

REVIEW

The frequency and magnitude of non-additive responses to multiple nutrient enrichment

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Summary

1. Anthropogenic eutrophication is among the greatest threats to ecosystem functioning globally, often occurring via enrichment of both nitrogen (N) and phosphorus (P). As such, recent attention has focused on the implications of non-additive responses to dual nutrient enrichment and the inherent difficulty associated with predicting their combined effects.
2. We used a simple metric to quantify the frequency and magnitude of non-additive responses to enrichment by N, P and N + P in 653 experiments conducted across multiple ecosystem types and locations.
3. Non-additive responses were found to be common in all systems. Freshwater ecosystems and temperate latitudes tended to have frequent synergistic responses to dual nutrient enrichment, i.e. the response was greater than predicted by an additive model. Terrestrial and arctic systems were dominated by antagonistic responses (responses to N + P that were less than additive).
4. The mean of all experiments was synergistic because despite being less common, synergistic responses were generally of greater magnitude than antagonistic ones.
5. *Synthesis and applications.* Our study highlights the ubiquity of non-additive effects in response to dual nutrient enrichment and further elucidates the complex ways in which ecosystems respond to human impacts. Our results suggest how alternative nutrient limitation scenarios can be used to guide approaches to conservation and management of nutrient loading to ecosystems. This review provides the first published summary of non-additive responses by primary producers.

Key-words: Antagonism, co-limitation, eutrophication, interaction, nitrogen, nutrient loading, phosphorus, primary production, synergy

Introduction

The ecological impacts of excessive nutrient loading are substantial, driving losses of ecosystem services world-wide (Vitousek *et al.* 1997; Smith & Schindler 2009) and stimulating debate over how to most effectively regulate anthropogenic nutrient inputs (Conley *et al.* 2009). At the crux of the debate is whether controlling nitrogen (N), phosphorus (P) or both, should frame conservation initiatives (Carpenter 2008; Conley *et al.* 2009). The underpinning research that has informed this debate is generally based on quantifying the primary producer response to enrichment by these key nutrients. Most notably, measuring the production response to multiple nutrients, i.e. both N and P, has received much attention because many anthropogenic stressors tend to alter concentrations of both

nutrients simultaneously (Sala & Knowlton 2006; Halpern *et al.* 2008).

A recent study by Elser *et al.* (2007) demonstrated the prevalence of nutrient co-limitation across ecosystems. Here we define nutrient co-limitation as a greater response to simultaneous enrichment by both nutrients than enrichment by either nutrient individually. Some interpretations of these findings have suggested that they likewise imply a dominance of synergy in ecosystems, assuming that co-limitation is necessarily synergistic (Davidson & Howarth 2007; Elser *et al.* 2007). However, a synergism only occurs when the response is greater than additive, whereas co-limitation can also be an equal to or less than additive response. Understanding these different outcomes forms the basis of our ability to predict how an ecosystem will respond to nutrient enrichment and, therefore, our ability to develop effective management strategies.

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We developed a simple metric to quantify the relative response to additions of both N and P compared to predicted additive effects in plant production to: (i) quantitatively assess the generalities of non-additive responses to nutrient enrichment and (ii) distinguish different types of co-limitation across ecosystem types and latitudinal gradients. We also test the hypothesis that the distribution of these data is consistent with null distributions based on random values. Our results suggest how alternative nutrient limitation scenarios can be used to guide approaches to conservation and management of nutrient loading to ecosystems.

Materials and methods

We developed the interaction effect index (IEI) to quantify the response of primary producers to N and P additions:

$$\text{IEI} = \ln[\text{response NP}/(\text{response N} + \text{response P})]. \quad \text{eqn 1}$$

Where response NP is the primary producer biomass (and in some cases the change in mass) reported for N + P treatments (hereafter NP) and response N and response P are primary producer biomass responses in those treatments. Taking the natural log of the quotient proportionally centers the IEI values around zero. For example, an IEI value generated from an experiment, where response NP is two times greater than response N + response P (i.e., $\ln(2)$) is equal to the absolute value of an experiment, where response N + response P is two times greater than response NP (i.e., $\ln(0.5)$).

