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How nutrient retention and TN:TP ratios depend on ecosystem state in thousands of Chinese lakes

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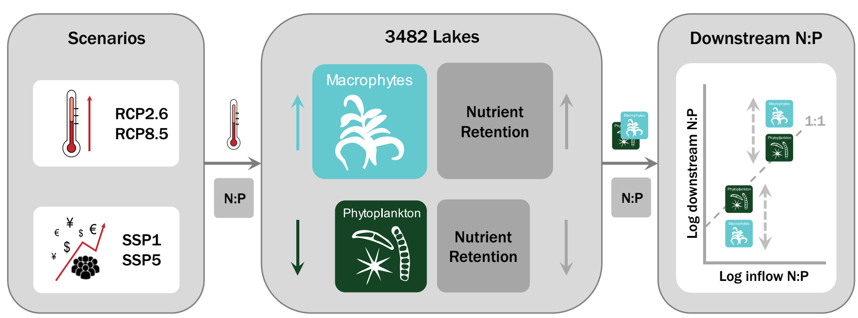
HIGHLIGHTS

- Anthropogenic activities aggravate eutrophication in hydrologically connected systems.
- We show how nutrient retention affects downstream nutrient loading.
- Nutrient retention fractions are higher in macrophyte-dominated lakes.
- Outflow TN:TP ratios depend on lake ecosystem state and inflow TN:TP ratios.
- Nutrient pollution reduction may stimulate reinforcing feedbacks on water quality.

GRAPHICAL ABSTRACT



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ABSTRACT

Worldwide, anthropogenic activities threaten surface water quality by aggravating eutrophication and increasing total nitrogen to total phosphorus (TN:TP) ratios. In hydrologically connected systems, water quality management may benefit from in-ecosystem nutrient retention by preventing nutrient transport to downstream systems. However, nutrient retention may also alter TN:TP ratios with unforeseen consequences for downstream water quality. Here, we aim to increase understanding of how nutrient retention may influence nutrient transport to downstream systems to improve long-term water quality management. We analyzed lake ecosystem state, in-lake nutrient retention, and nutrient transport (ratios) for 3482 Chinese lakes using the lake process-based ecosystem model PCLake+. We compared a low climate change and sustainability-, and a high climate change and economy-focused scenario for 2050 against 2012. In both scenarios, the effect of nutrient input reduction outweighs that of temperature rise, resulting in more lakes with good ecological water quality (i.e., macrophyte-dominated) than in 2012. Generally, the sustainability-focused scenario shows a more promising future for water quality than the economy-focused scenario. Nevertheless, most lakes remain phytoplankton-dominated. The shift to more macrophyte-dominated lakes in 2050 is accompanied by higher nutrient retention fractions and less nutrient transport to downstream waterbodies. In-lake nutrient retention also alters the water's TN:TP ratio, depending on the inflow TN:TP ratio and the ecosystem state. In 2050 higher TN:TP ratios are expected in

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the outflows of lakes than in 2012, especially for the sustainability-focused scenario with strong TP loading reduction. However, the downstream impact of increased TN:TP ratios depends on actual nutrient loadings and the limiting nutrient in the receiving system. We conclude that nutrient input reductions, improved water quality, higher in-lake nutrient retention fractions, and lower nutrient transport to downstream waterbodies go hand in hand. Therefore, water quality management could benefit even more from nutrient pollution reduction than one would expect at first sight.

1. Introduction

Globally, nutrient inputs and retention have increased over the 20th century, as well as nutrient transport to the oceans (Bouwman et al., 2005; Beusen et al., 2016). Nutrient pollution threatens water quality and is expected to continue to increase by anthropogenic changes such as human population growth, urbanization, agricultural intensification, and climate change (Bouwman et al., 2005; Seitzinger et al., 2010; Wang et al., 2020). Excess nutrients promote turbid, phytoplankton-dominated waters which may be toxic (Codd et al., 2005) and provide fewer ecosystem services compared to lakes with clear water (Janssen et al., 2020). Furthermore, climate change aggravates eutrophication effects (Moss et al., 2011) through rising temperatures that favor the growth of cyanobacteria over other primary producers such as other phytoplankton species (Paerl and Huisman, 2008, 2009) and submerged macrophytes (Mooij et al., 2007). Thus, with ongoing socio-economic developments and climate change, the risks of eutrophication are expected to rise. Nevertheless, water quality managers may be able to benefit from (natural) nutrient retention processes to partly prevent nutrient transport to downstream systems (van Gerven et al., 2017; Teurlincx et al., 2019) and lessen downstream eutrophication (van Wijk et al., 2021).

Limnological research increasingly considers multiple waterbodies within landscapes, including nutrient retention as an important and vulnerable regulating ecosystem service (Kling et al., 2000; Heino et al., 2021). Catchment-scale studies tend to primarily focus on nutrient retention on land and transport by rivers (e.g., Bouwman et al. (2005)). However, especially lentic systems — such as lakes — play an important role in nutrient retention in watersheds (Finlay et al., 2013; Maavara et al., 2015; Cheng and Basu, 2017; Liu et al., 2018; Schmadel et al., 2018). Recently, the importance of the feedback between nutrient loading, ecosystem state, and nutrient retention was highlighted in the context of such connected waterbodies (van Wijk et al., 2021). This is especially relevant for shallow lakes which may experience different ecosystem states (e.g. phytoplankton or macrophyte dominance) (Scheffer et al., 1993; Smith and Schindler, 2009). Since nutrient retention fractions are generally higher in clear, macrophyte-dominated than turbid, phytoplankton-dominated waters, the ecosystem state does not only depend on nutrient inputs into the waterbody but also influences nutrient transport to downstream systems (van Wijk et al., 2021). Yet, research on this spatial feedback theory is limited.

Furthermore, total nitrogen to total phosphorus (TN:TP) ratios have generally increased by changes in relative nutrient inputs and retention in waterbodies which may affect water quality (Jeppesen et al., 2005; Finlay et al., 2013; Glibert et al., 2018; Tong et al., 2020; Wu et al., 2022). As appeared in the 1970–80's, ecological water quality (i.e., ecosystem state) strongly depends on phosphorus levels (Nicholls and Dillon, 1978; Vollenweider and Kerekes, 1982; Ahlgren et al., 1988). More recently, the co-limitation effects of P and N (Paerl et al., 2016) and the importance of TN:TP ratios (Guildford and Hecky, 2000) have been put to the fore. More effective reduction of the point than diffuse nutrient sources, and (consequently) more effective P than N reduction, has led to increases in TN:TP ratios, for example, in the Ruhr River catchment (Westphal et al., 2020). Additionally, the higher removal efficiency of P than N in improved municipal wastewater treatment and imbalanced nutrient retention in lakes contributes to higher TN:TP ratios (Tong et al., 2020; Wu et al., 2022). On the other hand, Downing and McCauley (1992) found that oligotrophic lakes have higher TN:TP ratios because of the high TN:TP ratios of natural nutrient sources such as infertile terrestrial ecosystems. High TN:TP ratios relate to less toxic phytoplankton blooms in several hydrological systems (Chen et al., 2013; Harris et al., 2016). Nevertheless, others point to higher risks of algal blooms in coastal zones (Wu et al., 2022), and higher chlorophyll-*a* concentrations (Smith, 1982) and toxin contents in phytoplankton (van de Waal et al., 2014) with increased TN:TP ratios. Additionally, higher TN:TP ratios are associated with decreased drinking water quality and reduced lake food-web biodiversity (Wu et al., 2022). Yet, only a few studies assessed the relative retention of N and P in waterbodies and its implication for TN:TP ratios of loading to downstream systems (Grantz et al., 2014; Liu et al., 2018).

