TITLE PAGE

Title: Species richness – phosphorus relationships for lakes and streams worldwide

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ABSTRACT

Aim: We investigated the patterns of autotrophic and heterotrophic relative species richness along a total phosphorus (TP) concentration gradient. The relative species richness – TP relationships were calculated separately for four different regions [(sub)tropical, xeric, temperate, and cold] and two types of water bodies (lakes and streams).

Location: Global

Methods: Using data from peer-reviewed articles reporting the occurrence of freshwater species at specific TP concentrations, we determined the species richness along a TP gradient. Using log-logistic regressions, we then estimated the TP concentration at which the potential decrease of relative species richness (RSR) equals 0.5 and the slope at which the decrease occurs (β). The RSR is given as the ratio of species richness to maximized species richness along a TP gradient.

Results: The RSR of streams generally decreased more rapidly than that of lakes with increasing P, as illustrated by the steeper slope of the log-logistic functions for streams ($\beta_{lakes} < \beta_{streams}$). Although there was no consistent trend between autotrophs and heterotrophs in the different regions, we found that the TP concentration at which the RSR equals 0.5 was lower in cold regions (0.04 – 0.22 mg P/L) than in warmer regions (0.28 – 1.29 mg P/L).

Main conclusions: The log-logistic relationships between RSR and TP concentration vary considerably among regions of the world, between freshwater types (lakes and streams) and between species groups (autotrophs and heterotrophs). This variability may be attributed to differences between the two freshwater types in respect to their species groups and evolutionary patterns, nutrient demand, biogeochemical and hydrologic processes. We were not able to derive log-logistic regressions for all combinations of freshwater type or species type and region [e.g., (sub)tropical lakes]. For other areas, our results can be used to assess the potential impact of phosphorus eutrophication on freshwater biota.

Keywords: Autotrophs, heterotrophs, freshwater, log-logistic regression, total phosphorus, species sensitivity, relative species richness

INTRODUCTION

The intensification of agriculture, industrialization, and urbanization has led to increasing fluxes of phosphorus (P) worldwide (Liu & Wang, 2007). In freshwater systems, this nutrient is regarded as the main factor driving primary productivity (Schindler, 1974). In addition to increases in biomass, changes in autotrophic and heterotrophic species richness associated with P concentrations have been reported (McIntyre *et al.*, 2007; Penning *et al.*, 2008; Rumes *et al.*, 2011). For example, high crustacean species richness was found in eutrophic (sub)tropical lakes, while macrophyte species richness in temperate lakes (Rumes *et al.*, 2011) was maximized at intermediate total-phosphorus levels (Penning *et al.*, 2008). The rate of nutrient recycling in tropical streams has also been linked to fish species richness (McIntyre *et al.*, 2007), suggesting that total-phosphorus levels and faunal richness are strongly correlated.

Because aquatic eutrophication is currently considered one of the strongest threats to water quality and stream biodiversity worldwide (Björklund *et al.*, 2009; Vörösmarty *et al.*, 2010), it is important to identify the freshwater types and regions whose biotic communities are most affected by P imbalances. Many studies have focused on the effects of increasing P in one or more specific water bodies, species, or regions (Dodson *et al.*, 2000; Smith *et al.*, 2007; Struijs *et al.*, 2011b). However, to our knowledge, no study has outlined the effects of different P concentrations on relative species richness on a global scale. Understanding how decrease in relative species richness due to P increases may occur in different regions of the world and in different freshwater types is essential for the ecological assessment of eutrophication impacts.

The goal of this study was to compare the relationships between P concentration and the relative species richness of autotrophs and heterotrophs in lakes and streams in different regions of the world. We first performed an inventory of peer-reviewed observational field data, which yielded a large number of studies worldwide. We then derived concentration-response relationships based on this dataset. Given that the cause-effect relationships obtained from nutrient-addition experiments may reflect only small spatial and temporal coverage, observations from surveys make it possible to derive concentration-response relationships for other areas or periods.

Concentration-response relationships are commonly applied in toxicology and can be used to compare the sensitivity of different species groups to changes in the concentration of the stressor of interest. They can also be directly coupled with existing biogeochemical models of the fate of P in inland waters, such as those used in Global NEWS (Harrison *et al.*, 2005; van Drecht *et al.*, 2005), the Millennium Ecosystem Assessment (van Drecht *et al.*, 2009), life cycle impact assessments (Helmes *et al.*, 2012), or estimation of past or expected ecological risk of stressors (Leuven *et al.*, 2011; Fedorenkova *et al.*, 2012), to ultimately determine the relationships between environmental stressors and relative species richness in freshwater systems.

MATERIAL AND METHODS

Species richness – total P relationships

We chose total P (TP) as our stressor of interest because it is the recommended P fraction for water quality monitoring (Lewis *et al.*, 2011) and is commonly reported in water-quality studies. Based on observational studies of species occurrence, we calculated the relative species richness of autotrophs and heterotrophs along a TP gradient. Subsequently, we derived log-logistic regressions of the relative species richness in lakes and streams in (sub)tropical, temperate, cold, and xeric regions. Each step is described in detail below, and

97 the complete framework is illustrated in Fig. 1.

98 We computed the overall species richness (SR) as the number of species reported in
99 0.1 $\log_{10}$-transformed concentration intervals (C_i, mg P/L) for streams and lakes in different
100 regions as

101 where $O_{t,h,g}$ is the occurrence of a given species in species group *g* (autotrophs or
102 heterotrophs) at nutrient concentration C_i in freshwater type *t* (stream or lake) in region *h*. O
103 is one if the species is reported to be present and zero if the species is not present.

