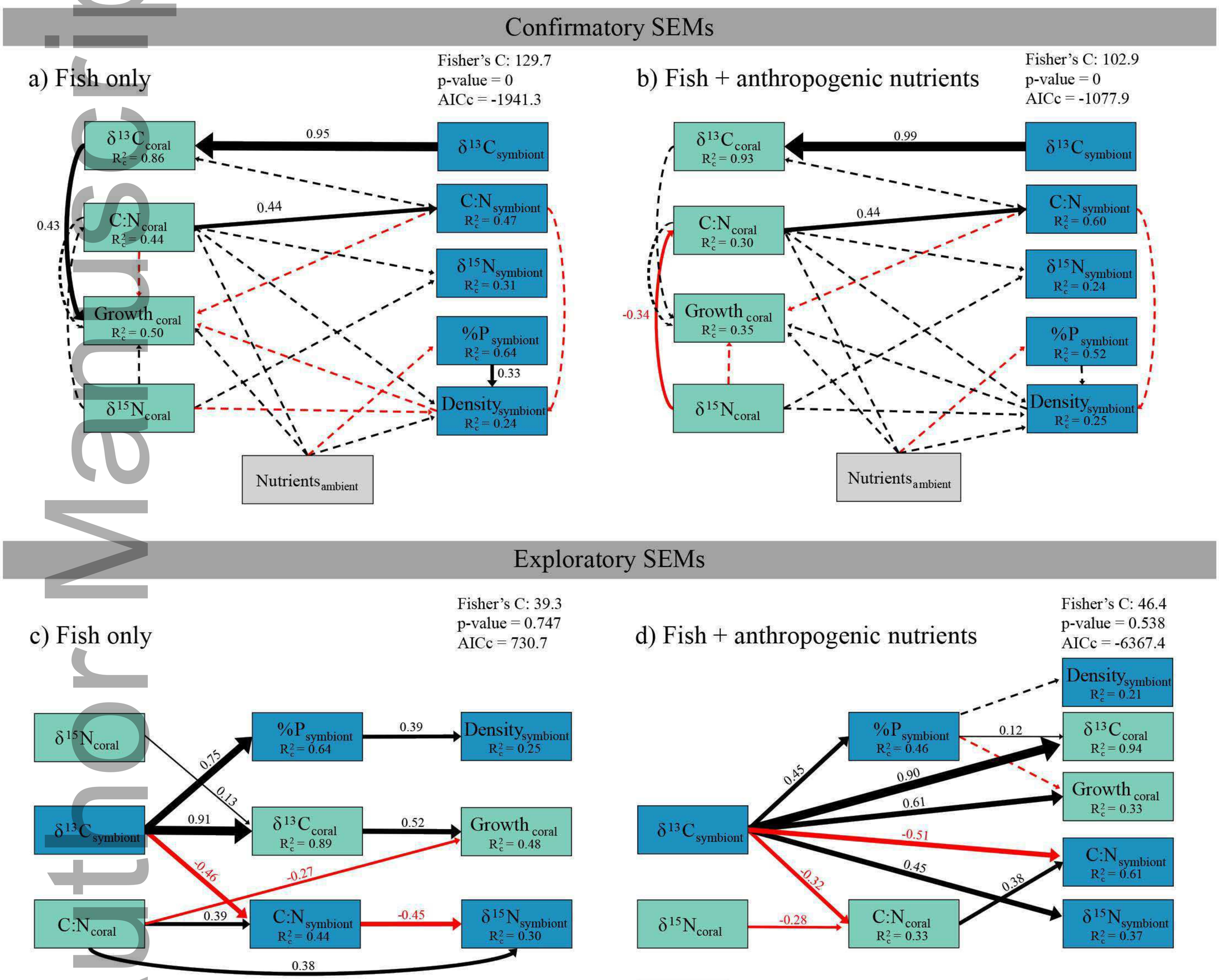

Figure 1

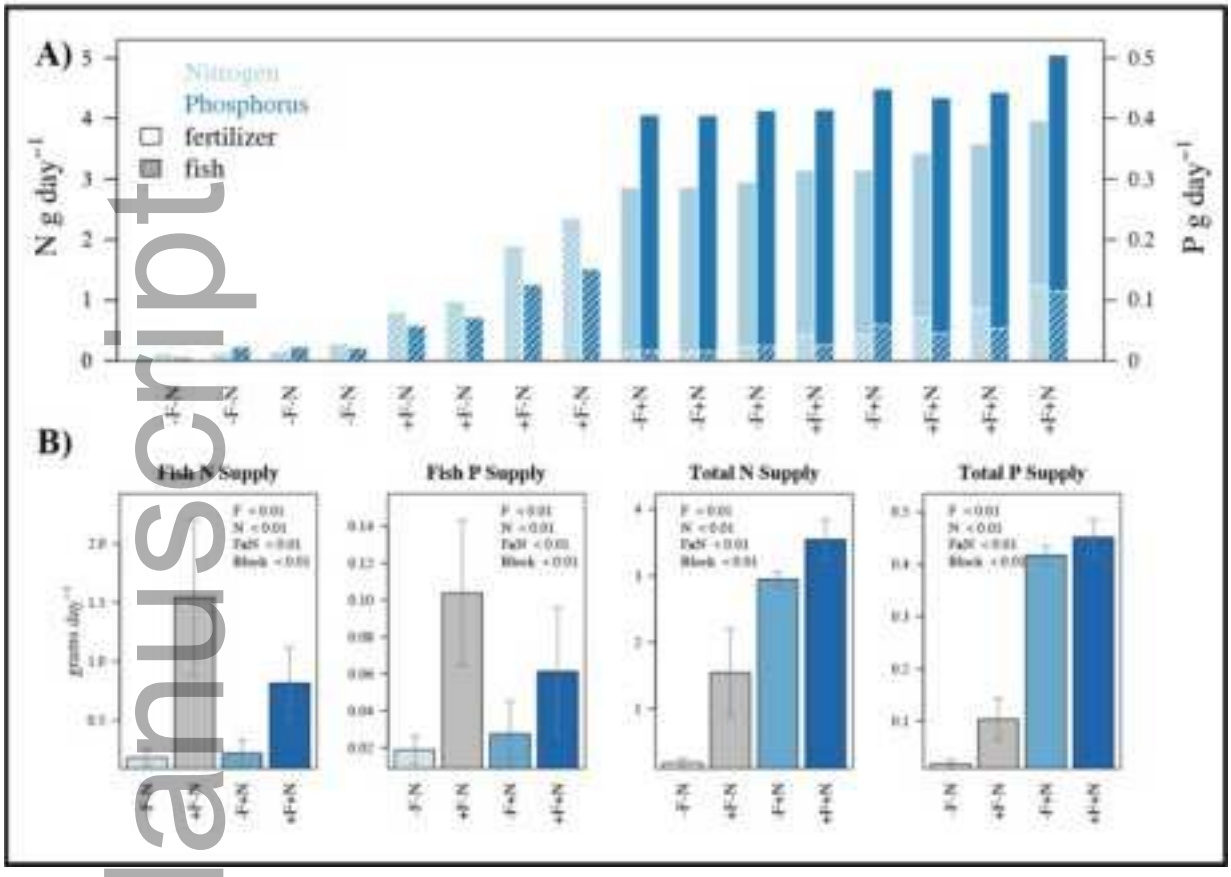

