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LETTER

Nutrient loading alters the performance of key nutrient exchange mutualisms

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Abstract

Nutrient exchange mutualisms between phototrophs and heterotrophs, such as plants and mycorrhizal fungi or symbiotic algae and corals, underpin the functioning of many ecosystems. These relationships structure communities, promote biodiversity and help maintain food security. Nutrient loading may destabilise these mutualisms by altering the costs and benefits each partner incurs from interacting. Using meta-analyses, we show a near ubiquitous decoupling in mutualism performance across terrestrial and marine environments in which phototrophs benefit from enrichment at the expense of their heterotrophic partners. Importantly, heterotroph identity, their dependence on phototroph-derived C and the type of nutrient enrichment (e.g. nitrogen vs. phosphorus) mediated the responses of different mutualisms to enrichment. Nutrient-driven changes in mutualism performance may alter community organisation and ecosystem processes and increase costs of food production. Consequently, the decoupling of nutrient exchange mutualisms via alterations of the world's nitrogen and phosphorus cycles may represent an emerging threat of global change.

Keywords

Coral, eutrophication, mutualism, mycorrhizae, nutrient loading, nutrification, parasitism, rhizobia, *Symbiodinium*, symbiosis.

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INTRODUCTION

Nutrient exchange symbioses are reciprocal partnerships in which a heterotroph provides limiting nutrients, primarily nitrogen (N) or phosphorus (P), to a phototrophic partner in exchange for photosynthetically fixed carbon. Over 80% of plant species partake in nutrient exchange symbioses (van der Heijden *et al*. 2015), while in marine environments these mutualisms sustain foundation species such as corals and sponges (Muscatine & Porter 1977; Cardini *et al*. 2014). In many natural systems, nutrient exchange mutualisms are essential for maintaining diversity and ecosystem function, while in managed systems they support agriculture by improving crop production and reducing fertiliser expenditures (Stachowicz 2001; Kiers *et al*. 2002). Furthermore, these partnerships can provide participants with benefits beyond direct nutrient exchange, such as improved tolerance to toxins, disease, drought and herbivory (Littman *et al*. 2010; van der Heijden *et al*. 2015). Thus, nutrient exchange symbioses are critical components of ecosystems worldwide.

However, cooperation is rarely favoured in nature and theory suggests mutualisms can best be viewed as reciprocal exploitations that provide a net benefit to each partner (Herre *et al*. 1999). Thus, nutrient exchange symbioses are not fixed as positive–positive interactions, but instead exist along a continuum from mutualism to parasitism depending on whether the benefits of interacting outweigh the costs for each partner (Johnson *et al*. 1997; Sachs & Simms 2006; Johnson & Graham 2013). Accordingly, changes in biotic and abiotic conditions can alter the costs and benefits for each partner and may jeopardise the performance and stability of the mutualism (Johnson 1993; Johnson *et al*. 1997; Akçay & Simms 2011). These tradeoffs variously predict linear, nonlinear and threshold relationships in partner performance, with the outcome often dependent on how the symbiosis is maintained (e.g. Doebeli & Knowlton 1998; Neuhauser & Fargione 2004; Wyatt *et al*. 2014). Given the importance of these mutualisms and the scale at which humans are altering the planet, it is critical to examine how global change will influence the performance of these partnerships.

Human activity now dominates global N and P cycles. Over the last century, anthropogenic nutrient delivery has increased to such an extent that anthropogenically derived nutrients dwarf natural nutrient sources (Vitousek *et al*. 1997; Bennett *et al*. 2001). Empirical evidence suggests that this pervasive addition of limiting nutrients may disrupt important nutrient exchange mutualisms (Treseder 2004; Shantz & Burkepile 2014). Nutrient loading can alleviate phototroph dependence on heterotrophically derived N and P, decreasing the net benefit of associating with heterotrophic symbionts and causing phototrophs to reduce the amount of C allocated to their partners (e.g. Dennison 2000; Kiers *et al*. 2003, 2011). Yet, the mechanisms that mediate nutritional symbioses are diverse. For example, plants and mycorrhizal fungi use a system of reciprocal trade that provides both partners a degree of control over the symbiosis (Kiers *et al*. 2011). In contrast, plant–rhizobia relationships can be maintained via resource sanctions in which plants reduce the amount of

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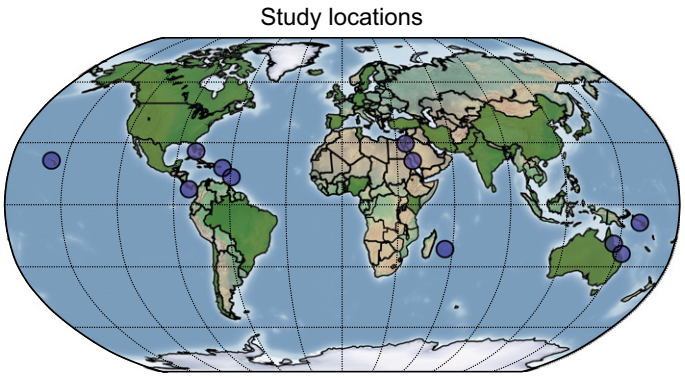

Figure 1 Map of the locations and countries where marine (blue dots) and terrestrial (green shading) experiments used in our analyses were conducted.

carbon delivered to under-performing symbionts (Kiers *et al.* 2003; Akçay & Simms 2011). Corals may display yet another strategy by keeping phototrophic algal symbionts nutrient limited to maximise carbon return (Falkowski *et al.* 1984; Wooldridge 2010). As a result, nutrient loading may have fundamentally different effects on different types of nutrient exchange mutualisms.

Several studies have synthesised the responses of single partners (e.g. phototrophs or heterotrophs only) to enrichment in some of the better-studied mutualisms such as mycorrhizae (Treseder 2004; Karst *et al.* 2008; Hoeksema *et al.* 2010) and corals (Shantz & Burkepile 2014). However, no study to date has tested how nutrient enrichment may impact the predicted fundamental tradeoffs in partner performance (e.g. Johnson *et al.* 1997; West *et al.* 2002; Kiers & van der Heijden 2006). Furthermore, we still lack a general understanding of how global increases in nutrient availability may affect the integrity of different types of nutrient exchange mutualisms.

