







RESEARCH ARTICLE

Effects of nutrient enrichment on freshwater macrophyte and invertebrate abundance: A meta-analysis

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Funding information

Deltares, Grant/Award Number:
11209190-003

Abstract

External nutrient loading can cause large changes in freshwater ecosystems. Many local field and laboratory experiments have investigated ecological responses to nutrient addition. However, these findings are difficult to generalize, as the responses observed may depend on the local context and the resulting nutrient concentrations in the receiving water bodies. In this research, we combined and analysed data from 131 experimental studies containing 3054 treatment-control abundance ratios to assess the responses of freshwater taxa along a gradient of elevated nutrient concentrations. We carried out a systematic literature search in order to identify studies that report the abundance of invertebrate, macrophyte, and fish taxa in relation to the addition of nitrogen, phosphorus, or both. Next, we established mixed-effect meta-regression models to relate the biotic responses to the concentration gradients of both nutrients. We quantified the responses based on various abundance-based metrics. We found no responses to the mere addition of nutrients, apart from an overall increase of total invertebrate abundance. However, when we considered the gradients of N and P enrichment, we found responses to both nutrients for all abundance metrics. Abundance tended to increase at low levels of N enrichment, yet decreased at the high end of the concentration gradient (1–10 mg/L, depending on the P concentration). Responses to increasing P concentrations were mostly positive. For fish, we found too few data to perform a meaningful analysis. The results of our research highlight the need to consider the level of nutrient enrichment rather than the mere addition of nutrients in order to better understand broad-scale responses of freshwater biota to eutrophication, as a key step to identify effective conservation strategies for freshwater ecosystems.

KEYWORDS

biomass, eutrophication, freshwater ecosystems, invertebrates, macrophytes, nitrogen, phosphorus

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1 | INTRODUCTION

Human activities have caused massive increases of nitrogen (N) and phosphorus (P) in the environment, most notably through sewage disposal, fossil fuel combustion, and agricultural fertilizer applications (Lu & Tian, 2017; Rockström et al., 2009; Xie & Ringler, 2017). These enhanced nutrient concentrations lead to major ecological changes in both aquatic and terrestrial ecosystems (Jackson et al., 2016; Mantyka-Pringle et al., 2014). In freshwater systems, an increase in nutrient loading generally leads to increasing algal abundance, which in turn may cause oxygen depletion, acidification, and increasing toxicity (De Vries, 2021; Khan & Ansari, 2005; Smith, 2003; Smith & Schindler, 2009; Wurtsbaugh et al., 2019). The proliferation of algae may lead to a shift from clear water dominated by submerged macrophytes to turbid water dominated by phytoplankton (Carpenter, 2005; Scheffer et al., 1993). These processes may have cascading effects on other freshwater communities, depending on the species' abiotic preferences, their position in the food web, and predation pressure (Kido & Kneitel, 2021; Van der Lee et al., 2021; Wang et al., 2021). The abundance of stress-tolerant species likely increases with high nutrient concentrations, whereas less tolerant species may decline due to the loss of oxygen and light energy (Alexander et al., 2017; Scheffer et al., 1993; Schrama et al., 2018). Around the globe, eutrophication in freshwater ecosystems generally results in biodiversity loss (Ansari et al., 2010; Wang et al., 2021).

Freshwater eutrophication effects are commonly studied based on nutrient additions under field conditions or in controlled (mesocosm or laboratory) experiments. Nutrient addition experiments allow for observing the effects of eutrophication on biota while controlling for confounding factors, as opposed to observational studies exploring species assemblages in relation to a gradient of nutrient concentrations. However, it is difficult to generalize the results from single experiments, because responses may depend on the local context (Ardón et al., 2021; Nessel et al., 2021). Synthesizing data from multiple individual experiments through meta-analytical approaches represent a powerful approach to unravel general responses (Midolo et al., 2019). Several meta-analyses focused on the effects of nutrient additions in freshwater ecosystems, including studies on algae (Keck & Lepori, 2012), primary producers (Elser et al., 2007), invertebrates (Nessel et al., 2021), and combinations of trophic groups (Ardón et al., 2021). The scope of these studies was, however, limited to evaluating the effect of nutrient addition compared with a control situation with no addition. Thus, these studies did not consider the amount of nutrient added, while studies in terrestrial systems have revealed that this is highly decisive for ecological responses (Gallego-Zamorano et al., 2023; Midolo et al., 2019). Moreover, responses to nutrient additions have been more extensively studied for primary producers than for higher trophic levels. As Ardón et al. (2021) point out, the effects of nutrient enrichment for higher trophic levels remain elusive and require further research, as it is not obvious how the response to nutrient addition differs between aquatic species groups (Kido & Kneitel, 2021; Lyche-Solheim et al., 2013).

The aim of our study was to synthesize the effects of nutrient enrichment on multiple freshwater species groups along a gradient of both N and P concentrations. We aimed to assess and compare the abundance responses of macrophytes, invertebrates, and fish to N and P nutrient additions in freshwater systems (rivers, lakes, and marshes) by synthesizing data from experimental nutrient addition studies. We used three complementary metrics to quantify abundance: the abundance of individual taxa in an observation (hereafter, individual abundance [IA]), the mean abundance across all taxa in an observation (hereafter, mean abundance [MA]), and the total abundance across all taxa in an observation (hereafter, total abundance [TA]). We used a meta-analytical regression modeling approach, synthesizing results across experimental studies with different setups (laboratory, mesocosm, and field) and covering a range of different environmental conditions. In line with the results of various recent studies (Ardón et al., 2021; Nessel et al., 2021), we expect both N and P to induce abundance responses. Under nutrient-poor conditions, we expect additional N and P to serve as nutrients, thereby causing an increase in abundance. Under nutrient-rich conditions, we expect additional nutrients to cause a decrease in abundance due to oxygen depletion, increasing turbidity and algal toxicity (De Vries, 2021; Wurtsbaugh et al., 2019). Thus, we expect unimodal (hump-shaped) abundance responses to nutrient additions. For macrophytes, we expect the strongest response, due to their strong dependency on light and oxygen (Bornette & Puijalon, 2011; Carpenter, 2005). For higher trophic levels (invertebrates and fish in our study), we expect the response to become progressively weaker due to a loss of energy and biomass across trophic levels, as well as the variability of nutrient requirements among taxa (Cross et al., 2005; Liess & Hillebrand, 2005). Furthermore, we expect that few stress-tolerant taxa may profit disproportionately from excessive nutrient concentrations (Kido & Kneitel, 2021); hence, that IA and MA will show a larger decrease at high N and P concentrations than TA.