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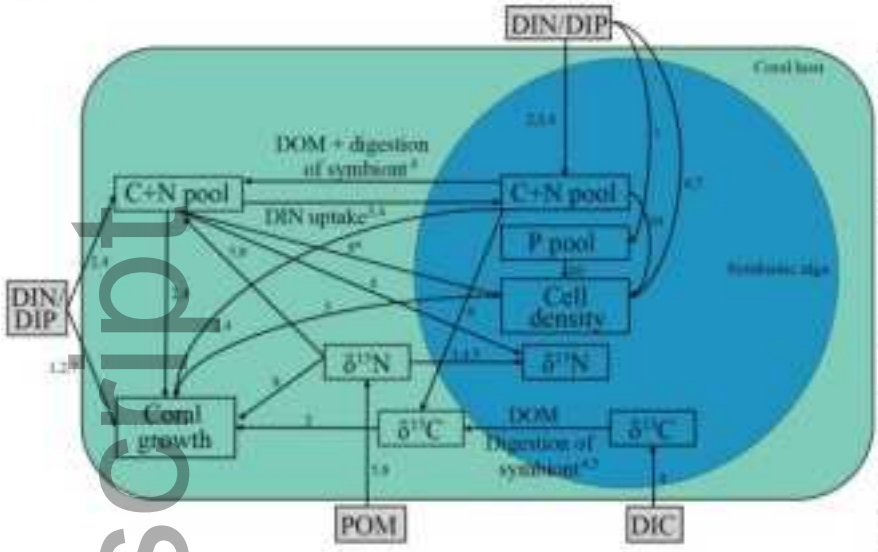
Figure 2