To address this gap, we used meta-analyses to assess the extent and consistency to which anthropogenic nutrient pollution disrupts a diverse array of nutrient exchange mutualisms. We identified 306 experiments from 76 studies, spanning three ocean regions and every habitable continent, which recorded the performance of both phototroph and heterotroph partners to control and nutrient-enriched conditions (Fig. 1; see Table S1 for details). For each experiment, we examined the simultaneous responses of both heterotroph and phototroph partners to nutrient enrichment. Our results reveal a nearly ubiquitous response to enrichment across mutualism types, in which phototroph performance improves at the expense of their heterotrophic partners. These tradeoffs were context dependent and mediated by the identity of the heterotrophic partner and the identity of the enriched nutrient. Together, these data show that nutrient enrichment affects a wide array of nutrient exchange mutualisms by altering the costs and benefits of interactions.

METHODS

Study selection and performance criteria

To identify studies for our analyses, we conducted an extensive literature search using ISI's Web of Science (1977–2014). We used multiple search terms that included 'mutualism' and nutr* or enrich*, and multiple mutualism types crossed with these terms [e.g. 'coral' and (enrich* or nutr*)] and identified additional studies from the references of papers from these searches. We identified six mutualism types with sufficient data available to be used in our analysis. (1) *Symbiodinium* exchanging C for N from Tridacnid clams (Algae–Clam). (2) *Symbiodinium* exchanging C for N from corals (Algae–Coral). (3) Algae or cyanobacteria exchanging C for N from fungi to form lichen (Algae/Cyanobacteria–Fungi). (4) Plants exchanging C for N and/or P from arbuscular mycorrhizal fungi (Plant–AM Fungi). (5) Plants exchanging C for N and/or P from ectomycorrhizal fungi (Plant–EM Fungi), which unlike AM Fungi do not form intracellular connections with host plants and may possess saprotrophic capabilities (Read *et al.* 2004). (6) Plants exchanging C for N from root-nodulating rhizobia (Plant–Bacteria).

To be included, studies needed to report at least one performance metric for both heterotroph and phototroph partners under control and nutrient-enriched conditions. Phototroph performance was measured as increases in above-ground biomass for plants. For algae, performance was measured as areal cell density, cells per clam (two studies), or chlorophyll *a* cm^{-2} in one instance, which was used as a proxy for cell density. Heterotroph performance was measured as growth as determined by changes in mass or extension rates (corals, clams and lichen), chitin (a proxy for fungal mass in lichen), hyphae mass or per cent of root colonisation calculated from equal-sized root samples (mycorrhizal fungi), or nodule biomass or number (rhizobia). Response metrics were standardised for area (e.g. equal sized root samples in plants, symbiont cells cm^{-2} in corals) to minimise correlation between phototroph and heterotroph responses. When multiple metrics were available, we used measurements of mass rather than other metrics to avoid including multiple response metrics within analyses that could be differentially sensitive to nutrient enrichment. Although these metrics are often not ideal measurements of performance, they are the most commonly used measurements available in the published literature for these groups and provide a strong indicator of an organisms' ability to flourish, grow and occupy their available habitat.

We identified 76 studies containing 306 experiments (5 studies, 19 experiments for Algae–Clam mutualisms; 13 studies, 31 experiments for Algae–Coral mutualisms; 3 studies, 19 experiments for Algae/Cyanobacteria–Fungi mutualisms; 24 studies, 84 experiments for Plant–AM Fungi mutualisms; 5 studies, 38 experiments for Plant–EM experiments and 26 studies, 115 experiments for Plant–Bacteria mutualisms; Table S1). Data were taken from the text or extracted from digital PDFs using DataThief III V1.6 (Tummers 2006). When studies included multiple independent experiments at different nutrient levels or with different species, each experiment was treated as an individual replicate. For marine studies, enrichment magnitudes ranged from 1 to 109 μM for N and 0.2 to 18.6 μM for P. In terrestrial systems the units of enrichment were variable but ranged from 2 to 20 times greater than control conditions for N and 1.5 to 220 times greater for P. These values represent a gradient from low

anthropogenic impact to severe pollution (see Table S1 for details).

To examine the impact of nutrient addition on nutrient exchange mutualisms, we calculated the log response ratios (RR) for both phototroph and heterotroph partners from each study. We used Bayesian meta-analyses to calculate effect sizes with 80 and 95% Bayesian credible intervals to examine the overall effect of enrichment and of different enrichment types (e.g. N vs. P) on both partners for each mutualism type and an overall effect across all mutualism types (see *Models and analysis* for details). Measuring the simultaneous response of both partners rather than single partner responses limited the number of studies available but allowed us to capture tradeoffs between partner performance that have not been examined in other meta-analyses (e.g. Treseder 2004; Hoeksema *et al.* 2010; Shantz & Burkepile 2014). We tested for tradeoffs in performance between partners using hierarchical Bayesian regressions for each mutualism type.

Models and analysis

A frequent problem for meta-analyses in ecology is poor reporting of ecological data. Approximately 40% of the studies failed to properly report sample sizes or variances. Therefore, we first conducted an unweighted Bayesian meta-analysis that allowed us to make use of the entire data set, regardless of deficiencies in reporting, followed by a weighted Bayesian model for comparison (see below for model details). Weighting can improve the power and precision of tests, but may sacrifice replication by excluding studies where data are poorly reported (Gurevitch & Hedges 1999; Stewart 2010). Although weighted analyses are preferred, unweighted tests are encouraged when potentially large amounts of data would otherwise be lost (Gurevitch & Hedges 1999). Weighting reduced our data set by ~ 40% to a subset of 191 experiments from 51 studies (Table S1), but yielded nearly identical results as our unweighted model (see Table 1). Funnel plots revealed no evidence of publication bias in either model. Given the substantially larger data set and the fact that both analyses showed quantitatively similar patterns, we focus on the unweighted model here and present results from the weighted analyses in the supplemental material.