We applied the IEI to 653 experiments from marine, freshwater and terrestrial ecosystems that tested for primary producer responses to enrichment in all three treatments: N, P and NP (compiled in Elser *et al.* 2007; obtained via the National Center for Ecological Analysis and Synthesis). Experiments that used the metric of biomass per unit area or volume were included, but proxy variables for biomass were also allowed (e.g. chlorophyll *a* concentration, ash-free dry mass, carbon mass, biovolume, per cent cover; Elser *et al.* 2007). We included only studies that reported mean community-level biomass responses to nutrient enrichment. Thus, the only single species responses that

were included were drawn from communities dominated by single species. One hundred and twenty-nine studies were conducted in laboratory settings; the rest of the experiments were conducted *in situ*. A total of 39 of the 653 experiments included additional manipulations (e.g. grazer exclusion), but only data from unmanipulated controls (e.g. grazers at natural densities) were included. Because of the nature of our categories, all experiments were classified simultaneously in two categories (based on ecosystem type and latitudinal zone)

A simple prediction regarding dual nutrient enrichment is that NP response would be equal to the sum of individual N and P responses (i.e. an additive response; Fig. 1b). Our metric provides a continuous measure to assess the relative departure from additivity. IEI values close to zero, either positive or negative, can be characterized by additive co-limitation (AD; Fig. 1b). As IEI increases or decreases, the non-additive effect becomes more pronounced and can be classified into one of three response categories: synergistic co-limitation (SC), antagonistic co-limitation (AC) and absolute antagonism (AA; Fig. 1a,c,d).

Co-limitation implies that the producer is limited by both nutrients (Arrigo 2005; Davidson & Howarth 2007), and is demonstrated when the response to both nutrients is greater than either nutrient individually. Synergistic co-limitation results when there is a positive non-additive response, whereby NP response is greater than the sum of N and P responses (Fig. 1a). Antagonistic co-limitation is a less than additive response that occurs when NP response is less than the sum of N and P responses, but is still greater than response to either single nutrient. Absolute antagonisms occur where NP response is less than at least one of the single nutrient enrichments. The relative strength of the non-additive effect (i.e. SC, AC, AA) increases as the IEI value deviates from zero, either positively (SC) or negatively (AC, AA).

The term nutrient co-limitation has been subject to various interpretations and requires specific clarification (Arrigo 2005; Lewis & Wurtsbaugh 2008). According to Liebig's law of the minimum, only one nutrient can functionally limit primary production at a given point in time. However, with dual nutrient enrichment, an individual (or producer assemblage with similar physiological nutrient demands) may oscillate between single nutrient limitation of two nutrients (here N and P). In this case, the supply of one nutrient is

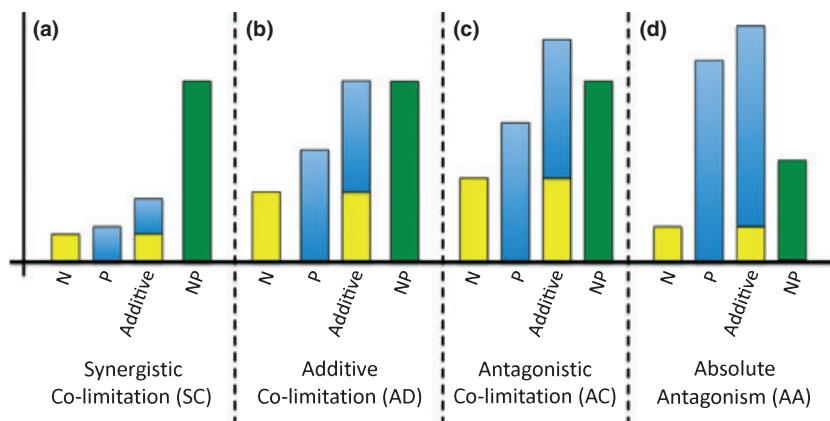


Fig. 1. A conceptual diagram of possible responses from enrichment by N, P and NP. An additive response is indicated in each panel by summing the individual N (yellow) and P (blue) responses. (a) Synergistic co-limitation (SC) such that the biomass or production response to dual enrichment (NP) is greater than the additive response of both single nutrient treatments (N and P alone). (b) Additive co-limitation (AD), whereby the response to NP is equal to that of the sum of N alone and P alone. (c) Antagonistic co-limitation (AC), whereby the response to NP is greater than that of either N or P alone, but not their sum. (d) Absolute antagonism (AA), whereby NP results in less biomass or production than either N or P alone.

sufficient to shift demand towards that of the other, next most limiting nutrient. This interplay continues until either another factor becomes limiting or a saturation state is reached (Davidson and Howarth 2007). As such, over the course of time, e.g. an experimental time period, an individual producer (or producer assemblage) may be considered functionally co-limited, even though a single factor may always be limiting at any instantaneous point.

