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Future nutrient pollution poses a threat to Africa’s freshwater fishes

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Abstract

Excessive levels of nutrients, particularly nitrogen and phosphorus, trigger eutrophication leading to harmful algal blooms and oxygen depletion that endangers freshwater fish species. Despite widespread awareness of these risks, efforts to protect freshwater fish species remain largely ineffective, especially under climate change and other anthropogenic pressures. Here, we assess present and future nutrient pollution risks across African river systems using two water quality models, IMAGE-GNM and SWAT+, under the SSP5–RCP8.5 scenario for 2010 and 2050. We evaluate total nitrogen (TN) and total phosphorus (TP) concentrations against ecological thresholds derived from fish metrics for freshwater fish species (0.7 mg N/L and 0.07 mg P/L). Both models project increasing nutrient pollution risks between 2010 and 2050 across major river basins and ecoregions, although SWAT+ consistently estimates higher impacts than IMAGE-GNM. By 2050, IMAGE-GNM projects that 42% of freshwater fish species will have at least half of their geographical range threatened by nutrient pollution, while SWAT+ projects similar high threats for more than 70% of species. Across all ecoregions, the potentially affected fraction of species is projected to increase between 2010 and 2050 with major river basins such as Niger, Volta and Turkana having over 80% of their fish species potentially affected by 2050. High risk conditions are particularly evident in habitat types such as temperate upland rivers, coastal rivers, and large lake basins. Our findings highlight regions where proactive management and policy interventions should be prioritised to mitigate the adverse effects of nutrient pollution on freshwater fish biodiversity in Africa.

Keywords: Total Nitrogen, Total Phosphorus, SWAT+, IMAGE-GNM, freshwater fish species

1. Introduction

Nutrient pollution, driven predominantly by nitrogen (N) and phosphorus (P), is a critical environmental issue impacting water quality worldwide. Elevated levels of these nutrients lead to eutrophication, characterized by excessive algal blooms, diminished oxygen levels, significantly affecting aquatic ecosystems (Devlin & Brodie, 2023). Sources of nutrient pollution include agricultural runoff, urban wastewater, and industrial discharges, all of which contribute to the degradation of freshwater and marine systems, with their impacts likely exacerbated by climate change (Suresh et al., 2023). Nutrient consumption is increasing rapidly in developing countries, primarily due to population growth, with these economies projected to account for 75% of global nutrient use by 2050 (Sutton et al., 2013). This poses significant challenges for Africa, where rapid population growth and economic development are outpacing the implementation of effective water management practices (Krishnadas & Matysik, 2024). Studies have shown that upcoming shifts in water quality driven by socio-economic changes, climate change, and rising hydroclimatic extremes will significantly affect both people and ecosystems (Beusen et al., 2022; van Vliet et al., 2023), with Sub-Saharan Africa increasingly becoming the dominant hotspot of surface water pollution (Jones et al., 2023).

The fishing industry is vital in Africa, supporting over 10 million people, including 7 million in West Africa alone (Westlund et al., 2008). This sector significantly contributes to food security and economic livelihoods (Temesgen et al., 2019). However, many regions are already experiencing adverse effects from nutrient enrichment such as impaired water quality and reduced biodiversity due to eutrophication and toxicity (Nyenje et al., 2010; Zhou et al., 2023). Pollution is recognized as one of the most significant threats to freshwater fish (Sayer et al., 2025), often resulting in eutrophication which can lead to hypoxia. This process alters the water's physical and chemical properties by lowering pH levels to toxic thresholds for fish that impair their ability to grow, reproduce and survive (Mustafa et al., 2024). Higher nutrient levels promote algal blooms which affect both uptake and supply of dissolved oxygen (Camargo & Alonso, 2006; Yan et al., 2021). These blooms reduce aquatic life's ability to find food by blocking sunlight, potentially driving species away or causing local extinctions (Villacorte et al., 2015). Additionally, they can clog fish gills and produce toxins that lead to illness or death in fish (EPA, 2015). As a key indicator of ecosystem health (Villéger et al., 2017), numerous studies have evaluated the impacts of nutrient pollution on fish biodiversity in various regions worldwide (Tilak et al., 2007; Gaber et al., 2013; Wagenaar & Barnhoorn, 2018; Zhou et al., 2024). However, the effects of N and P pollution on freshwater fish biodiversity in tropical regions are rarely studied (Dudgeon & Strayer, 2024), with studies lacking in spatial and temporal coverage, especially in Africa.