We used a hierarchical Bayesian model to conduct both unweighted fixed effects and weighted random effects meta-analyses. This Bayesian method is similar to frequentist methods used in traditional meta-analyses, allowing for group-level predictors and random effects while providing the flexibility to conduct Type II hierarchical regressions (Sutton & Abrams 2001). Furthermore, Bayesian methods allowed us to calculate exact posterior probabilities of effects, improving the interpretation of results when compared with traditional significance levels.

We calculated the log response ratio (RR) for each experiment as $\ln(\mu_{trt}/\mu_{cont})$, where μ_{trt} is the mean of the nutrient-enriched treatment group and μ_{cont} the mean of the control group. A positive RR means that nutrient enrichment increased performance, whereas a negative RR means that nutrient enrichment caused a decline in performance. When sample size and variances were appropriately reported, the standard error of the RR for each partner in each experiment was calculated using an unpooled variance estimate:

$$SE = \sqrt{\frac{\sigma^2_{cont}}{n_{cont}\mu^2_{cont}} + \frac{\sigma^2_{trt}}{n_{trt}\mu^2_{trt}}} = s_i,$$

where σ^2_{cont} and σ^2_{trt} are the respective control and treatment group variances and n_{cont} and n_{trt} are sample sizes of each group. Thus, each experiment produced a log response ratio RR_i and ~ 60% of experiments (Table S1) also produced known standard deviation of the response s_i for use in weighted analyses.

We first conducted our unweighted model including only a single error term for between-study variance so we could incorporate experiments that did not report estimates of variance. This model assumes that the response ratio for each study varied around the group-level means directly. That is, the *i*th study in the *j*th mutualism type was normally distributed around the mutualism mean ($\widehat{y_j}$) with a between-study variance (τ_j):

$$RR_{ij} \sim N(\widehat{y_j}, \tau_j)$$

Thus, there was no assumption of homogeneity of variances among mutualism types. The mean for each type was a linear function of the overall mean (μ) and a deflection from the overall mean for each mutualism type (δ_j):

$$\widehat{y_j} = \mu + \delta_j$$

In this model, mutualism types were fixed effects. We imposed sum-to-zero constraints on the deflections δ_j.

The weighted, random effects model considered the RR of each study as randomly varying around the 'true' study value θ_{ij} with response ratio variance calculated for the study s^2_{ij}:

$$RR_{ij} \sim N(\theta_{ij}, s^2_{ij})$$

'True' study values were assumed to be normally distributed around the mean for each mutualism type ($\hat{y}$) with a between-study variance specific to that mutualism type (τ) as described in the fixed effects model:

$$\theta_{ij} \sim N(\widehat{y_j}, \tau_j)$$

The mean for each mutualism type was a linear function of the overall mean and a deflection from the overall mean as described above. This model allowed each study to have its own true response, where true responses of each mutualism type varied around the mutualism type mean.

To test for performance tradeoffs, we used Bayesian hierarchical regression that modelled the heterotroph RR as a linear function of phototroph RR in each mutualism type. This was a standard hierarchical regression for the full data set. For the restricted data set, both heterotroph and phototroph response ratios were assumed to be subject to sampling error with a known variance calculated as described above. Thus, for the *i*th experiment, both phototroph and heterotroph RR were assumed to be normally distributed around some 'true' value and a hierarchical linear regression was carried out that

Table 1 The mean log response ratio (RR) and upper and lower 95% Bayesian credible intervals for phototroph and heterotroph partners from each mutualism type overall and to each enrichment type. Data are provided for both the unweighted and weighted models for comparison