2 | METHODS

2.1 | Literature search

We collected peer-reviewed primary research papers by searching online databases for scientific literature, previously published meta-analyses, and cross-referencing. We searched for papers published until December 2022 in the electronic databases Web of Science, Scopus, and SciELO (Scientific Electronic Library Online). We constructed search strings for these databases by using the PICO (Population, Intervention, Comparison, Outcome) method (Morgan et al., 2018), such that each search string consisted of a combination of search terms describing the response variables (invertebrates, macrophytes, and fish), the ecosystem type, the nutrient species, and the words "addition," "treatment," and "experiment." We used separate search strings for invertebrates, macrophytes, and fish, and included an additional search string to cover whole-ecosystem nutrient addition experiments.

We searched for papers with search strings in English (Web of Science and Scopus) as well as Spanish and Portuguese (SciELO), and included papers in any of these languages in our analysis. We furthermore searched for research papers in the databases of the meta-analyses performed by Ardón et al. (2021), Nessel et al. (2021), and Elser et al. (2007). Lastly, we searched for relevant papers in the reference lists of papers eligible for full-text screening (see below). We provide more details on the search strategy and all search strings in Appendix S1.

2.2 | Study selection

We screened papers for relevant data in two rounds. First, we screened titles and abstracts to identify papers that may contain data about the effects of nitrogen and/or phosphorus addition on freshwater invertebrates, macrophytes, and/or fish. Next, we performed full-text screening to select papers for data extraction. FKN, HM, MAJH, AMS, and GG performed first-round screening, and FKN and HM performed full-text screening. Before screening, all authors involved discussed the inclusion criteria and went through a set of 30 papers together to align their application of the inclusion criteria. We selected papers that (1) describe nutrient addition experiments (N and/or P) including a control; (2) report quantitative abundance data for macrophytes, invertebrates (including zooplankton) or fish, expressed as density or biomass at any taxonomic level; and (3) report

measured nutrient concentrations (both N and P) for the treatment and control. We included papers reporting on multifactorial experiments only if other factors (e.g., light intensity and temperature) did not experimentally vary between treatment and control.

Our literature search yielded 9818 papers (1758 papers for invertebrates, 4611 papers for macrophytes, 1603 papers for fish, 1638 papers for ecosystem experiments, 203 papers identified from previous meta-analyses, and five papers identified through cross-referencing with other papers). After screening, we selected 131 papers for data extraction, of which 84 papers contained data for invertebrates, 50 papers for macrophytes, and four papers for fish (seven papers contained data for more than one taxonomic group). We provide an overview of the paper selection process in Figure S1.1 (adapted from Page et al., 2021). We provide a list of all selected papers in Appendix S2. For an overview of the geographic distribution of all papers considered in this study, see Figure 1.

2.3 | Data extraction

From all selected papers, we extracted for each species or higher-level taxon the MA values for the treatment and the corresponding control, including the sample variance and the number of measurements (replicates). We extracted abundance data reported per unit area or volume as either biomass or the number of individuals; for macrophytes, we also included data reported as mass per individual.