Here we use the lake ecosystem model PCLake+ (Janssen et al., 2019) to explore how water quality, in-lake nutrient retention, and nutrient transport to downstream systems may develop in the future. We aim to increase understanding of how nutrient retention may influence nutrient transport to downstream systems to improve long-term water quality management strategies. Our study considers TN and TP loading, and their ratios, since all are important for ecological water quality (i.e., biotic and abiotic aspects that determine ecosystem state). We explore two scenarios of socio-economic development and climate change for 2050 and compare them to the situation in 2012. For the economy-focused scenario, with modest nutrient loading reduction and strong climate change, we hypothesize that lake ecosystem states will deteriorate. For the sustainability-focused scenario, with strong nutrient loading reduction and less severe climate change, we hypothesize that lake ecosystems states will on average slightly improve.

We focus on Chinese lakes because Asia is one of the global hotspots of N and P inputs to rivers and coastal systems (Seitzinger et al., 2005; Li et al., 2022). For example, in the East China Sea downstream of the Yangtze River, the frequency and area of harmful algal blooms have increased together with TN:TP ratios between 1950 and 2007 (Li et al., 2014). Furthermore, despite water quality improvements in Chinese rivers, water quality, and ecological condition in most Yangtze River lakes decreased between 2008 and 2018 in the study by Qin et al. (2022). Other studies have focused on nutrient inputs to Chinese rivers and coastal eutrophication (Strokal et al., 2016; Wang et al., 2020). Alternatively, here we focus on the water quality of lakes and their influence on nutrient transport to downstream systems through nutrient retention. Our scenario analysis for 3482 Chinese lakes illustrates how model analyses may help to enhance sustainable management efforts to minimize adverse nutrient impacts and to protect surface water quality for future generations.

2. Methods

We used PCLake+ (Janssen et al., 2019) to calculate the baseline lake water quality (definition in Supplementary material A), nutrient retention, and TN:TP ratios of water outflows for 2012, as well as for two scenarios. PCLake+ is a lake ecosystem model to simulate water quality based on ecological interactions and covers a wide range of freshwater lakes differing in stratification regime and climate-related processes (Janssen et al., 2019). The model includes in-lake biogeochemical processes that mechanistically affect the net nutrient retention, such as sedimentation, resuspension, burial, consumption, mineralization and sorption (Janssen et al., 2019). We extended PCLake+ with equations for the net hydrological transport of nutrients out of the lake and net in-lake nutrient retention (Section 2.3). The extended model was applied to 3482 unique lakes in the five largest river basins in China with varying depths (0.7–205 m), surface area (0.1–255 km^2), and climate zones (temperate to tropical) (Table 1). To prevent model runtime errors, this selection excludes cases with unrealistic water balances (i.e., water flows ≤0), permanent ice cover, or without nutrient loading. Groundwater flows (i.e., seepage and infiltration) were assumed to be negligible and each selected lake has a water in- and outlet, which eases the net nutrient retention calculation. Moreover, we checked that each lake had N and P retention fractions between 0 and 1, to assume they had reached equilibrium with their inflowing nutrient loading. Model input for each lake consisted of average lake depth, fetch, and latitude from a dataset earlier published and used with PCLake+ (Janssen et al., 2021). Furthermore, the sediment characteristics of each lake were derived using the approach of Janssen et al. (2021), and surface water inflows were derived from the HydroLAKES (Messager et al., 2016) and ISIMIP (Inter-Sectoral Impact Model Intercomparison Project) databases (Golub et al., 2022) (Fig. B.1 in Supplementary material B). This data was supplemented with data on climate and nutrient loading (Supplementary material C) from the climate change and socio-economic development scenarios, respectively (Sections 2.1 and 2.2).

For each lake, we ran PCLake+ for a range of TP loadings for 2012 and the climate scenarios to derive nutrient response curves. The nutrient response curves present the potential annual average parameter values for the specific lake and climate scenario, depending on the nutrient loading, and — in the case of alternative stable states (as explained in Supplementary material A) — the initial ecosystem state. To this end, each lake was forced from an initial clear to a more turbid state and back by, respectively, increasing (eutrophication) and decreasing (oligotrophication) the TP loading. We estimated a minimum and maximum ecologically relevant TP loading per lake from a typical range of chlorophyll-*a* concentrations (1.6 to 160 μg chl-*a* l^{-1}) using the lake eutrophication model GPLake-S (Chang et al., 2022). To ensure that the nutrient loadings of the socio-economic development scenarios were also captured, we widened the range of the found TP loadings to the extent that the actual 2012 and 2050 loadings fall within the simulation range. For 2012 and the 2050 scenarios, each lake run was initiated with a 30-year spin up from the default initial clear state. Next, the core runs were started with the lake-specific minimum TP loading, slowly increasing the load in 300-year-steps towards the maximum TP loading (eutrophication). Consecutively, the run was continued for another 300 year-steps in reverse order; from the maximum to the minimum TP loading (oligotrophication). The long run was deliberately chosen to minimize the effect of the response time of lakes to the changes in loadings on the calculated annual average (i.e., approximately equilibrium) water quality, nutrient retention, and nutrient outflow parameters (cf., legacy effect (Cuddington, 2011)). From the resulting nutrient response curves, scenario-specific output parameter values were derived for initial clear and turbid states, being the intercept of the parameter value at the nutrient loading of the corresponding socio-economic development scenario (using the approx interpolation function in R). Furthermore, TN:TP mass ratios were calculated.

We analyzed future trends for two scenarios for the year 2050: the sustainability-focused and economy-focused scenario. The sustainability-focused scenario uses Representative Concentration Pathway (RCP) 2.6 as climate change scenario (van Vuuren et al., 2011) in combination with shared socio-economic pathway (SSP) 1 for China developed by Wang et al. (2017, 2020). The economy-focused scenario is based on RCP8.5 and SSP5. By this, the sustainability-focused scenario projects some temperature rise and a strong decrease in nutrient loadings whereas economy-focused scenario has a larger temperature rise and more modest decrease in nutrient loadings (see Sections 2.1 and 2.2 for more details). In our analysis we distinguish initial and equilibrium ecosystems states. Initial ecosystem state (clear or turbid) is an input parameter of PCLake+, whereas the equilibrium ecosystem state (macrophyte or phytoplankton dominance) is an output (see Supplementary material A for more details).

Table 1
Median, first and third quartile (Q1 and Q3) of key lake characteristics of the 3482 lakes included in this study. A detailed table with lake characteristics per lake can be found in the supplemented data repository.