Climate change and rapid socio-economic development undermine efforts to halt biodiversity loss in freshwater ecosystems already under significant stress (Birk et al., 2020; Capon et al., 2021). More specifically, climate change is currently threatening 50% of the world's freshwater fish species (Ahmed et al., 2022). Moreover, it intensifies other already established threats, such as water quality degradation and river fragmentation (Dudgeon & Strayer, 2024). It also alters the flows in streams and rivers and even if these don't dry out, reduced flows can lead to increased pollution concentrations or give rise to toxic algal blooms (Whitehead et al., 2009). On the other hand, high flows mobilize nutrients, sediments, toxic chemicals and aid in dispersal of non-native species (Dudgeon & Strayer, 2024). Abrupt changes in flow or temperature in rivers can substantially reduce fish species richness (Sabater et al., 2023), with decreased water levels inhibiting fish growth (Sanon et al., 2020). Therefore,

as climate change impacts on freshwater biodiversity are projected to intensify (Ahmed et al., 2022), it is important to assess the potential threat of future nutrient pollution on freshwater fish.

To effectively manage and mitigate nutrient pollution, it is crucial to establish future hotspots where nutrient levels are likely to rise. This foresight can enable detailed studies in the hotspot regions for targeted interventions and policy planning. In this sense, scenario-based projections offer valuable insights into how nutrient pollution might evolve under different socio-economic and climatic conditions (O'Neill et al., 2017). In this study, we focus on the high-end warming scenario SSP5-RCP8.5, characterized by high greenhouse gas emissions and rapid economic growth (Riahi et al., 2011; Kriegler et al., 2017). We employed two large scale water quality models namely the Integrated Model to Assess the Global Environment - Global Nutrient Model (IMAGE-GNM) (Beusen et al., 2022), and Soil and Water Assessment Tool (SWAT+) (Nkwasa et al., 2024) to project future nutrient pollution hotspots across Africa. Models are increasingly used to address data gaps in water research, especially in regions lacking water quality data and robust monitoring programs, such as Sub-Saharan Africa (Desbureaux et al., 2022). Importantly, these models are capable of simulating the impacts of climate change on future water quality (Strokal et al., 2024). Since changes in water quality will not only affect human water use (Jones et al., 2022), but also freshwater ecosystems (Bosmans et al., 2022), it is essential to investigate the risk they pose on freshwater fish species.

In this study, we assessed the threat of future nutrient pollution to freshwater fish species by first comparing total nitrogen (TN) and total phosphorus (TP) concentrations from two models: IMAGE-GNM and SWAT+. This comparison, focused on identifying nutrient pollution hotspots, based on simulations under the combined climate change and socioeconomic scenario SSP5-RCP8.5 for the years 2010 and 2050. Utilizing a regional dataset of 2,624 freshwater fish species (Snoeks & Theeten, 2025), we estimated the threat posed by elevated TN and TP levels to fish in different ecoregions and major river basins. This study is, to our knowledge, the first assessment of potential threats of future nutrient pollution on riverine African freshwater fish. These insights into hotspots for nutrient pollution are crucial for policymakers and stakeholders to safeguard water quality, protect aquatic ecosystems and to decide on policy interventions.

2. Materials and methods

2.1 Water quality models

2.1.1 IMAGE-GNM

IMAGE-GNM is a spatially explicit, dynamic model with a resolution of $0.5^{\circ} \times 0.5^{\circ}$ that has been validated with sampling station data. It simulates the pathways of N and P to surface water from concentrated point sources, such as wastewater from industrial, urban, and rural populations, as well as from diffuse sources like agricultural systems with fertilizer use and manure management at a yearly time step. Additionally, it considers natural ecosystems, surface runoff, shallow and deep groundwater, riparian zones, litterfall in floodplains, and atmospheric deposition (Beusen, Van Beek, et al., 2015). IMAGE-GNM uses the grid-based global hydrological model PCRaster Global Water Balance (PCR-GLOBWB) (Sutanudjaja et al., 2018), to quantify water stores and fluxes, volume, surface area, and thus depth of water bodies, and water travel time. In the model, grid cells receive water containing N and P from upstream cells, and N and P entering water bodies through diffuse, point and natural sources. Nutrient retention is calculated based on water residence time and nutrient uptake velocity before