104 We identified the concentration of TP at which $SR_{i,t,h,g}$ is at its maximum (SR_{max}).
105 This approach has been applied by Struijs *et al.* (2011b) for genus-level macroinvertebrate
106 richness in Dutch streams as a function of TP-induced stress and by Azevedo *et al.* (2013) for
107 vascular-plant species richness in biomes as a function of low-pH stress. The TP
108 concentration at which SR equals SR_{max} is hereafter referred to as the optimum TP
109 concentration, C_{opt}. To compare SR – TP concentration relationships between autotrophs and
110 heterotrophs, between lakes and streams, and among regions, we transformed SR into a
111 relative species richness measure as

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113 following Azevedo *et al.* (2013) and Struijs *et al.* (2011b), where eRSR is the empirical
114 relative species richness (eRSR) of species in group *g* at concentration C_i in freshwater type *t*
115 in region *h*. At C_{opt}, eRSR is one. Conversely, an eRSR of zero represents the complete
116 absence of species. At C_i values lower than C_{opt}, we consider that SR is no longer affected by
117 the excess P (Struijs *et al.*, 2011b). Thus, eRSR is here described only for C_i values larger
118 than C_{opt}. It is important to note that species richness – TP relationships are typical bell-
119 shaped curves, with species richness also decreasing at limiting nutrient levels (Penning *et*

120 *al.*, 2008; Struijs *et al.*, 2011b). In this study, we were interested in how individual species'
121 tolerance to high TP levels might influence species richness – TP relationships. Therefore, we
122 limited the analysis to the eutrophic side of the curve, i.e. at C_i greater than C_{opt} (Struijs *et al.*,
123 2011b).
124 Next, we used a log-logistic model of the calculated RSR (cRSR) by fitting it to eRSR
125 as

$$cRSR = \frac{1}{1 + e^{\alpha + \beta \log_{10}(C_i)}}$$

126 The coefficient α indicates the $\log_{10}$ TP concentration at which relative species
127 richness is 0.5, and β indicates the slope of the log-logistic regression. We fitted both cRSR
128 coefficients (α and β) using logistic regression in SAS 9.2. The sample size for the log-
129 logistic regression is given by the number of $SR_{i,t,h,g}$ data points (at 0.1 $\log_{10}$ TP-concentration
130 intervals). We considered a log-logistic model to fail to fit the empirical data if it had a p
131 value > 0.05, a β coefficient non-different from zero at a 95% confidence level, or an α
132 coefficient outside the concentration range at which eRSR data were available (between C_{opt}
133 and the maximum observed TP level). To test for potential sampling bias resulting from
134 different sampling effort across regions, we tested whether the number of species or the
135 number of studies was correlated with our results for C_{opt}, α, or β.
136 **Sensitivity analysis**
137 We conducted a sensitivity analysis to investigate how our regressions might vary if
138 smaller spatial units were used. For this analysis, we used the methodology described above,
139 but at smaller spatial levels of detail: freshwater ecoregions [using the map delineated by
140 Abell *et al.* (2008)], regions within individual realms, and individual studies in our data
141 inventory. Azevedo *et al.* (2013) have suggested employing a sensitivity analysis based on
142 repeating the procedure using smaller spatial-aggregation levels to identify differences in

ecoregions within terrestrial biomes.

We repeated the sensitivity analysis to determine how our results would change if we distinguished among specific taxonomic groups within the autotrophic and heterotrophic groups. Autotrophs were divided into cyanobacteria, silicon-based algae, non-silicon-based algae, and macrophytes, while heterotrophs were divided into fish and invertebrates.

Collection and management of data

To acquire data about the TP-concentration ranges at which specific aquatic species were reported to be present, we selected peer-reviewed articles using a combination of relevant keywords in *Web of Science* (lake, freshwater, phosphorus, etc.). The specific keyword combinations can be found in Appendix S1 in the Supporting Information. We included only articles that reported the locations of their field surveys and that recorded TP concentrations and species occurrences at the same sampling location and time. We also included species records from the *Limnodata Neerlandica* database (STOWA, 2010), which includes invertebrate-occurrence data and water-quality measurements for inland waters in the Netherlands. We did not consider brackish or inland saline waters or anthropogenic ecosystems, such as fish ponds or wastewater-treatment plants.

We grouped ponds and reservoirs with freshwater lakes and springs, rivers, and creeks with streams. Wetlands were excluded from this study. Furthermore, based on the geographical location of each study, we assigned each freshwater system to a biogeographical region: (sub)tropical, temperate, cold, or xeric. This division was based on the major freshwater habitat types (MHT) of the world, recently developed by Abell and colleagues of the FEOW project (Freshwater Ecoregions Of The World, http://www.feow.org). We combined the regions designated as temperate coastal rivers, temperate floodplain rivers and wetlands, and temperate upland rivers into one temperate region. Likewise, we combined (sub)tropical coastal rivers, (sub)tropical floodplain rivers and wetlands and (sub)tropical

upland rivers into one (sub)tropical region. Although the MHT map delineated by the FEOW includes many freshwater types, such as temperate floodplain rivers and wetlands, we used the freshwater-type classification given by each inventoried study. Montane and polar freshwater systems were combined and referred to as the cold region. Studies located in the MHT classes Oceanic Islands, Large Lakes, and Large River Deltas (such as studies located in the Great Lakes and Lake Peipsi regions, the Paraná River basin, and the Azores Islands) were assigned to the closest adjacent habitat.

We selected species belonging to the following groups: autotrophs (comprising cyanobacteria, silicon-based algae, non-silicon-based algae, and macrophytes) and heterotrophs (comprising aquatic invertebrates and fish). We used the Integrated Taxonomic Information System database (www.itis.gov) for the nomenclature of invertebrates and fish, the PlantList (www.theplantlist.org) for macrophytes, and the AlgaeBase (www.algaebase.org) for cyanobacteria, silicon-based algae, and non-silicon-based algae (for details on the allocation of each organism, see Table S2.1). We included records at taxonomic levels lower than species (i.e., variety and subspecies) when they were available, considering them as species-level records. Next, we standardized the different reporting methods in each study (e.g., biomass and abundance) into an occurrence/non-occurrence dataset for each species. For example, if biomass was greater than zero, then we considered the species as occurring.