Variable	Q1	Median	Q3
Average water depth (m)	2.1	3.0	5.1
Lake surface area (km^2)	0.18	0.31	0.68
Hydraulic residence time (d)	65	119	236
Catchment surface area (km^2)	2.4	6.3	22.3

2.1. Climate change scenarios

We applied the RCP2.6 and RCP8.5 as climate change scenarios for the sustainability-focused and economy-focused scenarios, respectively. RCP2.6 (i.e., 2.6 W m^{-2} radiative forcing in 2100) is the lowest of the intermediate radiative forcing scenarios, including the use of bio-energy and carbon capture and storage, and requiring rigorous climate policies to limit emissions (van Vuuren et al., 2011). In contrast, RCP8.5 (i.e., 8.5 W m^{-2} radiative forcing in 2100) is a highly energy-intensive scenario with high population growth, a lower rate of technology development, and no climate policy (van Vuuren et al., 2011). The radiative forcing per 2050 RCP scenario was interpreted according to the ISIMIP2b approach (Golub et al., 2022) to produce input parameters for the hydrological model VIC-LAKE (Hostetler and Bartlein, 1990; Hostetler, 1991; Bowling and Lettenmaier, 2010). Typical climate years were defined from these VIC-LAKE simulations by taking the daily average over a 30-year period prior to the simulated year. For 2012, we used existing validated data (R^2_{adj} between 0.84 and 0.87) from VIC-LAKE simulations (Janssen et al., 2021). The resulting dataset of 365 values for each, the 2012 baseline, the sustainability- and economy-focused scenario, were used as climate input for PCLake+ (Table C.1 in Supplementary material C). The distribution patterns of the resulting lake epilimnion temperature kernel density curves are similar, but the lakes in the sustainability- and economy-focused scenario are on average 0.63 and 0.78 °C warmer than in 2012, respectively (Fig. 1, top left panel). The hydrological input parameters were kept constant in 2012 and the 2050 scenarios (Supplementary material B and C.1).

2.2. Socio-economic development

Our 2050 scenarios for socio-economic development follow the SSP storylines and associated gridded data of N and P losses to rivers from agriculture and sewage for China developed by Wang et al. (2017, 2020). We used SSP1 and SPP5 for the sustainability-focused and economy-focused 2050 scenario, respectively. We converted the N and P losses in 2012 and 2050 of these two scenarios to nutrient loadings to lakes based on the in-river retention equation from Behrendt and Opitz (2000) (Eq. B.1–6 and Fig. B.2 in Supplementary material B). The resulting dataset was used as input for PCLake+ in the form of TN and TP loadings and their ratio for 2012, the sustainability- and the economy-focused scenario. In SPP1, a dramatic (but gradual) shift towards sustainability is assumed with a strongly improved connection to and treatment of sewage, an increased low-meat diet preference, and a strong increase in nutrient recycling (e.g., manure recycling) in the food production system and agricultural productivity whilst minimizing overfertilization. As a result, nutrient loadings per lake generally decrease (on average 86 % and 53 % reduction for TP and TN, respectively) and TN:TP ratios increase compared to 2012 (Fig. 1). In SSP5, steps towards sustainability are taken in a more conventional way assuming a priority for economic development and urbanization with a moderate improvement in connection to and treatment of sewage, an increased food demand, particularly for meat products, and a moderate

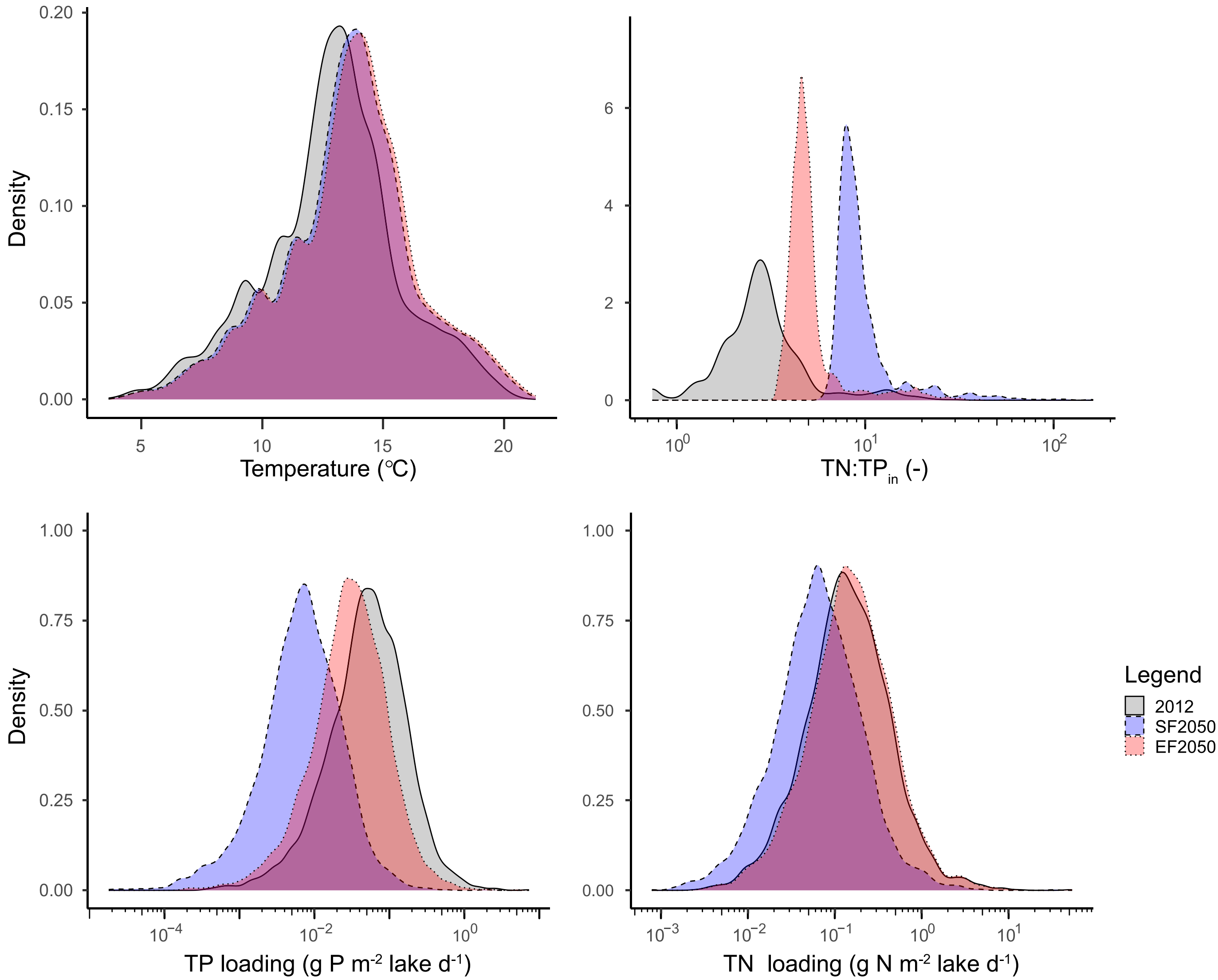

Fig. 1. Kernel density plots of scenario epilimnion temperature (°C; top left), TN:TP ratio of the inflow (unitless; top right), and TP and TN loading from the socio-economic development scenarios input (g nutrient m^{-2} lake d^{-1}; bottom panels). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050). The TN:TP plot has 1.5 times the standard band width.

increase in nutrient recycling in the food production system. In this scenario, TP loading slightly decreases whilst TN loading hardly changes compared to 2012, resulting in increased TN:TP ratios (Fig. 1). The increase in TN:TP ratio relative to 2012 is on average three times larger for the sustainability- than the economy-focused scenario.