	Mean RR and 95% Bayesian credible interval			
Unweighted analysis	All nutrients	N	P	N + P
Algae–Clam (Phototroph)	RR = 0.75 CI_{95} = 0.55, 0.93	RR = 0.54 CI_{95} = 0.20, 0.85	RR = 0.40 CI_{95} = 0.12, 0.67	RR = 0.99 CI_{95} = 0.68, 1.29
Algae–Clam (Heterotroph)	RR = 0.61 CI_{95} = 0.45, 0.76	RR = 0.54 CI_{95} = 0.11, 0.86	RR = 0.29 CI_{95} = −0.29, 0.73	RR = 0.67 CI_{95} = 0.29, 0.94
Algae–Coral (Phototroph)	RR = 0.50 CI_{95} = 0.28, 0.72	RR = 0.37 CI_{95} = 0.17, 0.59	RR = 0.20 CI_{95} = −0.15, 0.64	RR = 0.84 CI_{95} = 0.35, 1.34
Algae–-Coral (Heterotroph)	RR = −0.37 CI_{95} = −0.56, −0.18	RR = −0.38 CI_{95} = −0.60, −0.16	RR = 0.17 CI_{95} = −0.24, 0.42	RR = −0.49 CI_{95} = −0.94, −0.01
Algae/ Cyano–Fungi (Phototroph)	RR = 0.14 CI_{95} = −0.06, 0.36	RR = 0.10 CI_{95} = −0.13, 0.33	RR = 0.16 CI_{95} = −0.27, 0.68	RR = 0.64 CI_{95} = 0.03, 1.26
Algae/ Cyano–Fungi (Heterotroph)	RR = −0.15 CI_{95} = −0.27, −0.02	RR = −0.13 CI_{95} = −0.27, 0.02	RR = −0.03 CI_{95} = −0.59, 0.55	RR = −0.26 CI_{95} = −0.77, 0.30
Plant–AM Fungi (Phototroph)	RR = 0.52 CI_{95} = 0.39, 0.66	RR = 0.36 CI_{95} = 0.15, 0.58	RR = 0.57 CI_{95} = 0.37, 0.77	RR = 0.51 CI_{95} = 0.27, 0.80
Plant–AM Fungi (Heterotroph)	RR = −0.28 CI_{95} = −0.42, −0.14	RR = −0.20 CI_{95} = −0.44, 0.03	RR = −0.29 CI_{95} = −0.48, −0.10	RR = −0.24 CI_{95} = −0.79, 0.33
Plant–EM Fungi (Phototroph)	RR = 0.72 CI_{95} = 0.49, 0.95	RR = 0.34 CI_{95} = 0.05, 0.66	RR = 0.58 CI_{95} = 0.22, 0.98	RR = 0.93 CI_{95} = 0.59, 1.30
Plant–EM Fungi (Heterotroph)	RR = −0.08 CI_{95} = −0.26, 0.10	RR = 0.41 CI_{95} = 0.03, 0.75	RR = −0.27 CI_{95} = −0.66, 0.12	RR = −0.16 CI_{95} = −0.33, 0.01
Plant–Bacteria (Phototroph)	RR = 0.36 CI_{95} = 0.26, 0.46	RR = 0.19 CI_{95} = 0.12, 0.26	RR = 0.36 CI_{95} = 0.22, 0.49	RR = 1.0 CI_{95} = 0.51, 1.57
Plant–Bacteria (Heterotroph)	RR = −0.36 CI_{95} = −0.53, −0.18	RR = −0.56 CI_{95} = −0.75, −0.36	RR = −0.01 CI_{95} = −0.26, 0.26	RR = −0.48 CI_{95} = −1.25, 0.26
Overall (Phototroph)	RR = 0.50 CI_{95} = 0.42, 0.58	RR = 0.32 CI_{95} = 0.20, 0.43	RR = 0.38 CI_{95} = 0.24, 0.54	RR = 0.82 CI_{95} = 0.62, 1.03
Overall (Heterotroph)	RR = −0.10 CI_{95} = −0.17, −0.04	RR = −0.05 CI_{95} = −0.17, 0.05	RR = −0.02 CI_{95} = −0.22, 0.15	RR = −0.16 CI_{95} = −0.38, 0.06
Weighted analysis	Overall	N	P	N + P
Algae–Clam (Phototroph)	RR = 0.76 CI_{95} = 0.56, 0.95	RR = 0.52 CI_{95} = 0.20, 0.85	RR = 0.35 CI_{95} = 0.03, 0.62	RR = 1.04 CI_{95} = 0.73, 1.35
Algae–Clam (Heterotroph)	RR = 0.56 CI_{95} = 0.40, 0.73	RR = 0.43 CI_{95} = −0.16, 0.78	RR = 0.20 CI_{95} = −0.25, 0.65	RR = 0.64 CI_{95} = 0.27, 0.94
Algae–Coral (Phototroph)	RR = 0.44 CI_{95} = 0.25, 0.64	RR = 0.33 CI_{95} = 0.16, 0.52	RR = 0.12 CI_{95} = −0.14, 0.45	RR = 0.92 CI_{95} = 0.29, 1.54
Algae–Coral (Heterotroph)	RR = −0.41 CI_{95} = −0.59, −0.22	RR = −0.41 CI_{95} = −0.61, −0.20	RR = 0.11 CI_{95} = −0.29, 0.46	RR = −0.59 CI_{95} = −1.04, −0.05
Algae/ Cyano–Fungi (Phototroph)	RR = 0.17 CI_{95} = −0.02, 0.37	RR = 0.16 CI_{95} = −0.05, 0.35	RR = 0.08 CI_{95} = −0.34, 0.48	RR = 0.62 CI_{95} = −0.13, 1.48
Algae/ Cyano–Fungi (Heterotroph)	RR = −0.05 CI_{95} = −0.15, 0.03	RR = −0.05 CI_{95} = −0.16, 0.05	RR = 0.0 CI_{95} = −0.50, 0.51	RR = −0.13 CI_{95} = −0.81, 0.48
Plant–AM Fungi (Phototroph)	RR = 0.39 CI_{95} = 0.31, 0.49	RR = 0.31 CI_{95} = 0.19, 0.44	RR = 0.42 CI_{95} = 0.28, 0.57	RR = 0.41 CI_{95} = 0.27, 0.60
Plant–AM Fungi (Heterotroph)	RR = −0.25 CI_{95} = −0.37, −0.14	RR = −0.19 CI_{95} = −0.39, −0.01	RR = −0.22 CI_{95} = −0.37, −0.03	RR = −0.30 CI_{95} = −0.77, 0.20
Plant–EM Fungi (Phototroph)	RR = 0.90 CI_{95} = 0.48, 1.33	RR = 0.38 CI_{95} = −0.18, 1.06	RR = 0.15 CI_{95} = −0.07, 0.46	RR = 1.36 CI_{95} = 0.85, 1.83
Plant–EM Fungi (Heterotroph)	RR = −0.16 CI_{95} = −0.27, −0.06	RR = −0.08 CI_{95} = −0.73, 0.53	RR = −0.06 CI_{95} = −0.28, 0.21	RR = −0.23 CI_{95} = −0.42, −0.07
Plant–Bacteria (Phototroph)	RR = 0.66 CI_{95} = 0.39, 0.94	RR = 0.29 CI_{95} = 0.12, 0.46	RR = 0.22 CI_{95} = 0.10, 0.37	RR = 1.57 CI_{95} = 0.90, 2.16
Plant–Bacteria (Heterotroph)	RR = −0.32 CI_{95} = −0.61, −0.05	RR = −0.30 CI_{95} = −0.65, 0.04	RR = 0.00 CI_{95} = −0.20, 0.20	RR = −0.56 CI_{95} = −1.56, 0.36
Overall (Phototroph)	RR = 0.55 CI_{95} = 0.45, 0.66	RR = 0.33 CI_{95} = 0.20, 0.48	RR = 0.22 CI_{95} = 0.11, 0.36	RR = 0.99 CI_{95} = 0.76, 1.23
Overall (Heterotroph)	RR = −0.11 CI_{95} = −0.17, −0.04	RR = −0.10 CI_{95} = −0.26, 0.04	RR = 0.01 CI_{95} = −0.17, 0.18	RR = −0.20 CI_{95} = −0.45, 0.05

allowed model parameters to vary among the j groups. The 'true' heterotroph and phototroph values for each experiment in the jth group were normally distributed around some predicted value with a variance specific to the group:

$$\theta_{heteroij} \sim N(\hat{y}_{Hij}, \tau_{Hj})$$
$$\theta_{photoij} \sim N(\hat{y}_{Pij}, \tau_{Pj})$$