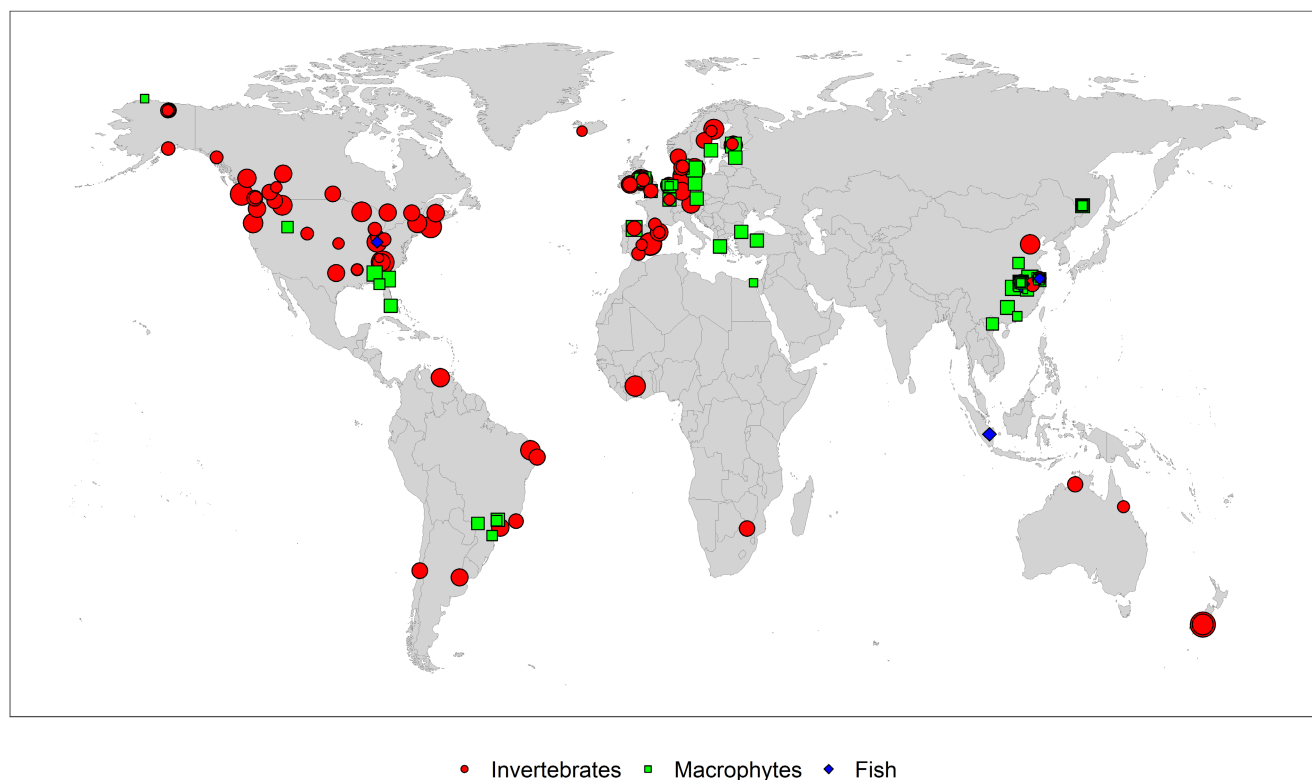


FIGURE 1 Map indicating the study locations included in the analysis, grouped according to taxonomic group. The point size indicates the number of data points that are included data for fish in the analysis after data extraction. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

When a paper reported data for multiple experimental durations, we extracted the data for each duration separately. We extracted the data from tables, figures, the main text or online databases; when a paper reported data in a figure, we extracted the values using WebPlotDigitizer (v4.6; Rohatgi, 2022). If needed, we converted standard deviations to standard errors to calculate sample variances; furthermore, when a study reported the median abundance value and/or inter-quartile range, we converted this to the MA and standard error (Wan et al., 2014). We harmonized the scientific names of the species and taxa based on the Catalogue of Life Checklist (Bánki et al., 2022). We gave each paper a unique study ID. Within each paper, we assigned a control ID to data points with different experimental treatment values sharing the same control. We extracted the nutrient concentrations for all nitrogen and phosphorus species reported in the paper, and converted these to mg/L if not already reported in this unit; furthermore, we reported the N and P reactive form that the authors measured. Our final dataset contained 5177 abundance measurements (4367 for invertebrates, 786 for macrophytes, and 24 for fish) for 297 taxonomic groups (239 for invertebrates, 55 for macrophytes, and three for fish). Because of the small number of observations obtained for fish, we excluded fish from the analysis. We provide a link to our database in the Data Availability Statement.

2.4 | Effect sizes

Based on the obtained data, we calculated three metrics representative of abundance responses: the IA ratio of each reported taxon, the MA ratio across taxa within a taxonomic group, and the TA ratio across taxa within a taxonomic group (Table 1). For all metrics, values >0 reflect increases and values <0 reflect decreases in abundance relative to the control (Hedges et al., 1999). The IA metric reflects the abundance response to nutrient additions of individual taxa. The MA metric considers the arithmetic mean of the IA ratios of all taxa within one observation. The TA metric considers the abundance response to nutrient additions for all taxa together within one observation. Thus, IA represents the responses of individual species or species groups, while MA and TA reflect the response of the entire assemblage or community sampled at a given site. While MA is representative of the mean response across the assemblage or community, TA is more indicative of productivity, as

it considers the abundance changes summed across all taxa. To prevent metrics from becoming indeterminate for measured abundance values of zero in either the treatment or the control, we transformed zero abundance values to the smallest possible measured non-zero MA. For abundance data expressed as density, we replaced the zero abundance value of the sample as follows (De Jonge et al., 2022; Pustejovsky, 2015):

$$\tilde{A} = \begin{cases} \bar{A}, & \bar{A} > 0 \\ \frac{1}{2nD}, & \bar{A} = 0 \end{cases}, \quad (1)$$

where \tilde{A} represents the adjusted MA, \bar{A} is the mean sample abundance as reported in the data, n is the sample size, and D is a scaling factor that represents the sampling effort at the level of the individual observation (e.g., a density value reported in #/mL based on 50 mL samples will get a scaling factor of $D=50$). For abundance data expressed as biomass, we could not apply this correction, because the smallest possible non-zero abundance value would depend on the precision of the scale instrument measuring biomass, which most studies did not report. We therefore replaced zero abundance values for biomass by the smallest possible abundance given the accuracy of data reporting. For data reported in a table, we replaced the zero abundance value with half the detection limit δ , as indicated by the least significant digit of the data reported in the table (e.g., a biomass value of 1.5 mg/L indicates $\delta=0.1$ mg/L). For data reported in a figure, we assumed we could measure data points with an accuracy of three significant digits, so we set the detection limit δ at 1/1000th of the axis length of the figure; to obtain the adjusted abundance value, we divided the axis length by 2×10^3 (i.e., half the detection limit δ). We applied a zero-abundance correction to 211 treatment-control abundance pairs (176 for invertebrates and 35 for macrophytes). In total, our dataset included 3054 effect sizes for IA (2540 for invertebrates and 514 for macrophytes) and 989 effect sizes for TA and MA (631 for invertebrates and 358 for macrophytes). Macrophyte effect sizes pertained mostly to the species level, with a few records at genus level; effect sizes for invertebrates also included higher taxonomic levels (Appendix S3).

We also calculated a weighting factor for each effect size (Table 1). For the IA metric, we calculated the weighting factor as the inverse of the sampling variance (VAR), calculated as (Hedges et al., 1999):

TABLE 1 Summary of the metrics and weights used in the meta-analysis. A_T and A_C represent the abundance of each taxon in the treatment and the control, respectively, n is the number of observations, c is the number of taxa in one observation, and VAR represents the sampling variance (Equation 2).