References:
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2	$\delta^{13}C_{coral}$	$C{:}N_{symbiont} + \delta C^{13}{}_{symbiont}$
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3	$C{:}N_{symbiont}$	$C{:}N_{coral} + Nutrients_{ambient}$
Ambient nutrients are expected to increase N concentrations in the algae (decreased C:N), and the recycling of nutrients via metabolic waste products are expected to influence the correlation between the coral C:N and algae C:N (Tanaka et al 2018, 2015, 2007). The SEM cannot account for recycling (called feedback loops) (Lefcheck et al 2016) and the direction of N flow therefore goes from the coral to algae. The recycling of C and N is also expressed in component model 2.		
4	$\%P_{symbiont}$	$Nutrients_{ambient}$
P concentrations in symbiotic algae tend to increase with ambient phosphate concentrations (Godinot et al 2011).		
5	$\delta^{15}N_{symbiont}$	$\delta^{15}N_{coral} + C{:}N_{coral}$
Coral heterotrophy of particulate matter from the water column, that is indicated by an increased $\delta^{15}N$ signature in the coral, can be a source of N that is mediated into the N cycling loop between the coral and algae (Muscatine et al. 2005, Tremblay et al 2015).		
6	$Density_{symbiont}$	$Nutrients_{ambient} + C{:}N_{symbiont} + \%P_{symbiont} + C{:}N_{coral}$
Algae can take up nutrients from the water column increasing the nutrient pool available for their growth (Tanaka et al 2018, 2015, 2007), which can lead to increased algal density cm^{-2} (Ezzat et al 2015, Wiedenmann et al 2012).		
7	$Growth_{coral}$	$C{:}N_{coral} + \delta^{15}N_{coral} + \delta^{13}C_{coral} + C{:}N_{coral} + \%P_{symbiont} + Density_{symbiont} + Nutrients_{ambient}$
Energy from algal photosynthates plus most other compartments will, to various degrees, have an influence on the calcification rates and growth (mg cm^{-2} d^{-1}) of the coral (Ezzat et al 2015, Houlbreque et al 2015, Tanaka et al 2007, Godinot et al 2011, Fernier-Pagès et al 2000).		