We then derived the TP-concentration range at which each species occurred in streams or lakes within each water body in each region following the method described by Azevedo *et al.* (2013). Each concentration range represents the tolerance of an individual species to TP levels in a given freshwater type and region. Outside of these concentration boundaries, the species was considered absent. The range of occurrence (minimum and maximum concentration values) was calculated using one of the following procedures, in

order of preference: (1) the lognormal variation distribution of 90% of the sample (Slob, 1994), (2) the minimum – maximum reported concentration range, or (3) the mean value alone. Finally, we considered the overall range of occurrence of each species to be represented by the lowest minimum and highest maximum concentrations obtained for that species in a given freshwater type in a given region. Species whose final minimum- and maximum-concentration values were equal were excluded from the dataset because this condition does not represent a true concentration range found in the environment.

Data set

Approximately 6800 studies were found using the keyword combinations, and 186 of these studies were applicable (see list of studies in Table S1.1). Most studies did not fulfill all the requirements of this data inventory, such as identifying organisms at the species level, sampling either lake or stream freshwater systems, and providing spatially explicit, field-observation data on TP concentrations.

Many studies (142) represented North American and European freshwater systems (Fig. 2). The number of studies conducted in lakes and streams was 155 and 35, respectively (see Table S1.1). The inventory included 2294 unique species, with 1318 and 1596 species-occurrence – TP-concentration records for autotrophs and heterotrophs, respectively (see Table S2.2 for specific species ranges). We found no data for autotrophs in cold-region streams or for autotrophs and heterotrophs in xeric-region streams.

RESULTS

We were able to derive log-logistic functions for eight of the thirteen combinations of species group (autotrophs and heterotrophs), freshwater type (lakes and streams), and region for which eRSR data were available (Fig. 3). The number of available species in each combination varied considerably, from 45 autotrophic species in xeric lakes to 835 heterotrophic species in temperate streams (Table 1). Fig. S2.1 shows the scatter-plots of

218 species richness vs. TP concentration that were used to define C_{opt} and to calculate eRSR.

219 The TP concentration at which species richness is maximized, C_{opt}, was lowest in
220 cold-region lakes (0.02 to 0.03 mg P/L, Table 1). C_{opt} was generally higher in streams (0.07
221 to 0.20 mg P/L) than in lakes (0.02 to 0.10 mg P/L). We found no clear distinction between
222 the C_{opt} values of heterotrophs and autotrophs across freshwater types and regions.

223 The log-transformed TP concentration at which RSR equals 0.5, represented by α,
224 was highest in temperate streams (for both autotrophs and heterotrophs) and in xeric lakes
225 (for autotrophs) (10^{α} = 1.0 to 1.3 mg P/L, Table 1). α was lowest for heterotrophs in cold-
226 region lakes (10^{α} = 0.04 mg P/L).

227 The sensitivity of species to increasing nutrient levels is represented by the slope of
228 the log-logistic function, β (the higher the β, the steeper the function). Heterotrophic RSR
229 was systematically more sensitive to increases in P compared to autotrophic relative species
230 richness, except in temperate streams. Autotrophs in temperate and cold lakes were the least
231 sensitive to TP increases (β = -0.53 to -0.63). The optimum concentration C_{opt} was positively
232 correlated with α [Fig. S3.1(a)]. However, we found no correlation between α and the slope
233 of the log-logistic function, β. In addition, we found no significant correlation between the
234 sampling effort in each region and the results of the log-logistic regressions (C_{opt}, α, and β)
235 (appendix S4).

236 **Sensitivity analysis**

237 To analyze the robustness of our results, we compared how the choice of spatial scale
238 would affect the log-logistic regression coefficients by aggregating the dataset into realms,
239 ecoregions, and individual studies. We found that there may be high spatial variability across
240 spatial units within a region (Appendix 5). However, the variability of the coefficients
241 obtained for spatial aggregation at the level of regions was within the range of results
242 obtained for these additional levels of aggregation.

The three phytoplankton groups showed similar sensitivity to TP changes within lakes in the same region (Table S5.5). The results for cyanobacterial species were not different for similar freshwater types across regions (Tables S5.5 and S5.6). On the other hand, phytoplankton species of temperate lakes (cyanobacteria, silicon-based and non-silicon-based algae) are less sensitive to TP changes than macrophytes (Table S5.5). However, invertebrates in cold-region lakes were more sensitive to TP changes than invertebrates in temperate lakes (Table S5.7). The overall heterotrophic group also showed greater sensitivity in cold-region lakes than in temperate lakes (Table 1). In the temperate region, the level of P at which heterotrophic lake species maintained 50% of their richness was similar to that obtained for invertebrates but higher than that obtained for fish (Table S5.7).

We were not able to derive log-logistic regressions for all smaller spatial units and specific taxonomic groups. For example, although there were nine ecoregions within the temperate region, we were able to derive regressions for stream autotrophs in only four of these ecoregions (i.e., Central & Western Europe, Northeast US & Southeast Canada Atlantic Drainages, Southeastern Korean Peninsula, and Upper Mississippi, Table S5.2). Likewise, no data were available for macrophytes in (sub)tropical streams; therefore, this species group was not evaluated.

DISCUSSION

We derived the concentration-response relationships between TP and the RSR of autotrophic and heterotrophic species in two freshwater types (lakes and streams) in temperate, (sub)tropical, xeric, and cold regions. Below, we explore the main uncertainties of our study and interpret our results.