Metric	Description	Calculation	Weight
Individual abundance (IA)	The log-transformed abundance response ratio for each taxon in an observation	$IA = \ln\left(\frac{\tilde{A}_T}{\tilde{A}_C}\right)$	$\frac{1}{VAR}$
Mean abundance (MA)	The mean log-transformed response ratio for all taxa in one observation	$MA = \frac{\sum \ln\left(\frac{\tilde{A}_T}{\tilde{A}_C}\right)}{c}$	$n \times \sqrt{c}$
Total abundance (TA)	The cumulative log-transformed abundance response ratio for all taxa in one observation	$TA = \ln\left(\frac{\sum \tilde{A}_T}{\sum \tilde{A}_C}\right)$	$n \times \sqrt{c}$

$$\text{VAR} = \frac{V_T}{n_T \times \tilde{A}_T^2} + \frac{V_C}{n_C \times \tilde{A}_C^2}, \quad (2)$$

where V_T and V_C are the sample variance, n_T and n_C are the number of replicates, and \tilde{A}_T and \tilde{A}_C are the adjusted MA in the treatment and the control, respectively. In order to calculate the sampling variance for abundance pairs with a zero or unreported sample variance, we used Bracken's approach to impute the sample variance (Bracken, 1992). We imputed the sample variance for 1020 IA effect sizes (955 for invertebrates and 65 for macrophytes). For TA and MA, we established a weighting factor based on the number of replicates and the number of taxa included in the estimate (Table 1). We used the square root of the number of included taxa in order to reduce the skewness of the counts across the dataset (Schipper et al., 2020).

2.5 | Statistical analysis

We analysed the data per taxonomic group and per metric, thus using six data subsets (two taxonomic groups and three metrics). First, we identified the best-supported random effects structure using the corrected Akaike's information criterion (AICc). We performed random-effects model selection using restricted maximum likelihood (REML) estimation and including the full set of fixed effects for each model run (Zuur et al., 2009). We always included experiment ID (σ_1^2) as a random effect to account for dependency of observations sharing a common control and for which we included data points of multiple measurements in a time series. We also included the reported nutrient species for both N (σ_2^2) and P (σ_3^2) in the random effects structure to assess potential heterogeneity in the data based on the measured freshwater nutrient fraction. We performed model selection on the study code (σ_4^2) to test for additional heterogeneity at the study level that was not captured by the experiment ID. For IA, we additionally performed model selection on the taxonomic group name (σ_5^2) in order to account for heterogeneity in the response across taxa within the overarching clade groups (invertebrates and macrophytes). We note that this was neither needed nor possible for TA and MA, because these metrics are calculated across species groups. For IA, we furthermore used the full variance-covariance matrix of the sampling errors of the control in order to account for calculated effect sizes that use a single control data point for multiple treatment calculations (Lajeunesse, 2011). For all random-effects terms, we assessed variability by fitting random intercepts, and we combined all terms in a crossed, non-nested manner.

After identifying the best-supported random-effects structure, we first performed a random-effects meta-analysis to assess the overall effect of nutrient additions without considering the resulting concentrations. Next, we established mixed-effects meta-regression models (IA metric) and mixed-effects linear regression models (TA and MA metrics) to explore the abundance response to the gradients in N and P concentrations. We performed

fixed-effect model selection on a set of candidate models with different combinations of experimental nutrient concentrations as fixed effects. Prior to model fitting, we log-transformed the experimental nutrient concentrations to reduce their positive skew. We tested candidate models that included at least the experimental treatment concentration (either N or P) as model term, as well as the null model (intercept only). We allowed candidate models to include a quadratic treatment concentration term only when the linear term for the respective nutrient was also included (Nelder, 1998). Furthermore, for both nutrients, we allowed candidate models to include the experimental control concentration in interaction with the corresponding treatment concentration. We fitted and ranked all candidate models based on their AICc value using maximum likelihood (ML) estimation. We identified the best-supported models as those with $\Delta\text{AICc} < 2$ relative to the top-supported model and refitted these models using REML estimation, after which we calculated the regression coefficients, standard errors and the marginal and conditional R^2 values (Zuur et al., 2009). Based on this subset of best-supported models, we calculated weighted average regression coefficients (β_j) and the corresponding standard errors (SE_j) across the best-supported models per data subset as (Burnham & Anderson, 2002):

$$\beta_j = \sum_{i=1}^R w_i \times \beta_{ij}, \quad (3)$$

$$\text{SE}_j = \sum_{i=1}^R w_i \times \sqrt{\text{SE}_{ij}^2 + (\beta_j - \beta_{ij})^2}, \quad (4)$$

$$\text{with } w_i = \frac{\exp(-0.5 \times \Delta\text{AICc}_i)}{\sum_{i=1}^R \exp(-0.5 \times \Delta\text{AICc}_i)}, \quad (5)$$

where R is the total number of models i within 2 ΔAICc units, w_i is the Akaike weight for model i , β_{ij} is model coefficient j for model i (set at zero when β_{ij} is not included in model i), and SE_{ij} is the standard error of model coefficient β_{ij} . We further calculated the importance of each moderator term as the sum of the Akaike weights for all models i in which moderator j is present (Burnham & Anderson, 2002). For each model i , we also calculated the marginal and the conditional R^2 .

We performed all analyses in R Statistical Software (v4.0.4; R Core Team, 2021). For screening the paper abstracts, we used the "abstract_screener" function of the R-package *metagear* (v0.7; Lajeunesse, 2016). We also used *metagear* to impute missing variance estimates, using the "impute_SD" function. For IA, we fitted models using the "rma.mv" function of the R-package *metafor* (v3.0-2; Viechtbauer, 2010). For TA and MA, we fitted all models with the 'lmer' function of the R-package *lme4* (v1.1.27.1; Bates et al., 2015). To calculate the conditional and marginal R^2 for the TA and MA models, we used the "get_variance" function of the R-package *insight* (v0.14.5; Lüdtke et al., 2019). For plotting the results, we used the "ggplot" function of the R-package *ggplot2* (v3.3.5; Wickham, 2016).