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Figure 3

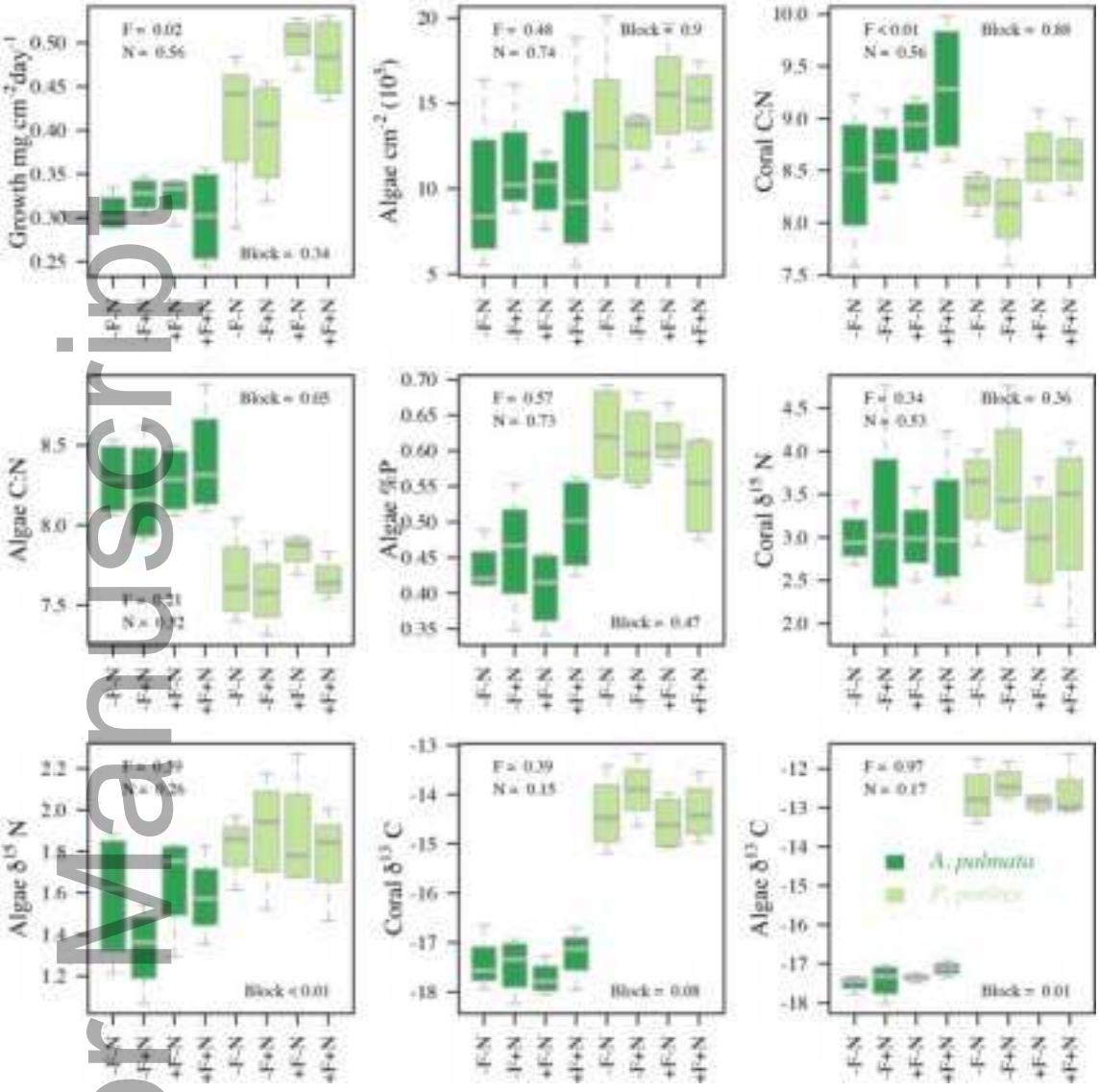

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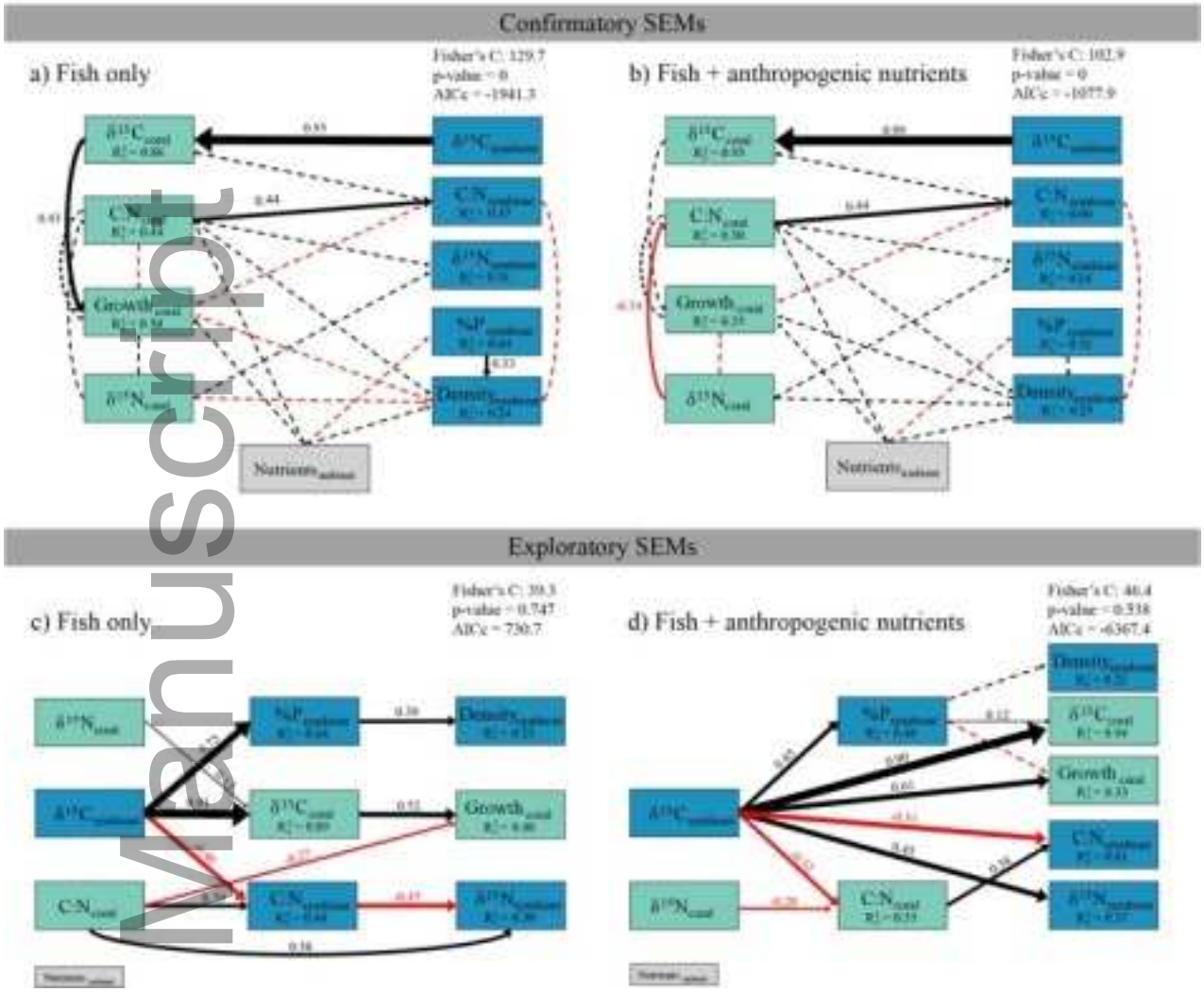
Figure 4



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