We test the hypotheses that the distribution of the data from each category (e.g. freshwater) was consistent with null distributions based on random numbers. To do this we compared the distribution of a given category (e.g., marine; $n = 105$) with the distribution of a randomly sampled data set of the same size, using Kolmogorov–Smirnov tests for 1000 permutations. Then we pooled the P -values from these permutations to determine the proportion of the model runs that showed statistical difference between the randomly generated and the observed distributions ($\alpha = 0.05$). The data set of artificial IEI values from which the null distributions for each category was sampled, was generated by randomizing each response variables (N, P and NP) from the original data set and recalculating IEI values based on these numbers. The null distribution for each permutation was then sampled from this data set.

Results

Synergistic co-limitation, AC and AA occurred in all ecosystem types and latitudinal zones (Fig. 2). When comparing the frequency of each response for all experiments combined, 37% were SC, 40% were AC and 23% were AA (Fig. 2). Across all six subcategories (marine, freshwater, terrestrial, arctic, temperate and tropical), SC occurred more frequently in all but terrestrial and arctic ecosystems, in which AC occurred 64% and 71% of the time, respectively (Fig. 2). AA occurred more frequently than SC in arctic (8% SC, 21% AA) and terrestrial

systems (18% SC and 18% AA), but never occurred more frequently than AC (Fig. 2). Across all categories, SC occurred substantially less frequently than antagonistic responses (i.e. AC and AA combined).

A study that incorporates multiple experimental units can be considered additive if the mean of all experiments does not significantly differ from zero (i.e. the 95% confidence intervals overlap zero). Because of the complex nature of our data set, applying such confidence intervals to individual studies was inappropriate. Thus to provide perspective as to the number of studies that were characterized by values close to additive (i.e. zero), we chose an arbitrary positive and negative interval of 10% from perfect additivity ($0.095 > \text{IEI} > -0.095$). Under these conditions, we found only 5% of experiments yielded additive responses (AD). Extending the interval to 15% ($0.139 > \text{IEI} > -0.139$), the frequency of such responses increased to only 11%.

All experiments combined reflect a mean SC response ($\text{IEI} = 0.12$, $P < 0.001$ for t -test of $\text{IEI} = 0$). Freshwater, temperate and tropical subcategories had mean net SC IEI values [$P < 0.005$ for t -test of $\text{IEI} = 0$ for freshwater and temperate; tropical did not differ from zero, $P = 0.43$ (see Appendix S1 in Supporting Information)]. Marine, terrestrial and arctic subcategories had mean AC IEI values [$P < 0.001$ for t -test of $\text{IEI} = 0$ for terrestrial and arctic, marine did not differ from zero $P = 0.83$ (Appendix S1)] (red lines; Fig. 3). SC values were on average of greater magnitude than AC or AA values in most subcategories (coloured bars; Fig. 3). Freshwater ecosystems had the greatest mean SC value ($\text{IEI} = 1.23 \pm 0.07$, NP responses 3.4× greater than additivity). Tropical and marine systems demonstrated the lowest IEI