2.6 | Robustness of results

We tested for publication bias by performing Egger's tests on the IA effect size metric, for which we modeled the residuals as a function of the precision, and checked for significance of the intercept coefficient (Egger et al., 1997). Furthermore, we assessed potential data asymmetry with respect to the best-selected random effects model by making funnel plots in which we plot the IA effect sizes as a function of the sampling standard error and the precision. We also selected two subsets of the data on which we performed full model selection as described above, and tested whether these data gave similar results compared to the model selection on the full dataset. For the first subset, we excluded effect sizes for which only one of the nutrients was added (leaving only effect sizes with both N and P addition). For the second subset, we excluded effect sizes with a small sample mean in either the treatment or the control (which may violate the assumption of a normal data distribution), based on Geary's rule (adjusted by Lajeunesse, 2015):

$$\frac{\tilde{A}}{SE} \left(\frac{4n}{1+4n} \right) \geq 3. \quad (6)$$

The dataset containing only data for both N and P addition consisted of 2223 IA effect sizes (1983 for invertebrates, 240 for macrophytes) and 611 data points for TA and MA (446 for invertebrates,

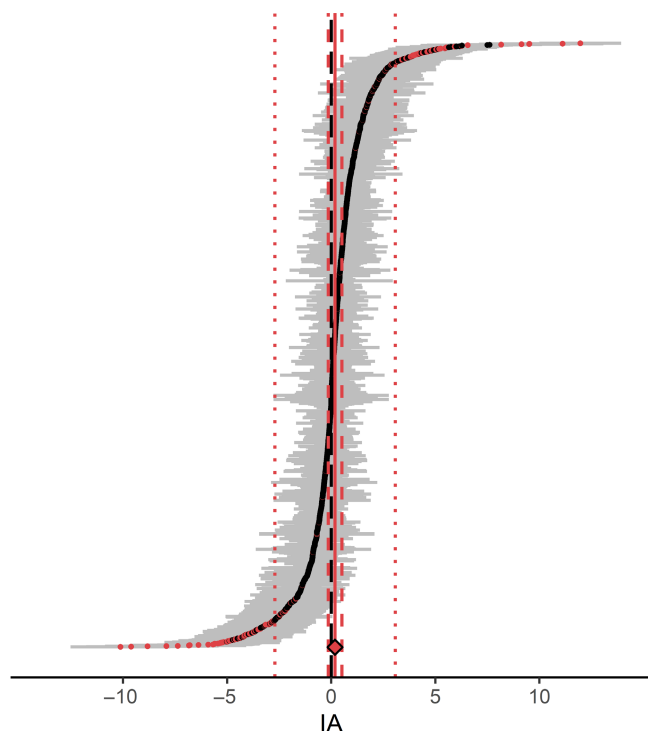
165 for macrophytes). The dataset containing only data that passed Geary's rule consisted of 2638 IA effect sizes (2177 for invertebrates, 461 for macrophytes) and 940 data points for TA and MA (597 for invertebrates, 343 for macrophytes).

3 | RESULTS

3.1 | Overall nutrient addition effects

Based on the random effects meta-analysis (no moderators), we found an overall positive response to nutrient addition only for invertebrate TA (mean effect size: 0.28 [95% CI: 0.08 to 0.48]). We observed no significant response of IA to nutrient addition for either invertebrates (mean effect size: 0.18 [95% CI: -0.14 to 0.51]) or macrophytes (mean effect size: 0.09 [95% CI: -0.22 to 0.39]) (Figure 2). Similarly, we observed no significant response of MA to nutrient addition for either invertebrates (mean effect size: 0.30 [95% CI: -0.03 to 0.64]) or macrophytes (mean effect: -0.01 [95% CI: -0.28 to 0.27]). For macrophyte TA, we did not observe an overall response either (mean effect size: -0.02 [95% CI: -0.31 to 0.28]). For all metrics, mean effects were similar based on the two data subsets (i.e., including only effect sizes for which both N and P were added, and including only effect sizes that passed Geary's rule) (Tables S4.1–S4.2).

(a) Invertebrates



(b) Macrophytes

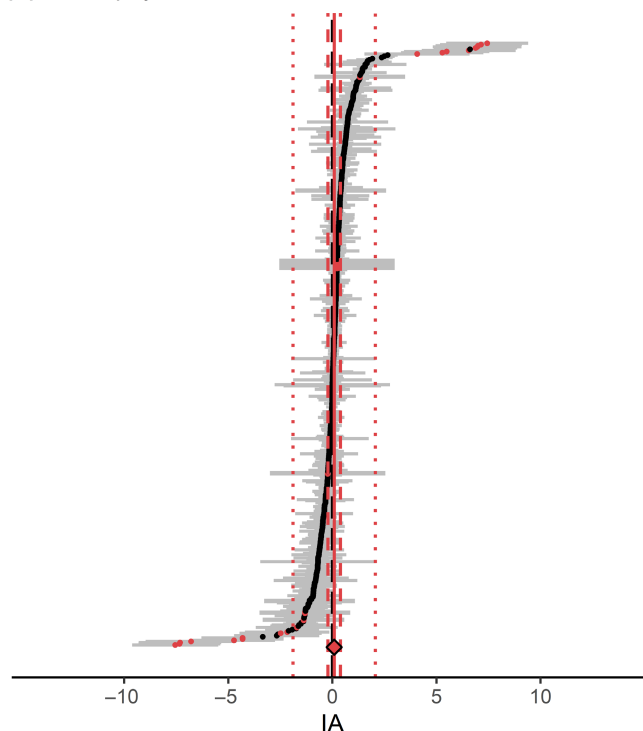


FIGURE 2 Forest plots for individual abundance (IA) effect size data (including 95% confidence intervals and 95% prediction intervals) for invertebrates (a) and macrophytes (b). Dots reflect IA effect sizes, where red dots indicate that the IA value was calculated using data point imputation. The dashed black line indicates an IA effect size of zero, the solid red line and diamond indicate the mean IA effect size, the dashed red lines represent the 95% confidence interval, and the dotted red lines represent the 95% prediction interval. We ran all models with the best-selected random effects structure and without moderators.