The 'true' heterotroph value was a linear function of the phototroph 'true' value:

$$\theta_{heteroij} = a_j + b_j\theta_{photoij}$$

such that each group j was allowed a different intercept and slope. The parameters a and b for each group were drawn from a normal distribution with means μ_a and μ_b and variances ω_a^2 and ω_b^2 respectively. The only difference between the models for the full data set and the restricted data set was that response ratios for the full data set did not vary around a 'true' value.

We calculated pseudo-R^2 values, which differ from R^2 in that they are calculated for each mutualism type within a hierarchical model for each posterior sample, following the standard formula for R^2 from linear regression. For each posterior sample of parameters, we calculated the sum-of-squared errors (SS_R) between observed and fitted data as a measure of residual variation and the sum-of-squared errors between observed data and the mean (SS_T). Pseudo-R^2 is then $1 - SS_R/SS_T$. We then took the median posterior value as the R^2 for each mutualism type.

Performance may also be expected to change with the level of enrichment or study duration. However, studies differed widely in the amounts of nutrients provided, duration and rate of nutrient addition (Table S1). To account for these differences, we assessed the effect of overall enrichment magnitude on performance and converted the reported enrichment levels into average enrichment per day by dividing the total amount of nutrients added by the experimental duration. Numerous studies reported enrichment in non-comparable units (e.g. mg nutrient kg^{-1} of soil vs. mg nutrient m^{-2}; Table S1). Therefore, rather than examining each metric and increasing the probability of committing a Type I error, we used whichever units of measurement provided the greatest replication. This reduced our available data by ~ 30% for Algae–Coral mutualisms, ~ 50% for Algae–Clam, Plant–AM Fungi and Plant–Bacteria mutualisms and 100% for Plant–EM Fungi mutualisms, which all used different enrichment metrics. We visually examined the impact of enrichment magnitude and enrichment per day on the response of each partner under both N and P enrichment by plotting effect sizes against enrichment. Quantitative regressions of these relationships were not possible due to poor replication across treatment levels.

Additionally, we examined potential differences in effect sizes between laboratory- and glasshouse-based experiments vs. those conducted in natural outdoor environments. As virtually all of the experiments involving clams, corals and lichen were conducted in highly controlled environments, we were only able to conduct these analyses on Plant–Bacteria and Plant–Fungi mutualisms.

Bayesian models were run in STAN, accessed via PyStan in Python v2.7 (available at python.org). In all models, coefficients were given weakly informative priors of $N(0, 4)$ and variance parameters given uninformative priors of $U(0, 10)$. We ran four MCMC chains simultaneously, each with 25 000 burn-in iterations followed by 25 000 sampling iterations, resulting in 100 000 posterior samples for each parameter. We verified chain convergence by ensuring that $\hat{R} = 1$ for all parameters and by examining posterior density plots.

RESULTS

Nutrient enrichment increased the performance of nearly all phototroph groups (Fig. 2a; Table 1). Although the median response across all studies was a nearly 65% increase in performance, there was significant heterogeneity among group responses. The weakest response occurred in the algae/cyanobacteria in lichen (Fig. 2a, Table 1) with a 15% greater performance under enrichment [Probability of an effect: Pr (RR > 0) = 0.92]. Phototrophs from all other mutualism types showed improved performance, ranging from ~ 45% greater performance in the Plant–Bacteria mutualism to ~ 110%

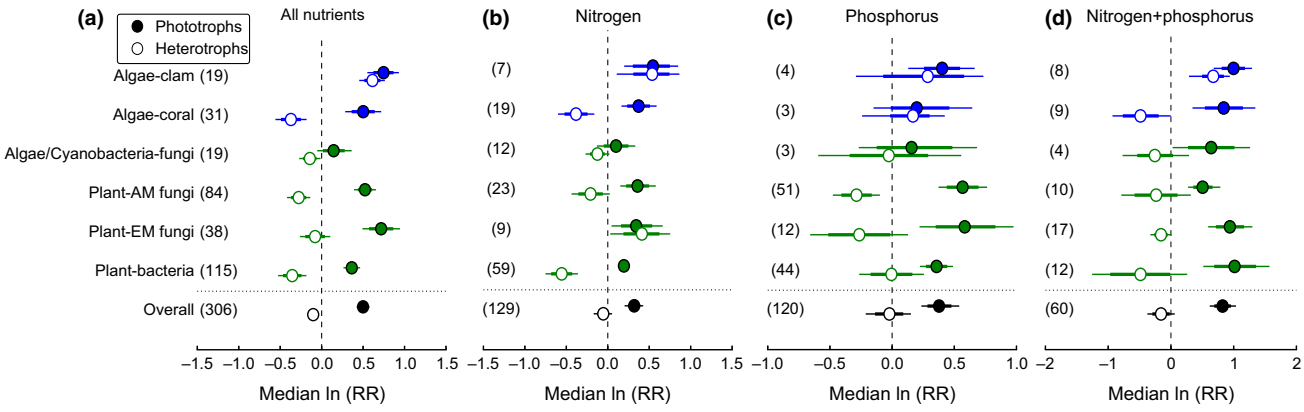

Figure 2 Estimated effect sizes based on log response ratios for phototrophs and heterotrophs from each mutualism type (blue = marine, green = terrestrial) and overall median response across all studies from the unweighted model as (a) pooled across all nutrients or under (b) nitrogen, (c) phosphorus, or (d) nitrogen + phosphorus enrichment. Thin and thick lines depict the 95 and 80% Bayesian credible intervals respectively. Numbers in parentheses denote the number of experiments used in each calculation.

increase in performance of *Symbiodinium* in the Algae–Clam relationship [Pr(RR > 0) = 1.00 for all other groups].