Uncertainties

First, the optimum concentration (C_{opt}) reported here corresponds to the maximal species richness found within an observed TP-concentration gradient. Thus, we assume that

the RSR – TP patterns we report are valid for TP levels above but not below C_{opt}. This concentration does not necessarily correspond to minimally disturbed, "baseline" conditions. Nonetheless, the calculated C_{opt} values are within the range of target values established by the European Union and the United States Environmental Protection Agency, which range from 0.01 to 0.15 mg P/L (European Commission, 2000; Smith *et al.*, 2003). The species used in the regression above C_{opt} may have been more represented by high-TP-tolerant algae and less by species that are typically present at low nutrient levels. In fact, many species in our inventory were present at TP conditions below C_{opt} (Table S2.3), suggesting that these species may also be adapted to survive at low TP levels.

Second, in our study, the response of organisms to stress was estimated based on phosphorus levels alone because this nutrient is considered the primary limiting nutrient in freshwater systems (Schindler, 1974; Carpenter *et al.*, 1998). We did not consider the influence of other stressors, although these can also influence freshwater species. For example, nitrogen has been reported to influence primary productivity as much as phosphorus, and co-limitation has also been reported to drive eutrophication (Elser *et al.*, 2007). Lower light availability due to increasing turbidity or growth of macrophytes may hinder the influence of P (Le Bagousse-Pinguet *et al.*, 2012). Likewise, grazing pressure, oxygen availability, chlorophyll concentration, substrate texture, stream width or area, and lake depth have been reported as factors to explain the variability in species-richness responses to P (Amarasinghe & Welcomme, 2002; Huszar *et al.*, 2006; Friberg *et al.*, 2010).

In addition to abiotic stressors, the nutrient demands of planktivores or higher-order consumers may vary widely (Hall, 2009). These differences are frequently addressed by biomanipulation experiments (Carpenter *et al.*, 2001). Although the present study did not account for each species' position in the food chain, we distinguished organisms according to their primary nutrition pathways (i.e., their ability or inability to perform photosynthesis).

293 Third, the type or number of species representing each species group (autotrophs and
294 heterotrophs) may depend on the research focus. For example, diatoms are commonly used
295 for water-quality monitoring, but the Dutch water-quality database we employed (STOWA,
296 2010) focuses on macroinvertebrates. In cold- and temperate-region lakes, the number of
297 invertebrate species was more than three times the number of fish species (Table S5.7). One
298 outcome of the high number of invertebrates is that the TP level at which 50% of the species
299 are maintained for the overall heterotrophic group was similar to that for invertebrates but not
300 to that for fish. Although taxa differ in their tolerance to high P levels (Caputo *et al.*, 2008),
301 we did not account for these differences in this study. Our results should therefore be
302 interpreted at the level of the overall autotrophic and heterotrophic species groups but not at
303 lower taxonomic levels.
304 Fourth, due to the strong research effort in Western Europe and in eastern North
305 America, we found numerous studies in the temperate region (Fig. 2). This prompted the
306 number of species employed to derive the RSR – TP functions in temperate systems to be
307 higher than elsewhere. However, neither the number of studies nor the number of species
308 used to derive our regressions influenced the results we obtained for C_{opt}, α, or β (appendix
309 4). In any case, the sensitivity analysis showed that there may be strong variability among
310 areas within a specific region. For example, while the 10^{α} and β coefficients for temperate
311 lake autotrophs were 0.30 and -0.63 mg P/L, respectively, individual studies yielded 10^{α}
312 values ranging from 0.02 to 4.07 and β values ranging from -0.53 to -0.01 (Table S5.1). The
313 choice of spatial units into which localities are aggregated to derive log-logistic regressions
314 (e.g., regions, ecoregions, or individual studies) remains under discussion. For example,
315 Azevedo *et al.* (2013) derived regressions at the biome level of spatial detail, while Struijs *et*
316 *al.* (2011b) and Amarasinghe & Welcomme (2002) defined their species-richness patterns per
317 country and per continent, respectively.

Fifth, we gathered data on TP concentration ranges at which freshwater species were present. In conditions outside this surveyed range, it is uncertain whether the species truly becomes absent because of life-threatening concentration levels. In contrast to controlled experimental studies, field-based observational studies like those surveyed here provide less certainty as to the exact boundaries between tolerable and intolerable stressor conditions (Struijs *et al.*, 2011b). Therefore, we cannot confirm factual species disappearance since the calculations of species richness are not based on verified species loss but on first-encounter species occurrence. Ultimately, there may be an underestimation of relative species richness estimations which are based on first-encounter analysis as opposed to confirmed species loss due to intolerable TP levels. This concern has been recently defined as 'dark diversity' (Pärtel *et al.*, 2011) and it is commonly under scrutiny when the stressor of interest is the potential loss of species caused by damage to the species living space as such (He & Hubbell, 2011). In observational studies such as ours, the issue caused by unconfirmed species loss may be alleviated by thorough monitoring of species occurrence and by coverage of a wide TP-concentration gradient, up to highly eutrophic levels.

Finally, to compare the potential impact of phosphorus across regions with evident differences in species richness (e.g., cold vs. (sub)tropical freshwater systems), we employed a relative measure of relative species richness. Despite our effort to gather data from the literature, we were not able to successfully estimate the RSR in regions for which very few or no data were found, such as xeric-region streams and (sub)tropical lakes.

This species-occurrence/non-occurrence approach simplifies an effect type previously described in a continuous manner (e.g., biomass or abundance) into a simpler binary dataset (presence and absence). This standardization has the advantage of combining the different ways in which effects have been reported by different studies. While abundance is more commonly reported for species that are visible to the naked eye, other organisms are more

frequently reported as present or absent in a given freshwater body.

Interpretation

Optimum TP

Our results show that the optimum TP concentrations are generally higher in streams than in lakes. This finding can be attributed to distinct biotic nutrient demands in the two freshwater types. First, because lakes require lower P levels than streams to reach the same net primary-productivity rate (Smith *et al.*, 1999), the optimum TP can be reached at lower concentrations in lakes than in streams. This pattern was observed across all autotrophic groups (cyanobacteria, silicon-based and non-silicon-based algae, and macrophytes) in the temperate region. Second, while nutrient surpluses in lakes are quickly reduced by widespread, fast-growing algae (Carpenter *et al.*, 1998; Doi, 2009), nutrient recycling in streams, especially those of lower size orders or with strong tree shading, depends primarily on the speed at which heterotrophs assimilate organic matter (Vannote *et al.*, 1980; Merritt *et al.*, 1984).