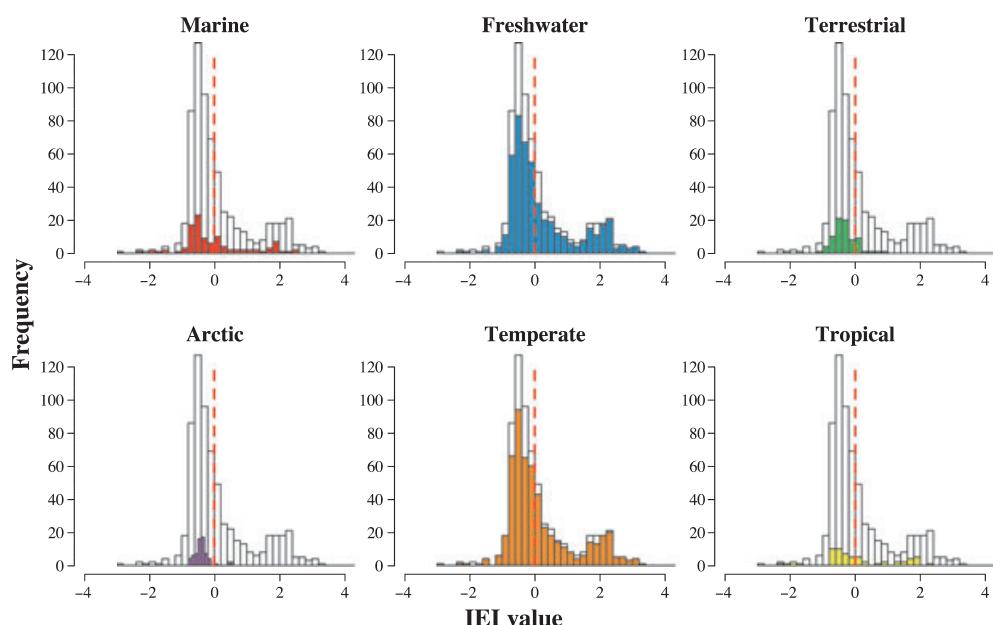


Fig. 2. Frequency of IEI values within each subcategory. In each plot, the white background bars indicate the frequency of IEI values for all experiments combined. A positive value represents synergistic co-limitation, a negative value indicates either antagonistic co-limitation or absolute antagonism and zero represents additive co-limitation. Categories are not orthogonal, thus experiments can be within multiple categories (i.e., temperate and marine).

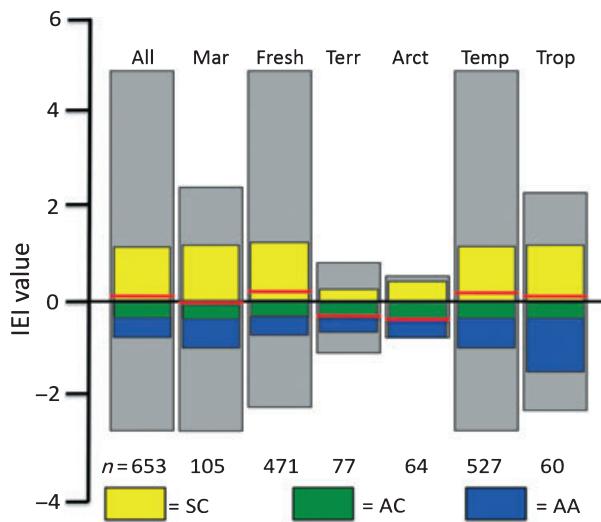


Fig. 3. Full range of all values (grey bars) and mean values for each response type (as indicated by the height of coloured bars; e.g. SC) for different ecosystem types and latitudinal zones. Positive and negative values as in Fig. 2. The red line indicates the net mean IEI value for the respective category. For context, an absolute IEI value of 0·69 or 1·09 indicate a 100% or 200% increase or decrease from additivity, respectively. The coloured bars indicate mean values for each category: yellow bars for synergistic co-limitation (SC), green for antagonistic co-limitation (AC) and blue for absolute antagonism (AA). Categories include fundamental ecosystem types (Mar = marine, Fresh = freshwater and Terr = terrestrial) and well as categories based on latitudinal zones [Arct = arctic (latitudes $> 66\cdot5^\circ$), Temp = temperate ($23\cdot5^\circ$ – $66\cdot5^\circ$) and Trop (latitudes $23\cdot5^\circ$ N to $23\cdot5^\circ$ S)].

values (IEI = $-0\cdot88 \pm 0\cdot5$, $-0\cdot92 \pm 0\cdot12$; NP responses 2·4× and 2·5× less than additivity, respectively). Terrestrial ecosystems and arctic latitudes were the categories that had greater absolute mean AA than SC values.

The highest IEI value (IEI = 5·01; NP response 150× greater than additivity) was from a benthic freshwater stream (Chessman, Hutton & Burch 1992). However, of the top 50 highest IEI values, all but two (both in benthic freshwater environments) experiments were conducted in pelagic freshwater and marine environments. The lowest IEI value (IEI = $-2\cdot81$; NP response 16× less than additivity) was conducted on the benthos of a temperate marine estuary (Taylor *et al.* 1995). Unlike the positive IEI values, the lower IEI values were not dominated by experiments from any category. A bimodal trend is apparent in freshwater, marine, temperate and tropical categories, whereby there is a secondary mode centred around IEI ≈ 2 (Fig. 2). Examination of the data showed that this trend was strongly driven by a single set of experiments in temperate lakes (62 of the 82 studies) (Maberly *et al.* 2002). Of the 82 experiments that fall within the range of $1\cdot5 < \text{IEI} < 2\cdot5$, we found that all but two were conducted in the pelagic zone of freshwater or marine environments, emphasizing that pelagic environments may tend towards relatively strong synergistic response to dual nutrient enrichment.