Similarly, there was an overall 10% decline in heterotroph performance with enrichment that varied substantially among different mutualism types (Fig. 2a). Coral, lichen, AM fungi and rhizobia displayed declines in performance ranging from 13% (lichen) to 31% (coral; Table 1). In contrast, EM fungi showed only minimal signs of impairment [average 8% decline, Pr (RR < 0) = 0.80], whereas clams showed an 85% increase in growth with nutrient enrichment [Table 1; Pr(RR > 0) = 1.00]. This pattern was nearly identical in the weighted model (Fig. S1a, Table 1). However, for lichens heterotrophs were less consistently impaired by nutrient enrichment in the weighted [Pr (RR < 0) = 0.90] vs. unweighted analysis [Pr(RR < 0) = 0.98] and for Plant–EM relationships EM Fungi showed greater and more consistent declines in the weighted model [Pr (RR < 0) = 1.00; Table 1].

The responses of different mutualism types to enrichment varied considerably with the identity of nutrients provided by the heterotroph (i.e. N vs. P). In the unweighted model, phototroph and heterotroph responses to N enrichment were nearly identical to those observed under all enrichment types, except EM fungi, which benefitted from N addition [Pr(RR) > 0 = 0.98; Fig 2b]. Phosphorus enrichment regularly improved phototroph performance in Algae–Clam, Plant–AM Fungi, Plant–EM Fungi and Plant–Bacteria mutualisms, but impaired heterotroph performance for AM and, to a lesser extent, EM fungi [Pr (RR < 0) = 1.00 and 0.92 respectively; Fig. 2c]. When experiments co-enriched with N + P, phototroph performance improved in all mutualism types. For heterotrophs, however, N + P enrichment resulted in a 95% increase in clam performance, reduced but variable performance of bacteria, AM fungi and the fungi in lichen and consistently impaired performance in corals and EM fungi (Fig. 2d; Table 1).

In our weighted analysis, phototroph responses to N enrichment were nearly identical (Fig. 2 vs. Fig. S1). For heterotrophs, fungi in lichen showed only a 5% decline in performance in the weighted analysis vs. a 12% decline in the unweighted model [Pr(RR < 0) = 0.74 vs. Pr(RR < 0) = 0.96 respectively]. Surprisingly, EM fungi performance improved by 50% under N enrichment in our unweighted analysis (Fig. 2b; Pr(RR) > 0 = 0.98), but showed no response to N in the weighted analysis (Fig S1b; Pr(RR) > 0 = 0.34), likely due to low replication (n = 2). For both P and N + P enrichments, the responses of both phototroph and heterotrophs were nearly identical between the models for all mutualism types except Plant–EM Fungi. EM fungi were impaired under P enrichment in the unweighted model (Fig. 2c) but not in the weighted model (Fig. S1c), while N + P enrichment impaired EM in the weighted model (Fig. S1d) but not the unweighted model (Fig. 2d).

We found evidence of linear tradeoffs between the performance of heterotrophs and phototrophs under nutrient enrichment in every mutualism type except for Algae–Clam and the Plant–AM symbiosis (Fig. 3). For Algae–Clam mutualisms, the response was opposite our predictions, with a positive relationship between clam and phototroph performance (Fig. 3a). However, Algae–Coral, Algae/Cyanobacteria–Fungi, Plant–EM and Plant–Bacteria mutualisms all showed linear declines in heterotroph performance as phototroph performance improved (Fig. 3; Table S2). The weighted model showed similar results with minor differences as tradeoffs were no longer detected in Algae/Cyanobacteria–Fungi or Plant–EM Fungi partnerships (Fig. S2). For Plant–EM interactions, the difference between models was largely due to a loss of over half the replicates in the weighted analysis. However, for Algae/Cyanobacteria–Fungi, replication was equal in both analyses and the different responses were entirely due to weighting.

Visual examination of the effects of enrichment magnitude and average daily enrichment on phototroph and heterotroph performance revealed few clear patterns (Figs S3 and S4). Rhizobia under N enrichment and AM fungi under P enrichment both declined in performance with increasing enrichment levels (Figs S3 and S4). However, for all other groups no clear patterns emerged. Enrichment levels were similar for Algae–Clam and Algae–Coral mutualisms. In terrestrial systems, P enrichment levels were much lower for Plant–EM Fungi experiments than for Plant–AM Fungi and Plant–Bacteria experiments, potentially contributing to the dissimilar patterns observed between these groups. Unfortunately, not enough studies reported baseline nutrient levels to assess how background levels may have influenced the results. Although it is reasonable to suspect that the magnitude of enrichment could impact the effect of nutrients on phototrophs and heterotrophs, there are not sufficient data to robustly test this hypothesis.

The overall effect of nutrients on mycorrhizal fungi and rhizobia were similar in both field studies and laboratory-based manipulations (Table S3). In both cases enrichment also positively impacted plant performance [Pr(RR) > 0 = 1.00 for both mutualism types in both types of studies]. Thus, it is unlikely that having a mix of field and laboratory-based studies in our analyses impacted our results.

DISCUSSION

We show that anthropogenic nutrient pollution presents a potentially serious threat to nutrient exchange mutualisms, with phototrophs benefitting at the expense of their heterotrophic partners. This general response was consistent across most mutualism types in terrestrial and marine environments. These patterns support the hypothesis that nutrient loading disrupts nutritional mutualisms by reducing the net benefit that phototrophs derive from their heterotrophic partners, leading the phototrophs to reduce the amount of C they reciprocate in return (Johnson *et al.* 1997). However, heterotroph identity, the enrichment type and the interaction between the two appeared to mediate the specific impact of nutrient enrichment.