Another reason for the higher optimum TP levels in streams compared to lakes is the differences in hydrological patterns that influence nutrient removal from the water column. Once nutrients are deposited in the sediment layer via the sinking of soil, animal fecal pellets or algae, they can be either transported back into the water column or immobilized in the sediment for long periods (Holtan *et al.*, 1988). In streams, strong water currents enhance sediment uplift, favoring the maintenance of high TP levels in the water column (Bahnwart *et al.*, 1998). In addition, the short residence times of water in streams, especially lower-order streams, may decrease phytoplankton exposure to nutrients hence hinder autotrophic growth (Vannote *et al.*, 1980). Conversely, lakes, especially cold ones (Carpenter *et al.*, 1999), may be subjected to thermal stratification for many months, confining nutrients to the surface layer, where net primary productivity and nutrient recycling prevails, and hindering the

368 vertical uplift of nutrient-rich sediments (Tylmann *et al.*, 2012).

369 Phosphorus loads are lower overall in the cold region than in the temperate and
370 (sub)tropical regions due to lesser anthropogenic nutrient release in cold regions, e.g.,
371 agricultural runoff (Harrison *et al.*, 2010). Smaller decomposition rates in colder regions may
372 also decrease nutrient release into water bodies. It is therefore likely that most species in cold
373 regions are adapted to low nutrient concentrations. Because we were not able to derive
374 regressions for both species groups in warmer regions [(sub)tropical and xeric], it is unclear
375 how the climatic gradient represented by the four regions may influence C_{opt} across the two
376 species groups.

377 *Regression coefficients*

378 Geological and evolutionary processes in freshwater systems will determine how
379 tolerant the biotic community is to a given stressor. As a result, species in nutrient-rich
380 environments will be more adapted to high nutrient levels than those unused to such
381 conditions (Köhler, 1994; Bontje *et al.*, 2011). In this study, we found that the freshwater
382 systems that could maintain half of the relative species richness at higher TP levels were also
383 those with high optimum TP levels, C_{opt}. Nonetheless, this trend does not imply that
384 organisms with high tolerance to elevated phosphorus levels are also less sensitive to
385 changing levels of this nutrient.

386 Heterotrophs have higher P demands than autotrophs because autotrophs have higher
387 N:P and C:P ratios (Elser *et al.*, 2000). Hence, heterotrophs are expected to be more affected
388 by P surpluses than autotrophs (and more sensitive to changing P levels). In our study,
389 however, this hypothesis was confirmed in temperate and cold-region lakes but not in
390 temperate streams (Table 1). Here, we propose three explanations for the lower sensitivity of
391 autotrophs in lakes compared to streams based on the difference in light availability and
392 photosynthetic rates between the two freshwater types. This analysis is verified once

phytoplankton species (cyanobacteria, silicon-based and non-silicon-based algae) are separated from macrophytes in the autotrophic group in temperate lakes. First, the increased production of N-rich protein and RNA by small organisms with high growth rates suggests that the biological demand for N may surpass that for P (Elser *et al.*, 1996). The lesser effect of P on autotrophs in lakes compared to streams may be due to more intense autochthonous phytoplankton activity in lakes than in streams (Doi, 2009). Second, the lower sensitivity of autotrophic richness to P changes can be attributed to the insensitivity of cyanobacteria to low-oxygen and high-P conditions (Downing *et al.*, 2001). Many cyanobacteria, including toxic groups (e.g., *Aphanizomenon*), compensate for their light demand in light-abundant lacustrine systems and for their N demand via N fixation; ultimately, P supplementation allows them to overcome their primary growth limitations (Camargo & Alonso, 2006). Third, macrophytes help to maintain algal diversity under increasingly eutrophic conditions by impeding the fast-growing, light-favored phytoplankton that prevail in eutrophic lakes (Le Bagousse-Pinguet *et al.*, 2012). Given that the proportion of macrophytes within the autotrophic group was considerably higher in temperate lakes than in streams, the buffering effects of increasing P may be more intense in lakes compared to streams in the temperate region.

The sensitivity of organisms could be compared across lakes and streams only in the temperate region. We found that heterotrophic species were less sensitive to TP changes in streams than in lakes. This difference may be due to the high dispersal ability of heterotrophs in lakes, generating stronger similarity between species assemblages and thus lower β-diversity in lakes compared to streams (Hof *et al.*, 2008). If lakes contain more similar species assemblages, which are expected to react in a more similar way following stress exposure, then relative species richness will change more rapidly in lakes than in streams because streams encompass more dissimilar species.

418 The comparison across regions was hindered by the scarcity of data for (sub)tropical
419 lakes and xeric streams. In addition, the influence of P on primary productivity is less
420 apparent in (sub)tropical lakes than in temperate lakes (Huszar *et al.*, 2006), which may
421 explain why we were not able to derive a log-logistic regression for this ecosystem. Huznar *et*
422 *al.* (2006) and Abell *et al.* (2012) have suggested that nitrogen may drive primary production
423 more than P does in (sub)tropical lakes because higher temperatures enhance nitrogen losses,
424 particularly through denitrification, and P transport to water bodies due to weathering (Abell
425 *et al.*, 2012).

426 **Relevance of research and application of results**

427 Global-scale assessments are available for the influence of P on net primary
428 productivity in freshwater systems (Elser *et al.*, 2007). However, changes in species richness
429 due to increasing P concentrations have previously been assessed in studies focusing on a
430 specific freshwater type or covering a smaller area, e.g., Struijs *et al.* (2011b) and Friberg *et*
431 *al.* (2010). The results of the present study show that the patterns of relative species richness
432 along a TP-concentration gradient can be described using logistic regressions.