Furthermore, both random effects on which we performed model selection were retained in the best-supported random-effects structure for all metrics and biotic groups (Tables S5.1–S5.6). The inclusion of study ID points at heterogeneity at the study level that was not captured by the control ID. For IA, species group name was selected as random effect for both invertebrates and macrophytes, reflecting that abundance responses to nutrient addition vary among species. We found no evidence for publication bias, either for invertebrates (Egger's test: intercept = -0.05 , $p = .221$) or for macrophytes (Egger's test: intercept = -0.10 , $p = .283$). Based on visual inspection, we did not observe funnel plot asymmetry (Figures S6.1–S6.2).

3.2 | Invertebrate responses to nutrient concentrations

Overall, we found that invertebrates respond to both N and P concentrations, yet the responses differed among metrics (Figure 3; Tables S7.1–S7.3, S8.1–S8.3, S9.1–S9.3). For IA, we observed a unimodal response primarily to N, with an abundance increase for moderate N concentrations (between 0.01 and 0.1 mg N/L, given average control concentrations of N). We further found a positive linear trend in the response to P, but less pronounced. For MA, we found a similar pattern, i.e. a unimodal response to N and a positive linear trend for

P, with the largest abundance increases for high concentrations of P (>1 mg P/L) and moderate concentrations of N (~ 0.1 mg N/L). For TA, the response was primarily driven by the P concentration, with the largest increase at high P concentrations. We observed that the experimental control N concentration modified the IA and MA responses, with more pronounced responses at low background concentrations, and larger increases and decreases in response to lower and higher N enrichment levels, respectively (Figure S10.1). In contrast, TA and MA responses to low levels of P enrichment were more pronounced (implying a larger decrease) at higher background P concentrations (Figure S10.2). When including only effect sizes from experiments with both N and P addition, we observed more positive IA and MA responses, especially for high N concentrations (IA) and high P concentrations (MA) (Figure S11.1). For the data subset with effect sizes passing Geary's rule, we observed a more positive response for all metrics (Figure S11.2). However, for both data subsets, the response patterns remained similar to those based on the main dataset.

3.3 | Macrophyte responses to nutrient concentration gradients

For macrophytes, we observed abundance responses to both N and P concentrations (Figure 3; Tables S7.4–S7.6, S8.4–S8.6, S9.4–S9.6).

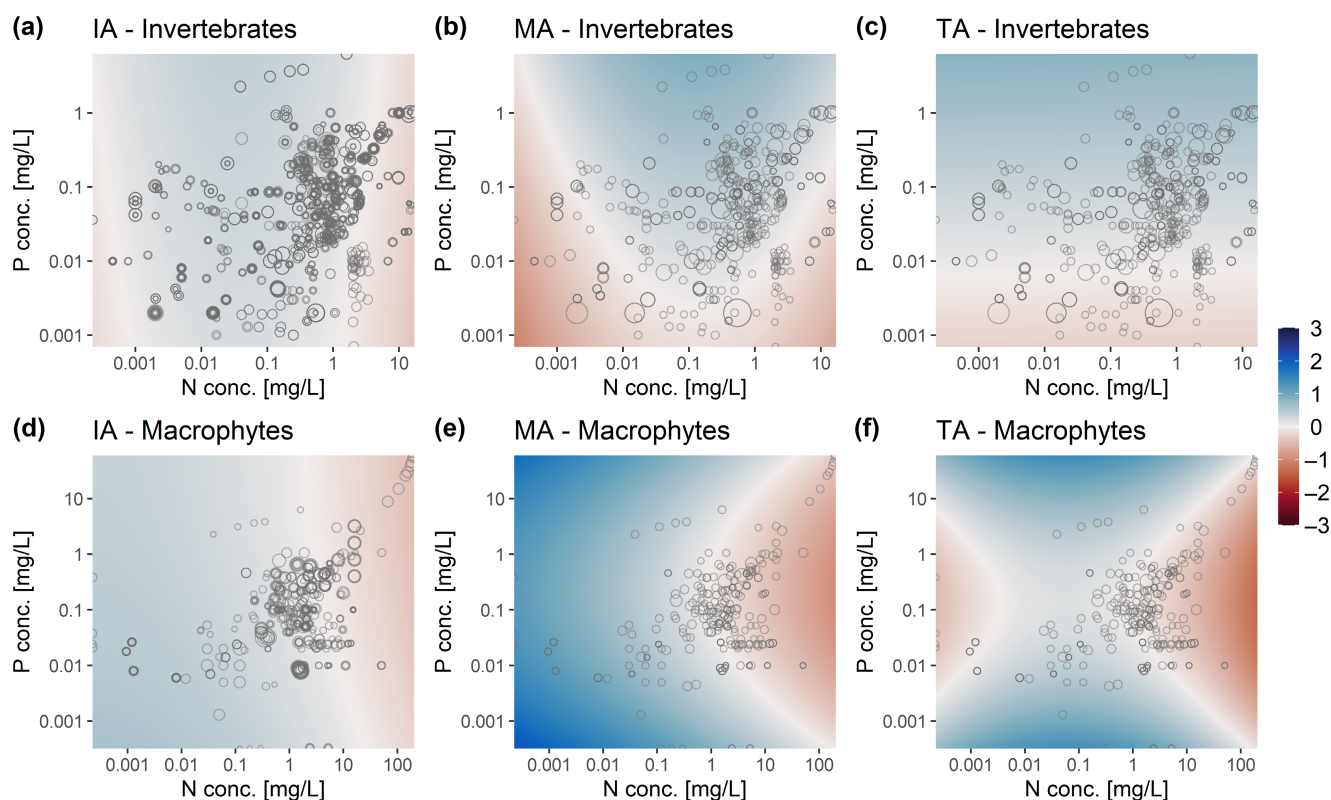


FIGURE 3 Heat maps indicating the responses of individual abundance (IA), mean abundance (MA) and total abundance (TA) values for invertebrates (a–c) and macrophytes (d–f). We used the fitted consensus models to visualize the responses along the gradients of both nutrients. Blue colors indicate an effect size >0 , and red colors indicate an effect size <0 . Data points are indicated with gray dots, and dot size indicates the weight for each data point. Coefficients of the underlying consensus models are provided in Appendix S9.