Nutrient loading should only alter the costs of resource trade if the enriched nutrient is limiting for the phototroph and of the same type as that provided by the heterotrophic partner (Johnson *et al.* 1997, 2015). In support of this, we found that the performance of rhizobia and corals, which primarily deliver N to phototrophs (Dennison 2000; Shantz & Burkepile 2014), declined substantially under N enrichment but not P enrichment (Fig. 2). In contrast, mycorrhizal fungi can facilitate both N and P uptake depending on the fungal type (e.g. AM vs. EM), plant and fungal stoichiometry and soil characteristics. However, due to the higher mobility of N vs. P in soil, mycorrhizae often benefit plants most through P

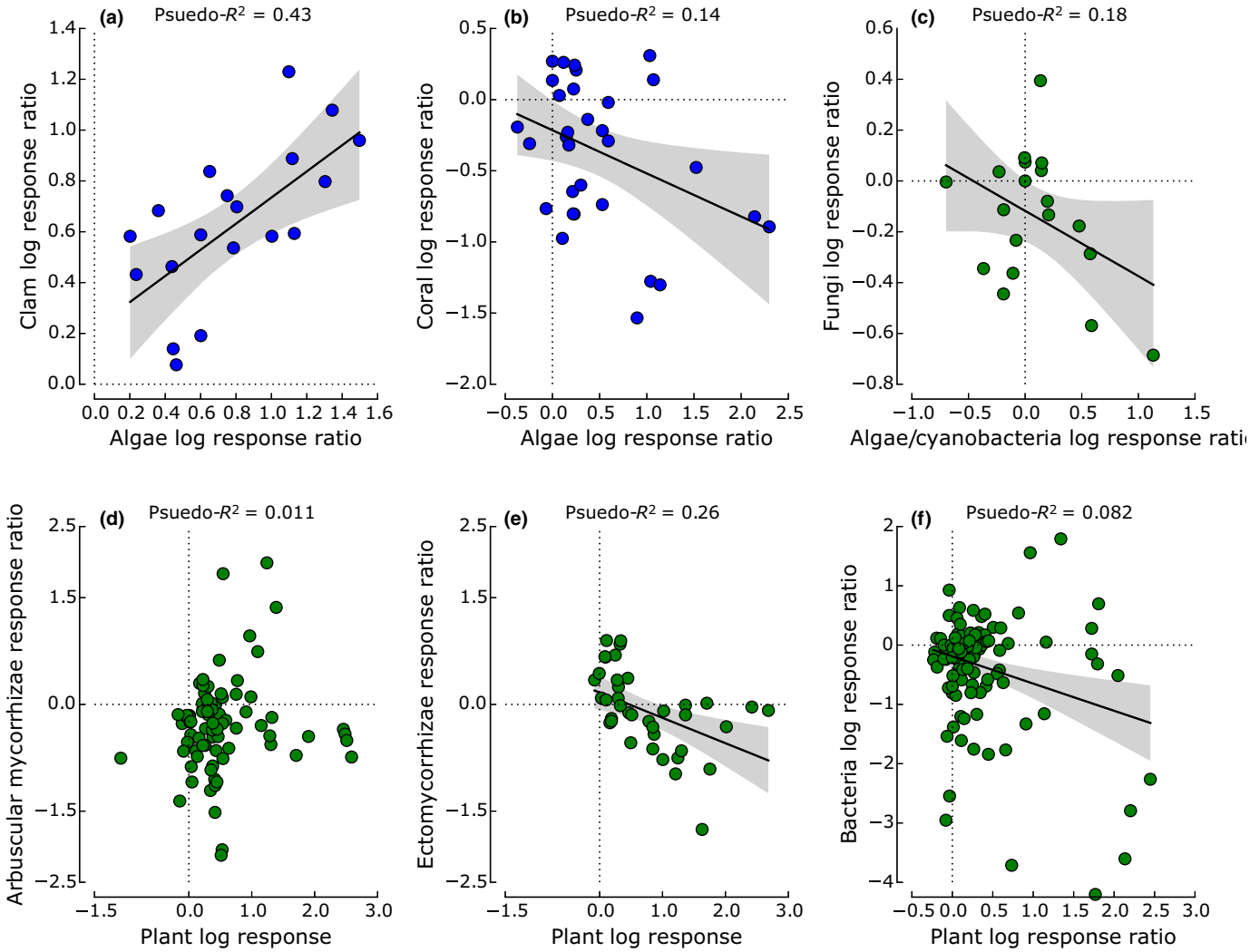

Figure 3 Results of Bayesian Type II regression of heterotroph log response ratios against phototroph log response ratios for the different mutualism types: (a) Algae–Clam, (b) Algae–Coral, (c) Algae/Cyanobacteria–Fungi, (d) Plant–AM Fungi, (e) Plant–EM Fungi and (f) Plant–Bacteria. Shaded area represents the 95% Bayesian credible interval of the regression.

supplementation (Smith & Read 1997; van der Heijden *et al.* 2015; Johnson *et al.* 2015). Accordingly, P enrichment impaired AM and EM fungi performance, while N enrichment resulted in moderate declines in performance only in our weighted model (Figs 2b,c and S1).

When experiments co-enriched with N + P, the effects on heterotrophs were generally smaller and more variable than the declines observed under single nutrient enrichments (Fig. 2). This suggests that the ratio of N : P provided plays a strong role in mediating the outcome of enrichment and that co-enrichment can still result in nutrient limitation, potentially maintaining phototroph demand for heterotroph-derived nutrients (Johnson *et al.* 2015). Thus, the identity of the heterotrophic partner and the nutrients they provide can reasonably predict how nutrient exchange mutualisms respond to different types of nutrient pollution.