433 We identified patterns in the RSR along a TP-concentration gradient for two species
434 groups (autotrophs and heterotrophs), in two freshwater types (lakes and streams), and in four
435 regions [(sub)tropical, xeric, temperate, and cold]. We found that lakes generally, but not
436 always, have lower optimal TP levels and that their species assemblages are less sensitive to
437 TP changes than those in streams. Furthermore, autotrophs and heterotrophs in cold regions
438 have lower optimal concentrations compared to those in other regions. The regressions can be
439 used to describe the potential decrease in relative species richness in a quantitative manner,
440 although it is important to note that factual causal relationships between species losses and P
441 increases are not tackled in this study. In combination with biogeochemical models of the fate
442 of nutrients, this procedure can assist in estimating the ultimate effects of stressors on species

richness maintenance (van Zelm *et al.*, 2007; Struijs *et al.*, 2011a; Verbrugge *et al.*, 2012).

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SUPPORTING MATERIAL

Appendix S1 Keyword combination and list of peer-reviewed articles

Appendix S2 Taxonomic classification, number of species, and list of species

Appendix S3 Pearson correlation results

Appendix S4 Bias test

Appendix S5 Internal validation

BIOSKETCH

The research team is involved in ecological risk assessment of environmental stressors with the use of mathematical models (http://www.ru.nl/environmentalscience). Author contributions: L.B.A., R.V.Z., R.S.W.E.L, A.J.H., and M.A.J.H. conceived the ideas and analyzed the data. L.B.A., P.E., J.S. and D.D.Z. collected and managed the data. All authors contributed to the writing of the manuscript.

Table 1 Number of studies, surveyed TP range (mg P/L), number of species (SR_{max}), optimum TP level in region (C_{opt}) and range of C_{opt} estimates across ecoregions (in parenthesis), relative species richness (RSR) coefficients α and β and 95% confidence intervals (in parenthesis), Pseudo-R^2 and p value of log-logistic regressions for two organism groups, in two freshwater types, and four world's regions.

Freshwater type	Species Group	Region	Number of studies	Surveyed TP range	Number of species	SR_{max}	C_{opt} in region (C_{opt} across ecoregions)	α	β	Pseudo-R^{2***} / p value
Lake	Autotroph	Cold	10	0.002 to 3.155	163	122	0.03 (0.005 to 0.03)	-0.64 (-0.76 to -0.52)	-0.53 (-0.67 to -0.40)	0.88 / < 0.001
		Temperate	74	0.001 to 41.970	614	459	0.05 (0.002 to 0.32)	-0.52 (-0.66 to -0.38)	-0.63 (-0.78 to -0.48)	0.88 / < 0.001
		Xeric	2	0.009 to 1.180	45	45	0.03 (0.03 to 0.03)	0.03 (-0.07 to 0.14)	-0.39 (-0.50 to -0.28)	0.91 / < 0.001
		(Sub)tropical*	7	0.003 to 35.000	95	42	15.85 (0.001 to 15.85)	1.58 (0.98 to 2.18)	-0.19 (-0.78 to 0.39)	0.72 / 0.0134
	Heterotroph	Cold	14	0.002 to 3.155	54	49	0.02 (0.003 to 0.02)	-1.37 (-1.43 to -1.31)	-0.12 (-0.18 to -0.07)	0.92 / < 0.001
		Temperate	61	0.001 to	682	488	0.10	-0.19	-0.24	0.98 /

				4.070			(0.003 to 3.2)	(-0.23 to -0.15)	(-0.281 to -0.21)	< 0.001
		Xeric	1	0.385 to 4.124	4	4	0.63*	No successful fit with the log-logistic regression		
		(Sub)tropical*	4	0.001 to 0.220	9	7	0.04 (0.005 to 0.04)	-0.82 (-0.86 to -0.78)	-0.03 (-0.07 to 0.01)	0.92 / 0.001
Stream	Autotroph	Temperate	11	0.001 to 2.625	182	146	0.20 (0.001 to 0.50)	0.01 (-0.02 to 0.04)	-0.17 (-0.20 to -0.15)	0.99 / < 0.001
		(Sub)tropical	6	0.001 to 5.088	203	199	0.07 (0.001 to 0.08)	-0.56 (-0.64 to -0.48)	-0.41 (-0.50 to -0.33)	0.94 / < 0.001
	Heterotroph	Cold	1	0.010 to 0.044	2	2	0.02*	No successful fit with the log-logistic regression		
		Temperate	16	0.007 to 17.000	835	697	0.10 (0.01 to 0.40)	0.11 (0.06 to 0.15)	-0.32 (-0.36 to -0.29)	0.99 / < 0.001
		(Sub)tropical*	3	0.052 to 1.225	9	8	0.40 (0.1 to 0.40)	0.13 (-0.02 to 0.29)	-0.15 (-0.29 to -0.01)	0.85 / 0.001

* Regression was not successfully derived since either β coefficient is not significantly different from zero at a 95% confidence level or 10^{α} coefficient was outside the TP concentration range of relative species richness (defined by C_{opt} to upper boundary of surveyed TP concentration)

** Minimum and maximum range of C_{opt} based on one ecoregion only

*** ————————, as defined by Schabenberger & Pierce (2001)

FIGURE LEGENDS

Fig. 1 Description of the steps taken for acquisition of data and derivation of response curves.

Fig. 2 World map (projection: Aitoff) with the location of the freshwater bodies used in this study allocated to four regions. The studies within "Other" areas (11), which represent large freshwater bodies and oceanic islands, were allocated to their closest region. Squares (155) and triangles (35) represent lakes and streams, respectively.