Comparing the distribution of the data within each category with that of a randomly generated null distribution allows inference as to the probability that these data were the product

of random organization of data, or some underlying pattern driving these trends. Over 99% of random permutations of the data set differed from the observed distribution of values from all the experiments combined. With the exception of marine and tropical categories, $> 95\%$ of the random permutations of the data set differed from the observed distribution of values in every category. These findings provide evidence that the distribution of these data is a product of underlying patterns that emerge from each subcategory.

Discussion

Synergies have garnered much attention in the ecological literature, often under the assumption that they occur frequently and with great magnitude (Myers 1995; Sala & Knowlton 2006; Halpern *et al.* 2008). Our findings provide more detail to this broad generalization. Though synergistic responses (SC) were often demonstrated, they occurred less frequently than antagonistic responses (the combination of AC and AA). However, where they occurred, SC tended to be of greater magnitude than antagonisms, as is supported by the bimodal distribution of the data with the second mode occurring approximately around 2. Thus, although the distribution of experiments is skewed towards negative IEI values (Fig. 2), the overall mean IEI is positive.

The presumed mechanism for synergisms results from primary production that is limited by both nutrients to such a degree that little production occurs under enrichment by a single nutrient. SC is generally a result of oscillating nutrient limitation, whereby ambient availability of nutrients is minimal, and given supply of one nutrient, limitation shifts towards limitation by the other (Davidson & Howarth 2007). Thus, limitation oscillates between nutrients (if supply rate of both nutrients is constant relative to demand) until either production is maximized or another factor becomes limiting. These conditions are often prevalent in extremely nutrient poor ecosystems (Arrigo 2005).

Antagonistic co-limitation, the most common response type, can be explained by a third (or additional) limiting factor. Other micronutrients (e.g. iron, magnesium, molybdate, silica), as well as physical factors (e.g. light, water), can limit production (Howarth, Marino & Cole 1988; Arrigo 2005; Davidson & Howarth 2007). Thus, stimulating production beyond a certain level may incur limitation by a resource(s) besides N or P. Another mechanism may derive from physiological and/or environmentally related limitations (e.g. maximum physical size, disturbance or grazing), whereby the upper bound of community or individual primary production is constrained in mass or size irrespective of nutrient resources (Rosemond 1993).

An additional plausible mechanism for AC may occur if increased supply of one nutrient concomitantly decreases the need for another. An example is the requirement of N for the anabolism of phosphatase enzymes which can be used to process organic P at low availability of inorganic or bioavailable P (Chrost 1991). In this case, enrichment of N can enhance net primary production (via increased production of phosphatase,

and thus increased access to inorganic P). However, under conditions of enrichment with N and P, the availability of inorganic P can simultaneously inhibit production of phosphatase resulting in potentially similar or only slightly higher production than with N additions alone. The net response to NP would then be less than additive, but still greater than the response to N or P alone (Ivancic *et al.* 2009; Rees *et al.* 2009; Scott *et al.* 2009).

Absolute antagonisms, perhaps the most counterintuitive response, were the most infrequent response category. The effect of grazing could lead to AA, whereby the grazer could selectively feed on the resource with the highest production rate, or potentially with the highest nutrient content from enrichment (DeMott, Gulati & Siewertsen 1998; Heck *et al.* 2006). However, there are multiple examples that suggest that antagonisms could simply be experimental artefacts. For example, Taylor *et al.* (1995) reports a strong AA response ($IEI = -2.81$) by eelgrass to enrichment by NP. The enrichment study was conducted in mesocosms where, under enriched conditions, phytoplankton, which was growing simultaneously with eelgrass, responded synergistically to nutrient addition (Taylor *et al.* 1995). This experiment was characterized by a large algal bloom, causing light limitation and thus reducing seagrass biomass. These findings are consistent with the widely predicted response of seagrass to nutrient enrichment at an ecosystem scale (Deegan *et al.* 2002), and arose due to complex interactions involving two different producer assemblages.