The effect of nutrient enrichment on nutrient sharing mutualisms may also depend on the heterotrophs' dependence on phototroph-derived C. Heterotrophs that are less reliant on phototrophs for C should suffer less from C-sanctions imposed by their phototrophic partners. We found that clams, which can obtain as much as 65% of their C by filter feeding (Klumpp *et al.* 1992) and digest up to 89% of newly formed algal symbionts (Maruyama & Heslinga 1997), benefitted from enrichment. In contrast, root-colonising rhizobia, AM fungi and corals are typically more dependent on their phototrophic partners for C (Dennison 2000; Houlbréque & Ferrier-Pagés 2009; van der Heijden *et al.* 2015) and enrichment largely impaired the performance of these groups (Fig. 2). Interestingly, the responses of EM fungi to nutrient enrichment were more variable than the consistent declines we observed in AM fungi performance. This increased variability in EM fungi responses might be expected if EM fungi can scavenge C from the environment via the decomposition of organic matter (Read *et al.* 2004), decoupling the performance of EM from their plant hosts. However, the ability of many EM to acquire biologically meaningful amounts of C through saprotrophy appears limited (Lindahl & Tunlid 2015) and the factors that shape potential differences in the response of AM and EM fungi to nutrient loading will be a fruitful area for future research. Overall, how-

ever, our data suggest that mutualisms in which heterotrophs are heavily dependent on photosynthetically derived C are particularly vulnerable to nutrient-induced decline.

Understanding whether resource trade is based on the direct exchange of nutrients for C, or balanced among multiple currencies, is essential to predict the effects of enrichment on nutrient exchange mutualisms. The linear relationships between the RR of heterotrophs and phototrophs in nearly all of the mutualisms we examined suggest that reciprocal trade of nutrients for C plays a strong role in maintaining most types of mutualisms. An interesting exception to this pattern appears to occur in AM fungi, in which no evidence of linear tradeoffs was observed (Fig. 3d). One potential explanation may be that the reciprocal reward system that mediates Plant–AM Fungi interactions provides more flexible responses to enrichment than the single partner control thought to mediate the other mutualism types. Another potentially important difference between AM mutualisms relative to the other groups is that AM fungi can provision both N and P (van der Heijden *et al*. 2015) and form common mycelia networks (CMNs) that allow interplant signalling (Johnson & Gilbert 2015), something not documented in EM networks. These CMNs create more complex interactions by allowing mycorrhizal fungi to interact with multiple plant partners (Walder *et al*. 2012; van der Heijden *et al*. 2015) and transport signalling compounds that improve plant defences against herbivory and infection among all of the network members (Song *et al*. 2010; Babikova *et al*. 2013). Thus, mutualisms between plants and AM fungi may be paid in multiple currencies and limit the direct negative tradeoffs between phototroph and heterotroph performance.

Understanding drivers of variation in the responses of different mutualism types to enrichment will require focused research on the physiological mechanisms that mediate individual mutualism types. However, continuing to identify general patterns in how nutrient exchange mutualisms respond to global change will provide more rapid and broadly applicable management and remediation strategies, as well as help guide future research efforts. In particular, exploring the importance of nutrient stoichiometry of both mutualist partners, the enrichment source and the form of enrichment (e.g. nitrate vs. ammonium) will likely be fruitful avenues of research (e.g. Johnson *et al*. 2015; Weidenmenn *et al*. 2012). For example, Shantz & Burkepile (2014) found that nitrate enrichment had no effect on the density of algal symbionts in corals but strongly suppressed coral growth, while ammonium enrichment increased *Symbiodinium* density but had no effect on coral growth. Thus, different sources of the same nutrient may generate different tradeoffs in mutualisms and may reveal even more context-dependency in how these mutualisms are regulated. Finally, the diversity and identity of partners in these symbioses may modify responses to nutrient pollution. For example, the genetic diversity of algal symbionts in corals and of microbial communities in soils can mediate the responses of Algae–Coral and Plant–Fungi mutualisms, respectively, to different environmental conditions (Hoeksema *et al*. 2010; Lesser *et al*. 2013; Cunning & Baker 2014). Future research examining the generalities that we identified in how mutualisms respond to nutrient pollution will help to better understand the context-dependent nature of these intricate symbioses.

Interestingly, the fundamentally different architecture of marine and terrestrial symbioses may play a strong role in dictating how systems respond to mutualism disruption. In marine systems such as coral reefs, the ecosystem engineers are often heterotrophic mutualists with endosymbiotic phototrophs. Thus, impaired heterotroph performance on reefs may negatively impact corals with cascading effects on the goods and services these systems provided (e.g. reef-dependent fisheries, shoreline protection, land accretion, etc.). In contrast, the ecosystem engineering mutualists of terrestrial systems are typically phototrophs that house symbiotic heterotrophs. As a result, the effect of enrichment-induced changes in mutualism strength on the structure, goods and services of terrestrial communities is harder to predict. For example, increased phototroph performance could provide greater above-ground carbon storage (Wieder *et al*. 2015), but this may be offset by impaired mycorrhizal sequestration of C in soils, which can account for as much as 70% of C storage in some ecosystems (Clemmensen *et al*. 2013). Similarly, increased productivity will benefit resource production, but declining heterotroph performance could bear financial costs. Nitrogen fixation by rhizobia in agricultural systems provides at least 70 million metric tons of N per year (Kiers *et al*. 2002), or roughly $28.7–$59.3 billion worth of fertiliser application (Nehring 2013), that must otherwise be replaced to maintain productivity if the plant–rhizobia relationship is drastically altered. Similarly, enrichment-driven declines in mycorrhizae performance may jeopardise the non-nutritional benefits that fungi confer to plants, such as tolerance to water stress, pathogens and soil toxins (van der Heijden *et al*. 2015). Accordingly, resolving the consequences and benefits of anthropogenic disruption of nutrient sharing mutualisms will be a critical aspect of understanding global change in the 21st century.

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AUTHOR CONTRIBUTIONS

A.A.S. designed the study with input from D.E.B.; N.P.L. conducted the analyses; A.A.S. wrote the manuscript with assistance from N.P.L. and D.E.B.

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