2.3. New equations in PCLake+

PCLake+ (Janssen et al., 2019) was extended with equations for the hydrological transport of nutrients out of the lake and net in-lake nutrient retention. Nutrient outflow ($L_{out,i}$ for nutrient i; g nutrient m^{-2} lake d^{-1}; Eq. (1)) is the transport of unretained (organic and inorganic) nutrients out of a lake along with the water discharge from the lake. This is the sum of the epilimnetic and hypolimnetic outflow nutrient concentrations ($[i]_{out,j}$ for nutrient i and water layer j; g nutrient m^{-3} d^{-1}), each multiplied by the depth of the respective water layer (z_j for water layer j; m; Eq. (1)):

$$L_{out,i} = [i]_{out,epi} \times z_{epi} + [i]_{out,hyp} \times z_{hyp} \tag{1}$$

Though, in practice this may be assumed to be dominated by epilimnetic outflow. In PCLake+, the nutrient loading into a lake is defined independent from the water inflow and represents the total external nutrient input into the lake ($L_{lake,i}$ for nutrient i; g nutrient m^{-2} lake d^{-1}; Eq. B.6 in Supplementary material B) from, for example, atmospheric deposition directly into the lake, and diffuse and point sources accumulating in the water inflow.

The difference between the nutrient outflow and the external nutrient input is the net nutrient retention, resulting from the combined effect of in-lake biogeochemical processes that contribute to or counter nutrient retention. This absolute amount of nutrients is retained in the system (aR_i for nutrient i; g nutrient m^{-2} lake d^{-1}; Eq. (2)), for example, by burial (i.e., permanently stored in the sediment) or denitrification (i.e., loss to the atmosphere).

$$aR_i = L_{lake,i} - L_{out,i} \tag{2}$$

The nutrient retention fraction (R_i for nutrient i; unitless; Eq. (3)) is derived by correcting for the external nutrient input as:

$$R_i = \frac{aR_i}{L_{lake,i}} \tag{3}$$

Nutrient retention fractions of zero means that in total the nutrient outflow equals the external nutrient input, and a fraction of one means that the absolute nutrient retention equals the external nutrient input.

3. Results

3.1. In-lake water quality and nutrient retention results

Our results for the 3482 lakes show a change in the distribution of macrophyte and phytoplankton levels between 2012 and 2050, depending on the initial state of the lakes (Fig. 2). We see a shift towards more lakes with high (> 10 g DW m^{-2}) macrophyte and low (< 5 mg chl-a m^{-3}) phytoplankton levels, especially in the sustainability-focused scenario. In all simulations, the macrophyte levels are bimodally distributed (i.e., either notably higher or lower than 10 g DW m^{-2}), with more lakes having low macrophyte levels when they are initially turbid (Fig. 2, left panels). These bimodal patterns are an indication of alternative stable states. When using the macrophyte to phytoplankton ratio of 1.75 g DW m^{-2} per mg chl-*a* m^{-3} as a threshold for the equilibrium ecosystem state (Supplementary material A), we find that only 18 % of the lakes are macrophyte-dominated in the 2012 run (Table A.1. in Supplementary material A). This percentage increases somewhat towards 2050 in the economy-focused scenario (24 %) and strongly in the sustainability-focused scenario (45 %) (Table A.1. in Supplementary material A). Despite the increase in the number of macrophyte-dominated lakes in the 2050 scenarios, most lakes are found to be phytoplankton-dominated.

As for the equilibrium ecosystem state, in-lake nutrient retention values show a bimodal pattern (Fig. 3, top panels). Nutrient retention fractions are bimodal with mostly low (<0.5) or high (>0.75) values which correspond with phytoplankton- and macrophyte-dominated lakes, respectively (Fig. 3, middle and bottom panels). In the sustainability-focused scenario, the kernel density distribution of both N and P retention fractions shifts to higher values than in 2012 (Fig. 3, top panels). This corresponds with a larger share of lakes being macrophyte-dominated (Table A.1 in Supplementary material A). For the economy-focused scenario, a similar but weaker pattern occurs for P, but the N retention fraction distribution hardly shifts (Fig. 3, top panels). When focusing on phytoplankton-dominated lakes, the kernel density distribution shifts to slightly lower nutrient retention values in 2050 compared to 2012 (Fig. 3, middle panels). The nutrient retention fraction thus strongly differs among individual lakes and depends on the ecosystem state, with the largest increase from 2012 to 2050 being expected in the sustainability-focused scenario.

3.2. Lake outflow TN:TP ratio results

For 2050, the scenarios show higher TN:TP ratios in the outflows of lakes than in 2012, especially for the sustainability-focused scenario. This correlates with the increasing TN:TP ratios of the inflow for 2012, and the sustainability- and economy-focused scenarios, respectively (Fig. 4). Notably, lakes with a low inflow TN:TP ratio (viz. <10) tend to have a lower TN:TP ratio at the outflow than at the inflow, whereas lakes with a higher TN:TP ratio (viz. >20) more often tend to have a higher TN:TP ratio at the outflow than in the inflow (see the spread of values around the dashed 1:1 line in Fig. 4). This pattern differs between equilibrium ecosystem states, with the regression line of macrophyte-dominated lakes deviating more from the 1:1 line (i.e., larger slope) than for phytoplankton-dominated lakes (Fig. 5). Thus, whether and how strongly the in- and outflow TN:TP ratios of lakes differ (i.e., deviating from the 1:1 line) depends on both the TN:TP loading of the inflow and the ecosystem state.

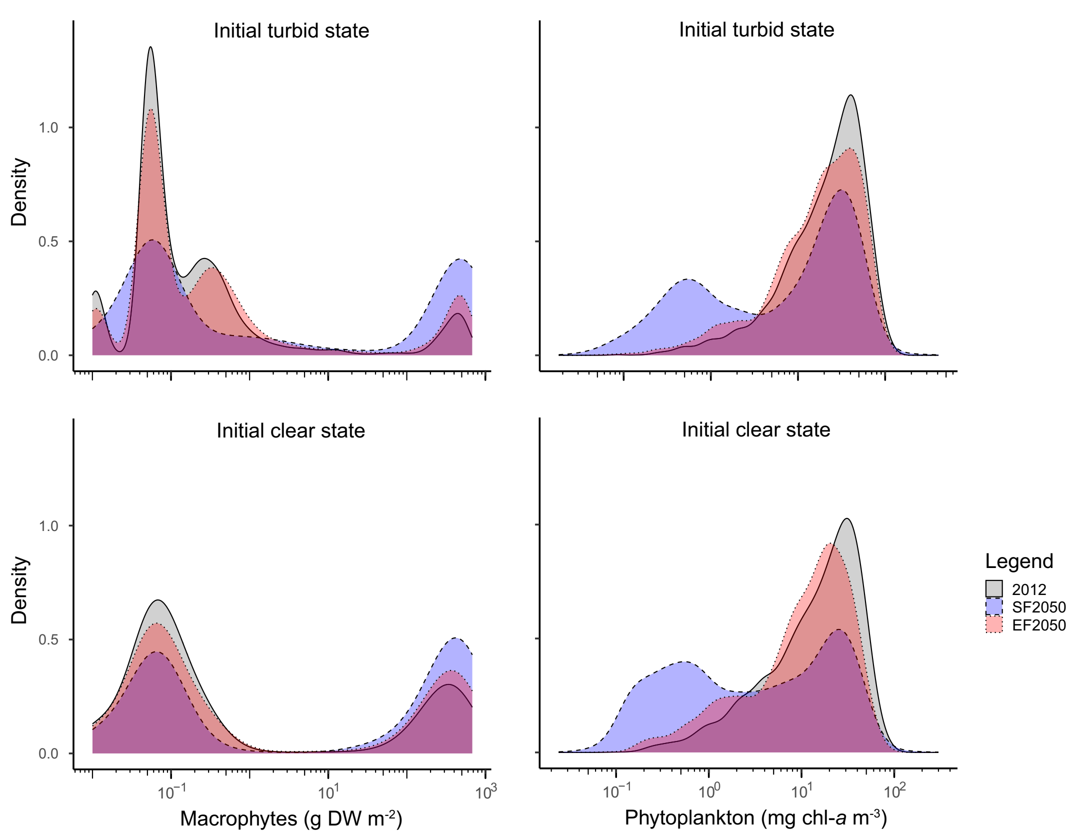

Fig. 2. Kernel density plots of macrophyte (g DW m^{-2}) (left) and phytoplankton levels (mg chl-*a* m^{-3}) (right) per initial state (top turbid, bottom clear). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050).