Fig. 3 Empirical (eRSR, circles) and the calculated (cRSR, lines) relative species richness of autotrophs along a total phosphorus (TP) gradient in lakes **(a)** and in streams **(b)** and of heterotrophs in lakes **(c)** and in streams **(d)**. Log-logistic coefficients used in the cRSR functions are shown in Table 1. Green, orange, rose, and blue represent the (sub)tropical, xeric, temperate, and cold regions, respectively (same color code as in Fig. 2).

FIGURES

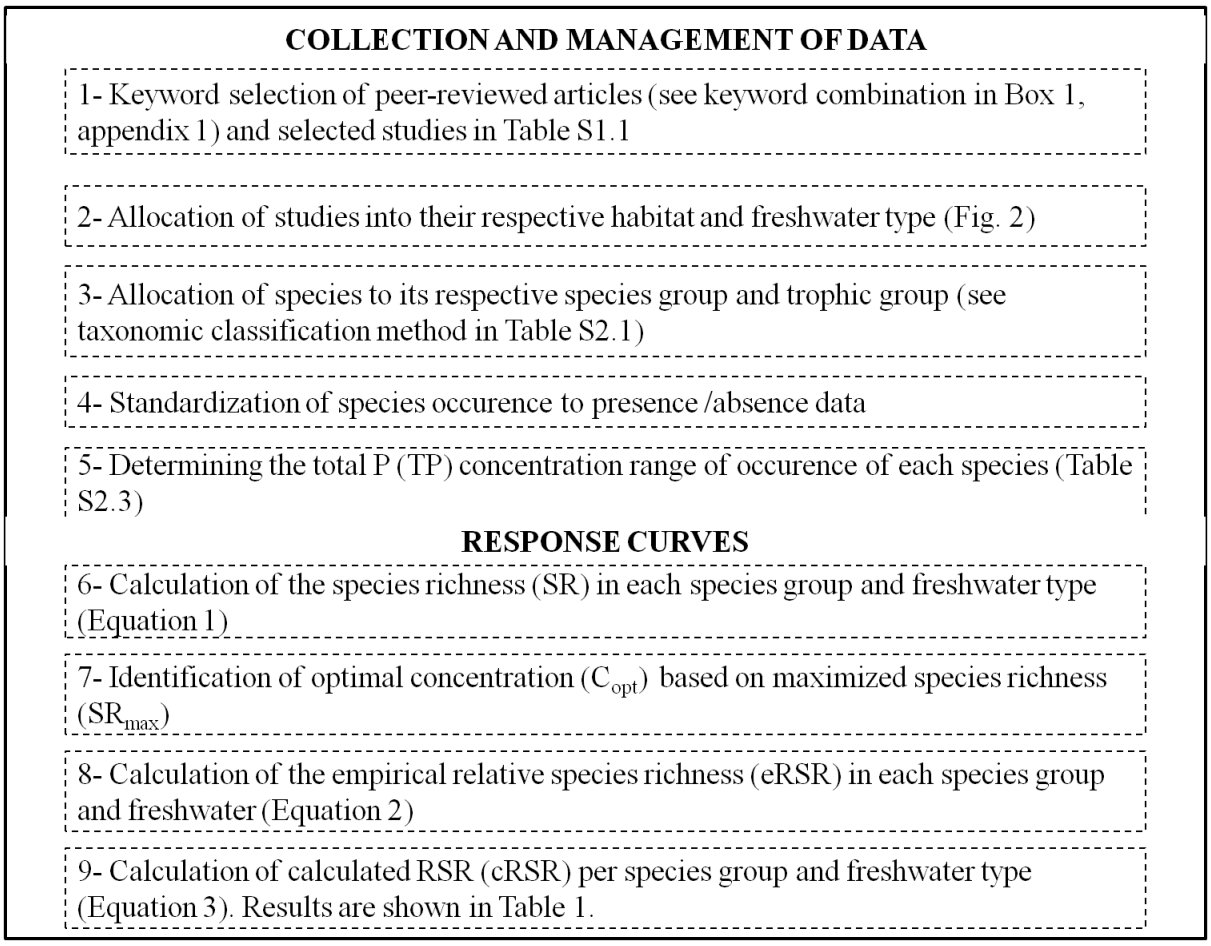

Figure 1

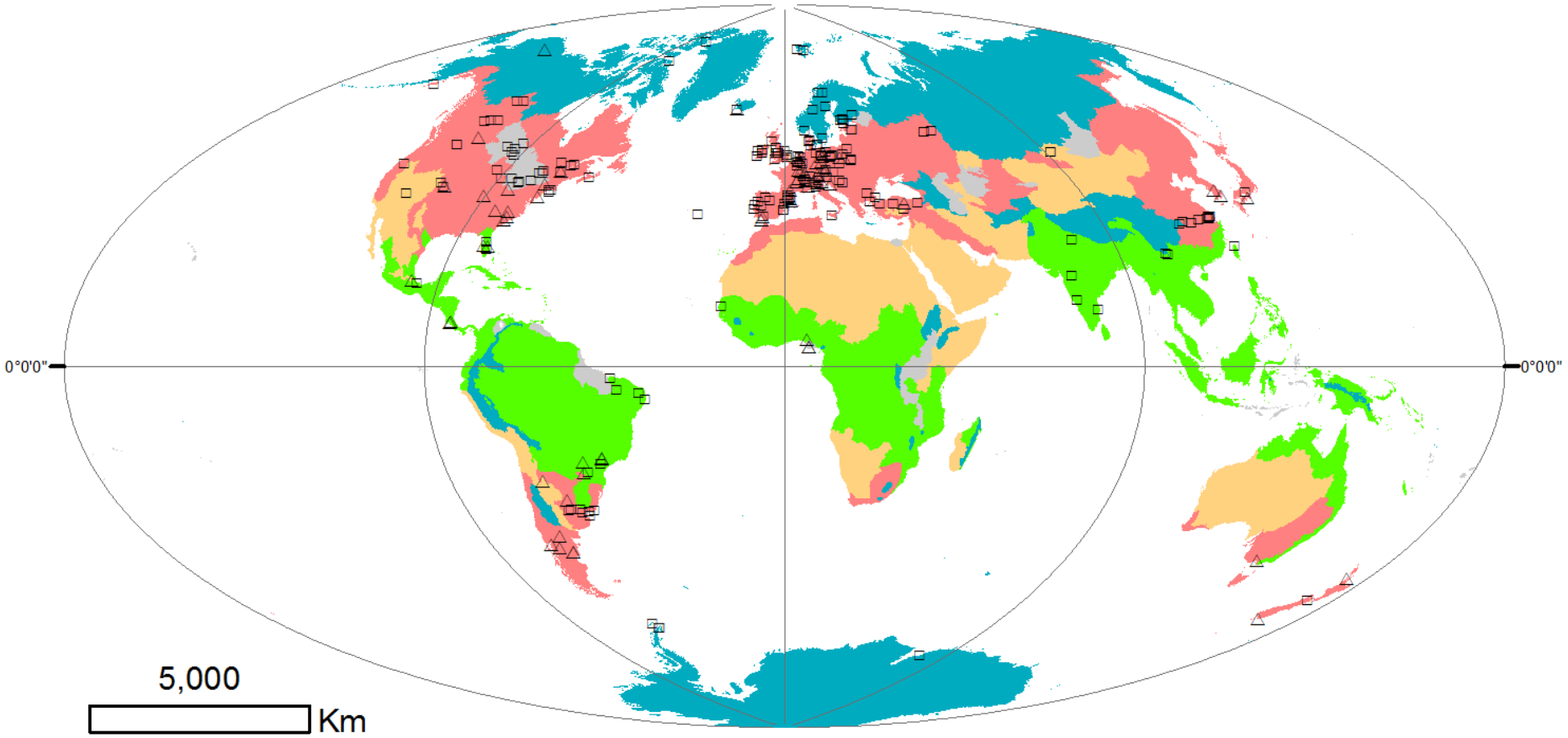

Figure 2

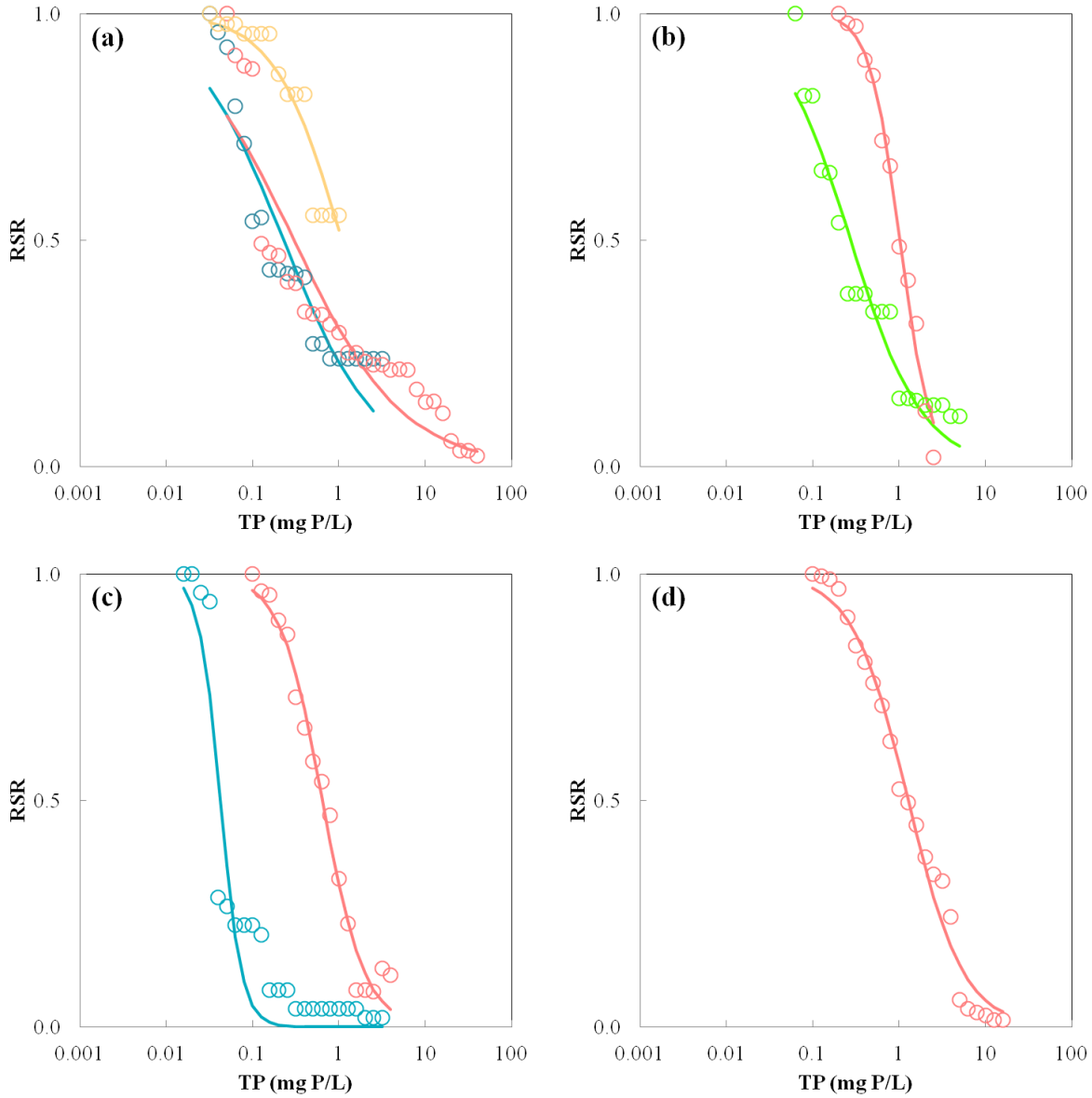

Figure 3