The experiments compiled in this study measured the biomass response to enrichment by monocultures (e.g. a stand of a single tree species) as well as entire assemblages of different producer species (e.g. a phytoplankton assemblage). The differences in response to nutrient enrichment between an individual species and a community of different species can be substantial. For example, a diverse assemblage of producers probably consists of organisms with varying physiological requirements (e.g. N limited or P limited) and growth potential (e.g. greater size/growth rate). As such, under various magnitudes and time duration of nutrient enrichment, differential non-additive responses may be expected, and knowledge of the existing community is required to fully understand the mechanisms behind these responses. These differences may help explain the disparity in findings between terrestrial and aquatic (freshwater and marine together) systems, whereby aquatic systems are characterized by a greater range in IEI values with notably greater frequency and magnitude of SC. Many aquatic studies were conducted on assemblages of producers, whereas the majority of studies conducted on monocultures were from terrestrial ecosystems. These findings are consistent with the fact that pelagic environments with mixed species assemblages (e.g. phytoplankton) tend to be particularly susceptible to large production responses (e.g. algal blooms) from multiple nutrient enrichment (Conley *et al.* 2009).

Distributional trends that emerge from these data appear to be the product of underlying ecological patterns as opposed to randomness within the data. Yet, isolating specific factors that determine the frequency of the type of non-additive effects are

difficult given the biological complexity (i.e. species life history, physical conditions, etc.) associated with interaction of multiple nutrients. A notable finding from our study was the dominance of antagonistic responses (AC and AA combined) in terrestrial and arctic subcategories. One explanation for terrestrial ecosystems may be that the growth rate is typically slower and generation time of terrestrial producers is typically greater than for producers in aquatic systems due to the greater requirement of structural and supporting tissue (Cebrian 1999; Chapin 2002). Thus, even given adequate experimental time frames, physiological constraints may hinder synergistic responses. Consistent with this observation, the strongest synergistic effects tended to occur in aquatic ecosystems, particularly in the pelagic zone, occurring among more speciose assemblages with relatively minimal structural demands (see Appendix S2). As for arctic regions, a less than additive response to nutrient enrichment may reflect the fact that producer growth rates are positively correlated with temperature and thus temperature could be a physical factor limiting synergistic responses (Chapin 2002). However, despite the similarity in frequency of response types between terrestrial and arctic subcategories, arctic experiments were primarily conducted in freshwater ecosystems (S2).

Our findings have important implications for management of nutrient loading to aquatic ecosystems. The prevalence of non-additive effects across all systems suggests that when possible, both nutrients should be controlled in conservation and management because the ecological repercussion of simultaneous nutrient enrichment is relatively unpredictable. This is particularly relevant in ecosystems where IEI is close to zero, as they are often characterized by a relatively large response to at least one, but more often both, nutrients individually (Fig. 1b,c). As the IEI value deviates from zero, positively or negatively, it may indicate the potential for effective control of nutrient loading by focusing on the single most limiting nutrient. For example, a large IEI value (i.e. a synergistic response) generally indicates that both nutrients are critical for enhancement of production, thus controlling the single most limiting nutrient (in the case of Fig. 1a; P is most important to control) may be an effective way to mitigate unwanted ecosystem responses. Likewise, an extremely negative IEI value (i.e. AA) generally indicates that only one nutrient is significantly limiting and thus suggests that controlling the loading rate of this most limiting nutrient may provide a significant reduction in ecosystem-scale responses.

In a perfect world, all stressors that negatively affect ecosystems would be carefully managed. Yet, conservation efforts are constrained by cost, time and societal will to manage ecosystems. Our findings show frequent and strong non-additive responses to nutrient enrichment across ecosystem types and locations. We emphasize that a single conservation model for mitigating nutrients is not appropriate and stress that future efforts need to account for the complex nature of dual nutrient limitation. We further highlight the importance of incorporating all treatments (N, P and NP) into enrichment experiments in conjunction with quantitatively assessing the nature of the interaction on a system-specific basis. These data are critical

for building effective predictive models needed to inform conservation and management decision-making regarding nutrient control.