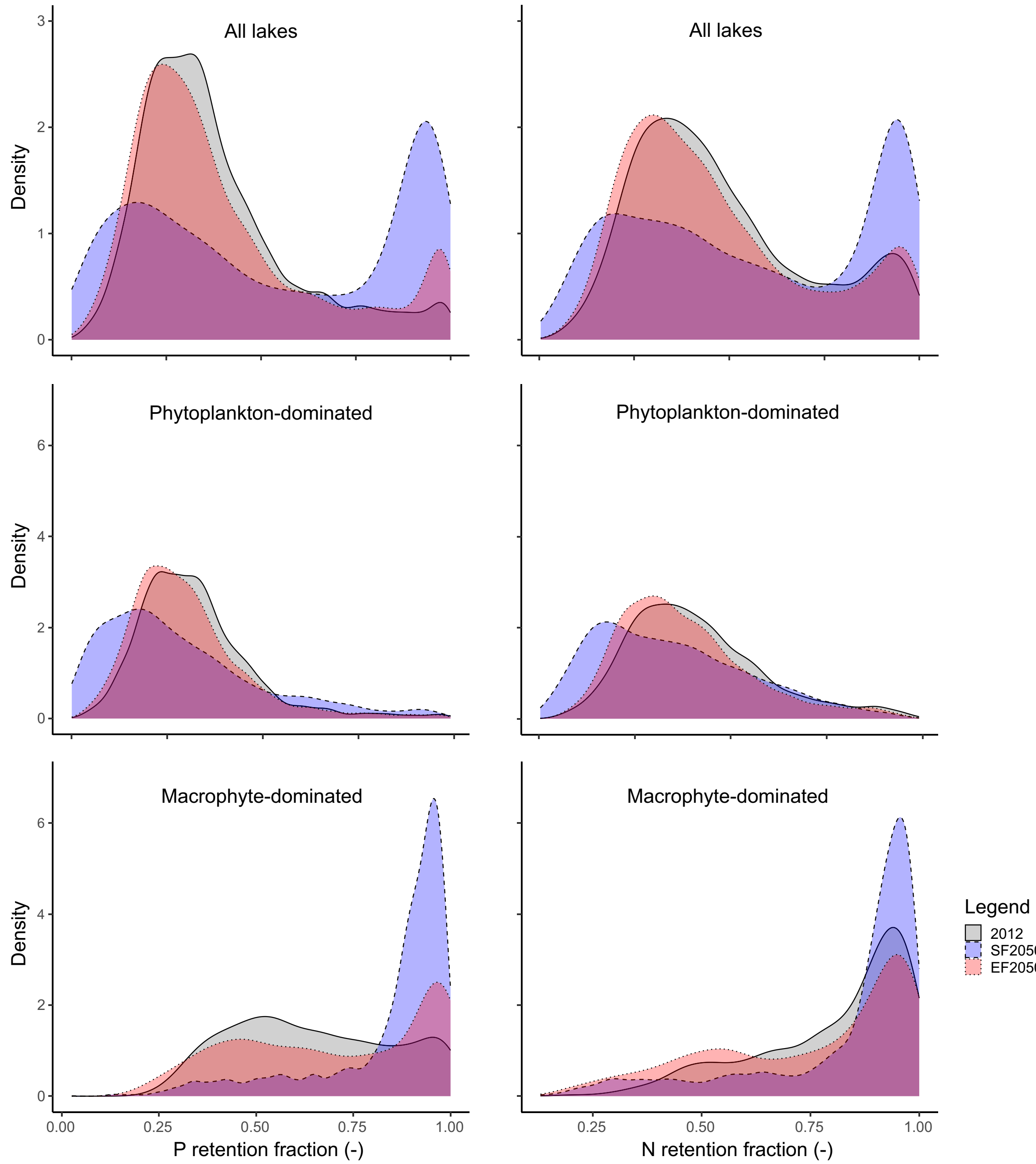

Fig. 3. In-lake nutrient retention fraction kernel density plots for P (left) and N (right) for all lakes (top), and subsets of phytoplankton- (middle) and macrophyte-dominated lakes (bottom) based on the macrophyte to phytoplankton threshold ratio (Supplementary material A). Lines (gray filling) indicate 2012, dashes (blue filling) the sustainability-focused scenario (SF2050), and dots (red filling) the economy-focused scenario (EF2050). Please note that in the top panels each density plot per scenario describes the spread over 3482 lakes for an initial clear and turbid state (i.e., 6964 data points), the middle and bottom panels differ in the number of lakes per density curve (for details see Table A.1 in Supplementary material A).

4. Discussion

4.1. In-lake water quality and nutrient retention

Our scenario analysis showed that more lakes are expected to be macrophyte-dominated and have higher nutrient retention fractions in 2050 than in 2012, with the strongest changes for the sustainability-focused scenario. This increase in the number of macrophyte-dominated lakes conforms to the decreased nutrient loadings but may seem unexpected based on the temperature increases from the 2050 scenarios (Fig. 1). In both scenarios, especially TP loadings decrease by among others improved connection to, and treatment of, sewage (see Section 2.2). In the sustainability-focused scenario this is a result of deliberate actions to reduce nutrient pollution, whereas in the economy-focused scenario this is merely a result of technological developments. The lower TP loadings and a corresponding increase in TN:TP ratios in the 2050 scenarios compared to 2012 (Fig. 1 and Section 2.2) may decrease the risk of dominance by toxic phytoplankton species (Chen et al., 2013). Nevertheless, the effect of TN:TP ratios on phytoplankton nuisance is debatable (see Sections 1 and 4.2) and the rising water temperatures in our scenarios potentially increase the risk of phytoplankton instead of macrophyte dominance (Mooij et al., 2007; Paerl and Huisman, 2008). Though, the latter also depends on the top-down control by the food web (Fragoso Jr et al., 2011).