IA responded mostly to N enrichment, with abundance increases at concentrations up to 10 mg/L. We further found a slight positive relationship between IA and P. MA also responded mostly to N enrichment, with strong abundance increases at low N concentrations. We further observed a decrease for high N concentrations (>1 mg/L), with the decrease most pronounced for moderate P concentrations (between 0.01 and 1 mg/L). The TA response was similar to MA for high N concentrations, but showed in addition a decrease for low N and moderate P concentrations. We observed that the experimental control N concentration caused the IA and MA response to increase, particularly at low concentrations (~0.001 mg/L), whereas we observed no effect for TA (Figure S10.1). For the control P concentration, we did not observe any response (Figure S10.2). When including only effect sizes from experiments with both N and P addition, we observed for IA a positive response for low-to-moderate N and P, and a negative response for high N and P (Figure S11.1). For MA and TA, we observed a response to N enrichment, with increases at low concentrations and decreases at higher concentrations (>0.01 mg/L). For the data subset based on Geary's rule, we observed responses largely similar to the default dataset (Figure S11.2). For IA, we observed a response mostly to N, with a maximal increase at moderate concentrations (~0.1 mgN/L) and a negative response for low and high concentrations (<0.001 mg/L and >10 mg/L). For MA and TA, we observed negative responses for low and high N concentrations, and positive responses for low and high P concentrations.

4 | DISCUSSION

4.1 | Overall abundance responses to nutrient addition

Eutrophication of freshwater systems has been one of the most pervasive influences of human activity on the biosphere (Rockström et al., 2009; Steffen et al., 2015). Although the effects of nutrient addition on freshwater ecosystems have been extensively researched over the past decades, these effects remain somewhat elusive, as ecological responses may differ with the amount of nutrients added, local environmental conditions, taxonomic groups, and the type of response studied (Wang et al., 2021). In line with this, we found a large heterogeneity in the responses of macrophytes and invertebrates to nutrient addition, with some taxa increasing and some decreasing in abundance (Figure 2). In our random effects meta-analysis (no moderators), we found a significant overall response only for total invertebrate abundance, which increased in response to nutrient addition. This positive response is in line with the positive responses reported for freshwater consumers by Ardón et al. (2021). However, it is in contrast to the findings by Nessel et al. (2021), who observed mainly decreases in freshwater invertebrate abundance and biomass in response to nutrient addition. For macrophytes, we observed no significant responses for any of the response metrics. This is in disagreement with both Ardón et al. (2021) and Elser et al. (2007),

who report an increase in biomass for primary producers. Possibly, these differences reflect how we treated zero-abundance values, which in general pose challenges to the calculation of effect sizes. We replaced zeroes by small non-zero values using both the sampling effort and the measurement precision (De Jonge et al., 2022; Pustejovsky, 2015, 2018). This allowed us to include data points with zero abundance in the control, which are commonly left out from meta-analytical studies (Benítez-López et al., 2017; Midolo et al., 2019). As we applied the same correction to zero treatment and zero control abundance estimates, we prevent a possible bias toward negative effect sizes by excluding species or taxa absent from the control yet present in the treatment.

4.2 | Abundance responses along gradients of N and P enrichment

In contrast to the results of the overall meta-analysis without moderators, our exploratory meta-regression models indicated that both nitrogen and phosphorus enrichment have an effect on the abundance of macrophytes as well as freshwater invertebrates. We note here that the amount of explained variance by the fixed effects in our models was relatively low (between 0.01 and 0.1; Appendix S8). Although such low marginal R^2 values are not uncommon for mixed-effect meta-regression models (compare De Jonge et al., 2022; Gallego-Zamorano et al., 2023), we nonetheless call for caution when interpreting the fixed-effect model selection results, as the parameter values in the consensus models explain only on a small proportion of the variance in the data. Nevertheless, the results of our meta-regression models point at the relevance of considering the level of nutrient enrichment rather than mere addition. The positive and unimodal responses to N and P, as observed for the invertebrates and for macrophyte IA, contrast the historical view that P supply is the main limiting factor for freshwater systems (Dodds & Smith, 2016; Dubey & Dutta, 2020; Schindler, 1974, 1977; Schindler et al., 2008; Srivastava et al., 2008), yet are in line with more recent studies pointing to limitation by N or co-limitation by N and P (Allgeier et al., 2011; Ardón et al., 2021; Elser et al., 2007; Paerl, 2009). On a global scale, P accumulates faster than N in many freshwater ecosystems, causing an 'N deficit' that might cause some taxa to benefit from N enrichment (Yan et al., 2016). For invertebrates, our results suggest that a moderate N concentration (IA and MA) and a high P concentration (IA, TA, MA) result in the largest abundance increase. The abundance increases in response to both N and P enrichment reflect that both N and P are essential nutrients for growth and reproduction. For invertebrate species, the internal tissue N:P ratio depends primarily on its nutrient requirements, which are related to for example its life history and body size, and much less on external nutrient concentrations (Karimi & Folt, 2006). However, nutrient requirements can vary significantly among taxa, whereby fast-growing species tend to have larger P requirements (Gillooly et al., 2005; Meunier et al., 2017). This is in line with our results showing a positive response of total invertebrate abundance

(indicative of productivity) primarily to P enrichment, whereas this is less so for the individual and mean assemblage level responses (IA, MA). Our results for both macrophytes and invertebrates further indicate that N becomes a stressor at high concentrations, in line with other studies pointing to N being impactful under high concentrations (Yu et al., 2015). For macrophytes, an increase in N concentration can lead to a change in community structure, with floating plants becoming dominant at the expense of plants rooted in the sediment (Feuchtmayr et al., 2009). A change in macrophyte community and increasing turbidity will in turn influence the invertebrate community, particularly benthic invertebrate groups that lose their habitat (Pan et al., 2015).