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References

- Arrigo, K.R. (2005) Marine microorganisms and global nutrient cycles. *Nature*, **437**, 349–355.
- Carpenter, S.R. (2008) Phosphorus control is critical to mitigating eutrophication. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11039–11040.
- Cebrian, J. (1999) Patterns in the fate of production in plant communities. *American Naturalist*, **154**, 449–468.
- Chapin, F.S.I. (2002) *Principles of Terrestrial Ecosystem Ecology*. Springer Science.
- Chessman, B.C., Hutton, P.E. & Burch, J.M. (1992) Limiting nutrients for periphyton growth in sub-alpine, forest, agricultural and urban streams. *Freshwater Biology*, **28**, 349–361.
- Chrost, R.J. (1991) *Environmental Control of Synthesis and Activity of Aquatic Microbial Ectoenzymes*. Springer-Verlag, New York.
- Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C. & Likens, G.E. (2009) Controlling eutrophication: nitrogen and phosphorus. *Science*, **323**, 1014–1015.
- Davidson, E.A. & Howarth, R.W. (2007) Environmental science – nutrients in synergy. *Nature*, **449**, 1000–1001.
- Deegan, L.A., Wright, A., Ayvazian, S.G., Finn, J.T., Golden, H., Merson, R.R. & Harrison, J. (2002) Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **12**, 193–212.
- DeMott, W.R., Gulati, R.D. & Siewertsen, K. (1998) Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnology and Oceanography*, **43**, 1147–1161.
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**, 1135–1142.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.
- Heck, K.L., Valentine, J.F., Pennock, J.R., Chaplin, G. & Spitzer, P.M. (2006) Effects of nutrient enrichment and grazing on shoalgrass *Halodule wrightii* and its epiphytes: results of a field experiment. *Marine Ecology-Progress Series*, **326**, 145–156.
- Howarth, R.W., Marino, R. & Cole, J.J. (1988) Nitrogen fixation in freshwater, estuarine and marine ecosystems: biogeochemical controls. *Limnology and Oceanography*, **33**, 688–701.
- Ivantcic, I., Radic, T., Lyons, D.M., Fuks, D., Precali, R. & Kraus, R. (2009) Alkaline phosphatase activity in relation to nutrient status in the northern Adriatic Sea. *Marine Ecology-Progress Series*, **378**, 27–35.
- Lewis, W.M. & Wurtzbaugh, W.A. (2008) Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. *International Review of Hydrobiology*, **93**, 446–465.
- Maberly, S.C., King, L., Dent, M.M., Jones, R.I. & Gibson, C.E. (2002) Nutrient limitation of phytoplankton and periphyton growth in upland lakes. *Freshwater Biology*, **47**, 2136–2152.
- Myers, N. (1995) Environmental unknowns. *Science*, **269**, 358–360.
- Rees, A.P., Hope, S.B., Widdicombe, C.E., Dixon, J.L., Woodward, E.M.S. & Fitzsimons, M.F. (2009) Alkaline phosphatase activity in the western English Channel: elevations induced by high summertime rainfall. *Estuarine Coastal and Shelf Science*, **81**, 569–574.
- Rosemond, A.D. (1993) Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. *Oecologia*, **94**, 585–594.
- Sala, E. & Knowlton, N. (2006) Global marine biodiversity trends. *Annual Review of Environment and Resources*, **31**, 93–122.
- Scott, J.T., Lang, D.A., King, R.S. & Doyle, R.D. (2009) Nitrogen fixation and phosphatase activity in periphyton growing on nutrient diffusing substrata: evidence for differential nutrient limitation in stream periphyton. *Journal of the North American Benthological Society*, **28**, 57–68.
- Smith, V.H. & Schindler, D.W. (2009) Eutrophication science: where do we go from here? *Trends in Ecology & Evolution*, **24**, 201–207.
- Taylor, D., Nixon, S., Granger, S. & Buckley, B. (1995) Nutrient limitation and the eutrophication of coastal lagoons. *Marine Ecology-Progress Series*, **127**, 235–244.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

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Supporting Information

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

Appendix S1. *T*-test results and confidence intervals for all designated categories (ecosystem type and latitudinal zone).

Appendix S2. Frequency of IEI values for each latitudinal zone (arctic, temperate, tropical) within each ecosystem type (freshwater, marine, terrestrial). In each plot, the white background bars indicate the frequency of IEI values for all experiments within that given ecosystem type (e.g. the first row the white bars indicate the IEI values for all experiments in freshwater ecosystems).

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