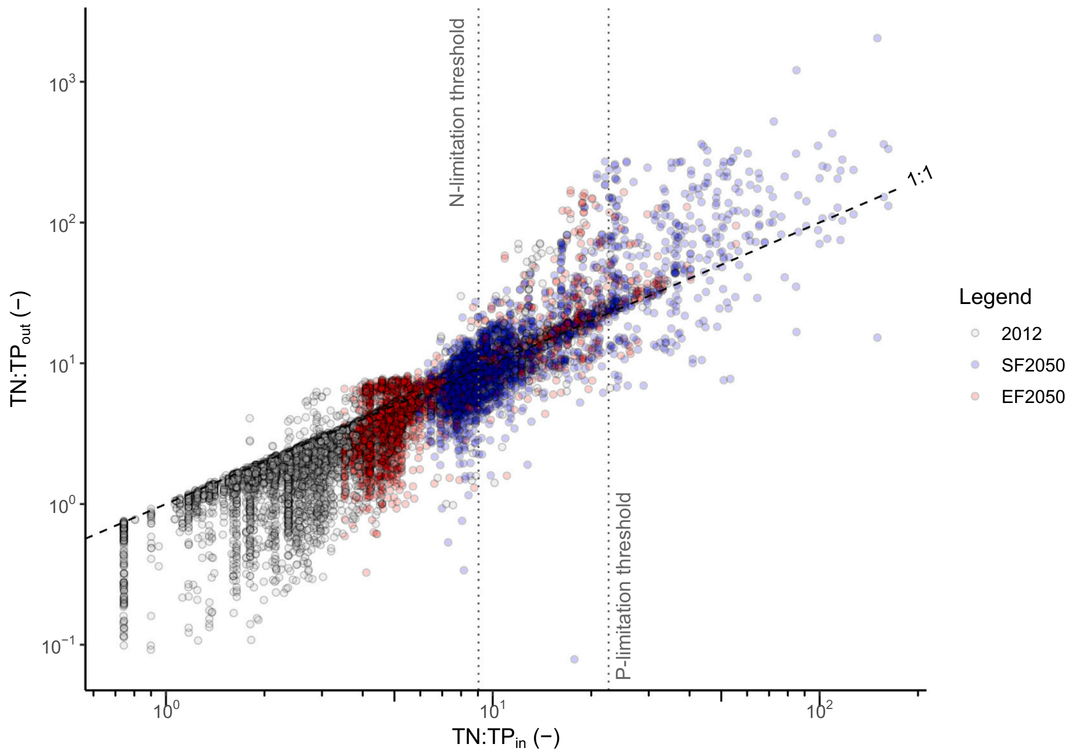

Fig. 4. TN:TP ratio of the outflow and inflow per lake for 2012 (gray), the sustainability-focused scenario (SF2050, blue) and the economy-focused scenario (EF2050, red). The dark gray dashed line is the 1:1 line indicating where the TN:TP ratio of the outflow equals that of the inflow. The vertical dotted lines represent the N- and P-limitation threshold for phytoplankton as defined by (Guildford and Hecky, 2000), converted to mass TN:TP ratios.

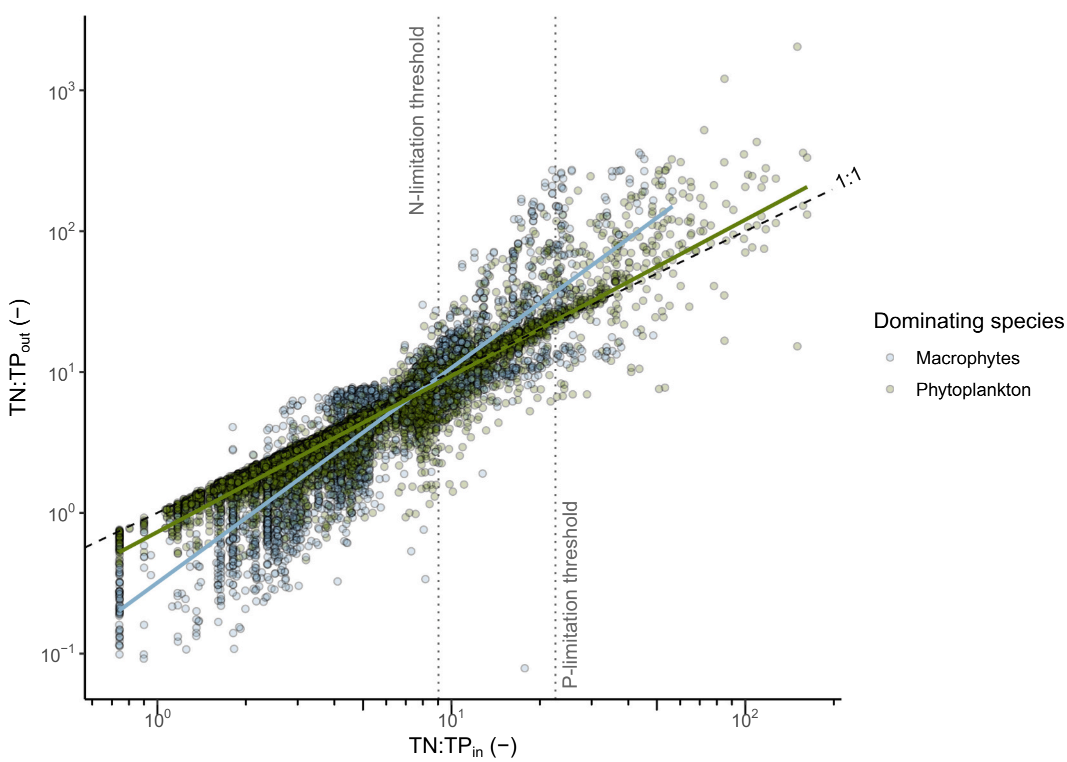

Fig. 5. TN:TP ratio of the outflow and inflow per equilibrium ecosystem state (macrophyte-dominated in blue and phytoplankton-dominated in green) per lake for 2012 and the 2050 scenarios combined. The light blue and dark green lines are the linear regression lines in log-log space (i.e., power functions in non-log space) for macrophyte- and phytoplankton-dominated lakes, respectively. The dark gray dashed line is the 1:1 line indicating where the TN:TP ratio of the outflow equals that of the inflow. The vertical dotted lines represent the N- and P-limitation threshold for phytoplankton as defined by (Guildford and Hecky, 2000), converted to mass TN:TP ratios.

In our 2050 scenarios, the increase in temperature is small relative to the decrease in TP loading (Fig. 1). We see a shift to more macrophyte-dominated lakes in 2050 (Fig. 2), especially for the sustainability-focused scenario with the lowest nutrient loadings (kernel density distribution peak around 0.005 g P m^{-2} lake d^{-1} in Fig. 1). This suggests that the effect of nutrient load reduction prevails. Similarly, across 55 European lakes studies, eutrophication was the overriding stressor and in cases of paired nutrient-thermal stress, nutrient effects were more pronounced in (cross-)basin studies (cf., our study) than in mesocosm experiments (Birk et al., 2020). Other model simulations have also shown the negligible effect of temperature increase (i.e., <1 °C in our study) for the establishment of macrophytes, and chlorophyll-*a* levels at low nutrient loadings (Rolighed et al., 2016), potentially due to nutrient limitation (Fragoso Jr et al., 2011). On the other hand, warming may even improve water quality in subtropical lakes with year-round macrophyte presence (Fragoso Jr et al., 2011). Nevertheless, in the far future (e.g., 2100) when climate change is expected to play a larger role, the positive effect of nutrient reduction could be diminished, especially under the RCP8.5 scenario (van Vuuren et al., 2011; Golub et al., 2022).