4.3 | Methodological reflections

We based our analysis on the concentrations of N and P in the receiving water bodies, rather than the amount of nutrient addition. Most studies did not report the amount of nutrient addition, and even if they did, additions were difficult to compare among studies because the volume of the receiving water body was often not reported. This contrasts with studies describing terrestrial nutrient addition experiments, which typically specify the nutrient addition per unit of area (Gallego-Zamorano et al., 2023; Midolo et al., 2019). A downside of our approach is that nutrient uptake in the system (e.g., the sediment or biota) will go undetected, hence that the observed response is not necessarily reflected by higher nutrient concentrations in the water. The fact that the studies in our database measured different nutrient species posed an additional challenge. We tackled this by including the N and P species as random effect in the analysis, and found that the variance explained by the nutrient species was negligible (Appendix S8). For N this is unexpected, as NO_3^- is considered non-toxic, whereas NH_4^+ and NO_2^- are considered toxic even at low concentrations (Kocour Kroupová et al., 2018; Mooney et al., 2019; Moore et al., 2021). However, nitrate concentrations in freshwater are generally higher than those for nitrite or ammonium, and there are studies that point to NO_3^- toxicity for values as low as 10 mg/L (Camargo et al., 2005), since NO_3^- can negatively influence growth and survival of freshwater organisms (Gomez Isaza et al., 2020).

We acknowledge that most studies in our dataset contained data for temperate regions in the northern hemisphere (North America, Western Europe, and East Asia; Figure 1). Although we increased the global coverage of our analysis by the inclusion of Spanish and Portuguese search strings in addition to English, we recognize that the addition of more languages might have led to a better global representation (Zenni et al., 2023). We are also aware of the fact that non-English language studies are more likely to publish results that are statistically non-significant (Konno et al., 2020). However, we did not find any proof for publication bias in our analysis. Interestingly, the regions that are best covered in our analysis are also identified as being at high risk for N and P eutrophication of freshwater systems (Steffen et al., 2015).

Finally, we note that the large residual heterogeneity in our models point at the influence of several relevant factors that we did not include in our analysis. For example, we did not account for seasonal variation among experiments, while N and P limitation may vary seasonally, with P being the limiting nutrient during spring, shifting to N limitation over the summer (Kolzau et al., 2014; Søndergaard et al., 2017). Furthermore, we could not account for possible confounding influences of temperature and acidity, because many studies did not report these factors. However, temperature may be a limiting factor for invertebrate species abundance (Bonacina et al., 2023), hence could affect the response to nutrient enrichment. For macrophytes, higher temperatures may increase the domination of floating plants on the system, causing a change in species dominance comparable to nutrient additions (Feuchtmayr et al., 2009). Furthermore, temperature has an effect on nutrient mobilization, with higher temperatures resulting in increasing mobilization of N species, causing more N compounds to become available for uptake (Jack Brookshire et al., 2011). This indicates an increasing role of climate change in the response of species to nutrient additions (Greaver et al., 2016).

4.4 | Concluding remarks

Our study shows that both N and P enrichment influence the abundance of freshwater macrophytes and invertebrates. All macrophyte abundance metrics and the IA and MA metrics for invertebrates tended to increase at low levels of N enrichment (0.001–0.1 mg/L), yet decreased at the high end of the N concentration gradient (1–10 mg/L). For macrophytes, MA and TA showed a noticeable decrease in abundance at high N concentrations, in particular at moderate P concentrations (0.01–1 mg/L). Overall, responses to increasing P concentrations were mostly positive. This was visible in particular for the TA of invertebrates, as indicator of total system productivity. We recommend future research to focus on more species groups, and to explore whether any differences in responses can be discerned between subgroups of invertebrates and macrophytes (e.g., according to ecological guild). Since eutrophication will continue to be a main environmental problem, a better and more detailed understanding of freshwater responses to nutrients remains crucial toward identifying appropriate management practices.

AUTHOR CONTRIBUTIONS

Floris K. Neijns: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing – original draft; writing – review and editing. **Hadassa Moreira:** Formal analysis; investigation; software; writing – original draft; writing – review and editing. **Melinda M. J. de Jonge:** Formal analysis; methodology; software; validation. **Bart B. H. P. Linssen:** Conceptualization; formal analysis; investigation; methodology; software. **Mark A. J. Huijbregts:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – original draft; writing – review and

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ACKNOWLEDGMENTS

We are thankful to Juan Gallego-Zamorano for his help with making the figures. We also would like to thank an anonymous reviewer for constructive feedback on our manuscript, and all authors who published their data.

FUNDING INFORMATION

FKN acknowledges funding from Deltares, project number 11209190-003.

CONFLICT OF INTEREST STATEMENT

The authors declare to have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that accompany this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.10251771>.

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How to cite this article: Neijnsens, F. K., Moreira, H., de Jonge, M. M. J., Linssen, B. B. H. P., Huijbregts, M. A. J., Geerling, G. W., & Schipper, A. M. (2023). Effects of nutrient enrichment on freshwater macrophyte and invertebrate abundance: A meta-analysis. *Global Change Biology*, 30, e17094. <https://doi.org/10.1111/gcb.17094>