Nutrient retention fractions mostly shifted to higher values between 2012 and the 2050 scenarios (Section 3.1). We found a bimodal pattern in nutrient retention fractions that is explained by the ecosystem state, especially for the sustainability-focused scenario. The effect of macrophyte versus phytoplankton dominance on the nutrient retention fraction may have been even stronger when distinguishing an intermediate state of co-existence, in addition to strongly macrophyte- and algae dominated states sensu Bachmann et al. (2002). The bimodal pattern is in line with the theory that macrophyte-dominated lakes have a higher nutrient retention capacity than phytoplankton-dominated lakes due to their influence on in-lake biogeochemical processes that affect nutrient retention (i.e., sedimentation, denitrification, nutrient uptake and consecutive burial) (Hilt et al., 2017; van Wijk et al., 2021). Similar to the spatial feedback theory used in the Smart Nutrient Retention Network concept (van Wijk et al., 2021), the increase in the number of macrophyte-dominated lakes by decreased nutrient loading is thus accompanied by higher nutrient retention fractions. Also, temperature could affect nutrient retention, since higher epilimnion temperatures may directly lead to higher biochemical process rates and thus potentially more nutrient retention. However, direct temperature effects might be counteracted by an ecosystem state shift to phytoplankton dominance or by temporary stratification which may increase P release from the sediment (Woolway et al., 2021). The net effect of temperature thus depends on the sensitivity of lake system processes and state shifts to changes in temperature and nutrient loading, as well as on stratification regimes. Especially in the sustainability-focused scenario, the effect of change in ecosystem state on nutrient retention by strong nutrient load reductions prevails.

We chose to focus on nutrient retention fractions (i.e., nutrient retention efficiency) because they correct for the influence of nutrient loading on the absolute amount of nutrients retained. Still, the absolute amount of nutrients retained might be important in the context of nutrient conservation sensu van Wijk et al. (2021). The lower the nutrient loading, the more lakes will have low absolute nutrient retention values (Supplementary material D) and the less nutrients are available for harvest and reuse. Nevertheless, macrophytes may be easier to harvest and reuse (e.g., Quilliam et al. (2015) and Bartodziej et al. (2017)) than phytoplankton. Thus, although the chance of macrophyte dominance is higher in lakes with low nutrient loading (Sections 2.2 and 3.1), they may still contribute to higher nutrient conservation potential. Our results show that even with relatively high nutrient loading (i.e., kernel density distribution peak around 0.05 g P m^{-2} lake d^{-1} for 2012 in Fig. 1), nutrient retention fractions are generally higher in macrophyte- than in phytoplankton-dominated lakes (Fig. 3). This shows the importance of ecosystem state-dependent nutrient retention fractions versus absolute amounts. Furthermore, the nutrient retention fraction can directly be used to translate nutrient inflows into nutrient outflows. For example, higher nutrient retention fractions in macrophyte- compared to phytoplankton-dominated lakes result in relatively lower throughflow of nutrients to downstream systems. As such, low nutrient retention in phytoplankton-dominated lakes could result in downstream eutrophication issues.

4.2. Lake outflow TN:TP ratios

Lakes may alter TN:TP ratio between their in- and outflow depending on lake characteristics such as water depth and hydraulic residence time, because these influence how strong and how long individual biogeochemical processes have time to act on the nutrients flowing through the system. For example, deeper water bodies may retain relatively more P through settling whereas in shallower systems more sediment-water contact leads to higher denitrification rates (Maranger et al., 2018). Therefore, TN:TP ratios may positively correlate with water depth. Moreover, reservoirs have shorter residence times and lower TN:TP ratios than natural lakes (Maranger et al., 2018). Nevertheless, in our study differences among outflow TN:TP ratios of lakes were not related to lake depth or hydraulic residence time (Supplementary material E). Vollenweider (1975) suggested that besides hydraulic residence time, lake-internal elimination (i.e., nutrient retention) processes determine the relative residence time of nutrients and therewith the relative nutrient retention rates of N and P. We found that the effect of lakes on TN:TP ratios depends on the inflow TN:TP ratio and lake ecosystem state (Figs. 4 and 5), with the latter representing different dominant nutrient retention processes.

A one-to-one relationship between in- and outflow TN:TP ratio would be expected when nutrients are proportionally retained. In our study, in general, the out- and inflow TN:TP ratios correlate positively, and the 2050 scenarios show higher in- and outflow TN:TP ratios compared to 2012 (Fig. 4). Moreover, our results deviated from the 1:1 line at the lower end (viz. <10) and the higher end (viz. >20) of inflow TN:TP ratios (Figs. 4 and 5). Especially the 2012 runs tend to have lower out- than inflow TN:TP ratios, whereas the sustainability-focused scenario for 2050 tends to have higher TN:TP ratios. This may be related to the higher nutrient loading in 2012, since denitrification rates may be higher in (hyper)eutrophic lakes and therewith lower TN:TP ratios (Downing and McCauley, 1992). On the other hand, saturation effects may reduce N removal efficiency in highly eutrophic systems (Maranger et al., 2018) and also changes in P retention should be considered. Additionally, the different trends for low and high inflow TN:TP ratios might be explained by relatively larger retention of the major limiting nutrient through biotic processes (e.g., uptake followed by sedimentation or burial). Finlay et al. (2013) argue that enhanced P limitation of phytoplankton increases N levels in the water column and outflows to downstream systems. Similarly, nutrient limitation of primary producers may explain why in our study lakes with a low inflow TN:TP ratio (i.e., more likely N-limited) tend to have a lower TN:TP ratio at the outflow (i.e., relatively more P in the water column) than at the inflow, whereas lakes with a higher TN:TP ratio (i.e., more likely P-limited) more often tend to have a higher TN:TP ratio at the outflow (i.e., relatively more N in the water column) than in the inflow (Section 3.2). Indeed, Elser et al. (2009) found that lakes with high TN:TP ratios were consistently P-limited.

Furthermore, the regression line of macrophyte-dominated lakes deviates more from the 1:1 line than for phytoplankton-dominated lakes (Fig. 5). The different correlations between in- and outflow TN:TP ratios may be explained by the distinct nutrient uptake mechanisms of the dominating group of primary producers. Phytoplankton directly consumes nutrients from the water column. Though, next to some direct uptake by their leaves, rooting macrophytes may take up nutrients from the sediment (Granéli and Solander, 1988). In our interpretation of TN:TP ratios, we assume that the sediment nutrient content depends on the nutrient loading into the water column at equilibrium, but the nutrient availability to macrophytes is modified by sediment characteristics and in-sediment nutrient retention. This decoupling of macrophyte nutrient uptake from the water column (Bachmann et al., 2002) as included in PCLake+ (Janssen et al., 2019), may explain why in- and outflow TN:TP ratios correlate less in macrophyte- than phytoplankton-dominated lakes. Moreover, the interpretation of the TN:TP ratio relationships is complicated by the fact that, contrary to macrophytes, in our study the phytoplankton nutrient content is part of the total nutrient concentrations of the water column and water outflow. This might also explain the closer correlation between in- and outflow TN:TP ratios in phytoplankton- than in macrophyte-dominated systems.

Contrary to other studies, we found that whether lakes increase or decrease outflow TN:TP ratios depends on whether a lake is N- or P-limited. For example, studies of hundreds of US lakes found mostly higher out- than inflow TN:TP ratios, explained by relatively higher in-lake retention of P by burial compared to N loss by denitrification (Grantz et al., 2014; Maranger et al., 2018; Wu et al., 2022). According to our results, this would be expected to be lakes with relatively high inflow TN:TP ratios (Section 3.2). Nevertheless, these US lake studies include relatively low input TN:TP ratios (e.g., on average 7.5 on a mass basis in Wu et al. (2022)). Thus, other studies do not report the TN:TP decreasing effect of more N-limited systems (i.e., low inflow TN:TP ratios) that we found. This might be explained by the relatively low TN:TP ratios captured in our 2012 simulations for China compared to historic (before 2007) data of temperate to tropical lakes with median in-lake TN:TP mass ratios of 10–32 (Abell et al., 2012). The relatively low TN:TP ratios in our study might be caused by the generally decreased inflow TN:TP ratios as calculated based on the in-river retention equation from (Behrendt and Opitz, 2000) (Supplementary material B).

Our results suggest that when nutrient loading and inflow TN:TP ratios are sufficiently reduced to enable macrophyte dominance, macrophytes will augment the decrease in TN:TP ratios in the water outlet. However, when TN:TP ratios are too high, macrophyte dominance may aggravate TN:TP ratios. Furthermore, care should be taken in conclusions on the effect of TN:TP ratios on water quality because this, among others, depends on which nutrient is limiting in the receiving system. For example, higher outflow TN:TP ratios may improve the water quality of downstream P-limited lakes, but threaten N-limited coastal ecosystems (Wu et al., 2022). Moreover, which (toxic) phytoplankton species dominates depends on TN:TP ratios (Dolman et al., 2012), the nutrient forms (Glibert, 2017), and the actual nutrient loading (Smith, 1982; Guildford and Hecky, 2000). Furthermore, which nutrient is limiting in the receiving waterbody may differ per season (Xu et al., 2015), and TN:TP ratios depend on the net effect of multiple (interacting) N and P loss processes (Downing and McCauley, 1992; Maranger et al., 2018). Therefore, we call for more research on the combined effect of nutrient loadings and alterations in their TN:TP ratios on water quality, and careful consideration of how nutrient- and lake management will influence TN:TP ratios.

4.3. Social and scientific outlook

Our scenario study considers the effect of changes in nutrient loading and epilimnion temperatures through SSP and RCP scenarios. However, climate change may also alter precipitation which is positively related to nutrient loading by runoff (Özen et al., 2010; Jeppesen et al., 2011; Meerhoff et al., 2022). For example, in the far future, large increases in riverine N loading are projected by precipitation increases in highly-fertilized eastern China (Sinha et al., 2017). Moreover, changes in precipitation will affect water residence times and therewith nutrient retention. We did not include such changes in hydrology and associated nutrient loading and nutrient retention in our scenario study because of uncertainty in how precipitation regimes will change. In China, expected changes in precipitation may differ per region and season (Gao et al., 2012). For example, in the Yangtze River basin, it has been shown that this depends on interplays of local, regional, and global drives of change (Li et al., 2021) but insignificant changes in annual mean precipitation are expected in the 2050s compared to 1961–1990 (Huang et al., 2011). When the effect of climate change on precipitation becomes more certain, future scenario studies can support water managers' understanding of the interplay between hydrology, nutrient loading, and nutrient retention.

In our study, we lumped the results into net retention of TN and TP, and their ratios. Through this, we made a first step to explore what water quality, nutrient retention, and downstream nutrient ratios may look like in 2050 for a large number of Chinese lakes. In the future, more detailed studies may help to better understand how lake outflow TN:TP ratios will change based on specific biogeochemical nutrient retention processes such as denitrification and P retention by settling and consecutive burial, and counteracting biogeochemical processes such as resuspension and mobilization. Also, exploration of the speciation of nutrients (e.g., particulate versus dissolved forms) in pollution sources and their role in nutrient retention processes is important to get a more thorough insight into how systems function and how water quality may develop in the future. The process-based PCLake+ model may be used for this because it includes the effect of different nutrient forms and in-lake biogeochemical nutrient retention processes. Moreover, the model is applied to various world regions (Janse et al., 2008; Janssen et al., 2019; Coppens et al., 2020) and may, therefore, be used to test our findings for lakes around the world.

We analyzed the effect of lakes on nutrient transport to downstream systems as the change in nutrient loading between the lakes' in- and outflow. However, studies of how connected waterbodies influence each other's water quality through nutrient loading and nutrient retention are needed in more complex network settings to prevent inconvenient surprises. For example, flushing may decrease the likelihood of alternative stable states in chains of lakes but still, abrupt changes between states may be possible in time and space (Hilt et al., 2011). Also, water quality may be surprisingly uniform among waterbodies in a homogenous network despite a downstream increase in water and nutrient flows (van Gerven et al., 2017). Moreover, other means of connectivity could be considered, such as transport by organisms (Teurlincx et al., 2019). For example, in heterogeneous landscapes with many lakes, the degree of mobility of anglers can lead to three types of spatial patterns in fish populations, including sequential collapses (cf., the collapse of a line of dominoes) (Carpenter and Brock, 2004). Carpenter and Brock (2004) conclude that a one-size-fits-all policy makes lake districts more vulnerable to change and this may be overcome by more lake-specific management approaches. We believe that studies of spatially connected systems may increase system understanding and help to find optimal water quality management strategies in hydrological networks.

5. Conclusion

We performed a scenario analysis of the effect of anthropogenic alterations of water temperature and (the ratio of) nutrient inputs on water quality and nutrient retention in 3482 Chinese lakes, and downstream nutrient loading. The effect of nutrient load reductions prevailed, showing that improved lake water quality (i.e., more macrophyte-dominated lakes), increased nutrient retention fractions and lower downstream nutrient loading go hand in hand. However, TN:TP ratios may be altered more in macrophyte- than phytoplankton-dominated lakes, and the impact of this on downstream waterbodies depends on the inflow TN:TP ratios, the nutrient loadings, and the limiting nutrient in the receiving system. In our 2050 scenarios, increases in inflow TN:TP ratios result in higher outflow TN:TP ratios in many of the studied lakes compared to 2012. The impact of these higher outflow TN:TP ratios on downstream systems will be waterbody-specific. Therefore, we call for careful analysis of connected systems and goal setting to guide water quality management.

Despite the uncertainties around the downstream impacts of alterations in TN:TP ratios, our simulations show that a number of Chinese lakes are projected to have better ecological water quality in 2050 than in 2012. Still, most of the simulated lakes are phytoplankton-dominated. Contrary to our hypothesis, in the economy-focused scenario, water quality, nutrient retention slightly increase, and nutrient loading (ratios) to downstream systems change slightly compared to 2012. In line with our hypothesis, the sustainability-focused scenario shows a more promising future with 45 % of the lakes being macrophyte-dominated with higher nutrient retention fractions and thus less nutrient loading to downstream ecosystems. The main reason for the expected water quality improvement lies in nutrient load reductions and the reinforcing feedback between nutrient loading, water quality and nutrient retention. Therefore, we conclude that earnest efforts are needed to drastically reduce nutrient loadings to reach this more sustainable future scenario for Chinese lakes, whilst minimizing epilimnetic temperature rise. Moreover, our study illustrates that water quality management around the globe could benefit even more from nutrient pollution reduction than one would expect at first sight.

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CRediT authorship contribution statement

Dianneke van Wijk: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Jan H. Janse:** Writing – review & editing, Visualization, Conceptualization. **Mengru Wang:** Writing – review & editing, Resources. **Carolien Kroeze:** Writing – review & editing, Visualization. **Wolf M. Mooij:** Writing – review & editing, Conceptualization. **Annette B.G. Janssen:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data underlying the article is available at https://doi.org/10.5281/zenodo.7808024.

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Supplementary materials A-E

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