water and nutrients are transported downstream. In this study, we used model estimates of river TN and TP for 2010, the latest non-scenario year, and for 2050 under the SSP5-RCP8.5 scenario. The model was validated against observed discharge, N and P concentrations in a number of different stations in a variety of rivers (Beusen et al., 2022). The data used in this study was taken from its updated version, the IMAGE 3.2 version detailed in Beusen et al. (2022), incorporating enhancements such as new input data, and an improved PCR-GLOBWB model with updated hydrological data.

2.1.2 SWAT+ model

SWAT+ is an enhanced version of the SWAT model, developed to offer greater flexibility in connecting spatial units and modelling management practices (Arnold et al., 2018; Bieger et al., 2017). The semi-distributed model simulates hydrological dynamics, crop growth, sediment transport, and nutrient loads by dividing hydrological basins into sub-basins and Hydrologic Response Units (HRUs), with each HRU representing areas of similar land use, soil type, slope, and management practices (Neitsch et al., 2005). SWAT+ also distinguishes upland and lowland processes through landscape units (LSUs) and uses the water balance concept as the foundation for all hydrological processes. The model simulates N and P cycles, tracking both inorganic and organic forms of these nutrients. Nitrogen movement and transformation are calculated based on water volume and soil nitrate concentration, while organic N and P transport via sediment is estimated using topsoil concentrations, sediment yield, and an enrichment ratio. The enrichment ratio accounts for the difference between the nutrient content of eroded sediment and the original soil, as finer particles transported during erosion tend to have higher nutrient concentrations compared to bulk soil. Nitrogen enters the soil through fertilizer and manure application, atmospheric deposition, and nitrogen fixation, while removal occurs via plant uptake, volatilization, denitrification, percolation, tile flow, lateral flow, and runoff. Phosphorus mainly enters through fertilizer and manure application and is removed by plant uptake, tile flow, lateral flow, percolation, and runoff.

Nutrients from the land phase can enter channels and move downstream through surface runoff and lateral subsurface flow (Neitsch et al., 2011). In-stream nutrient dynamics are simulated using the kinetic routines from the QUAL2E in-stream water quality model (Brown, 1987). The model tracks both nutrients dissolved in the stream and those attached to sediment particles. Dissolved nutrients travel with the water flow, while sediment-bound nutrients can settle onto the channel bed with the sediment. Additional information on nutrient processes in SWAT+ can be found in the SWAT documentation (Arnold et al., 1998; Neitsch et al., 2011). Details on the setup, calibration and validation of the Africa SWAT+ model using observed river discharge data, TN and TP concentrations, and river sediment loads, are provided in Nkwasa et al. (2024).

2.2 Future Socio-economic and Climate Scenarios

Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs) describe future possible developments in socio-economic and climatic conditions, respectively, offering integrated scenarios to explore uncertain future changes. Consistent scenario assumptions are important for enabling meaningful comparison of model outputs across different scales and variables. In this study, all models were driven using harmonized socio-economic assumptions based on SSP5 together with climate forcing from RCP8.5 to simulate future water quality conditions. SSP5 is characterised by high socio-economic growth with heavy fossil fuel use and increased high-tech agricultural production (O'Neill et al., 2017), whereas RCP8.5 considers a high level of greenhouse gas emissions (van Vuuren et al., 2011). The scenario assumes intensive agricultural practices to meet

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the growing food demand, with a diet rich in meat leading to increased manure production. This pathway projects significant economic and population growth, with Africa's gross domestic product (GDP) expected to rise by 60% and its population increasing by 70% to reach 1.7 billion people by 2050 (KC & Lutz, 2014). Despite the increase in sewage connections, inadequate wastewater treatment with poor environmental management policies will increase the risks to water quality and aquatic biodiversity. In addition, under SSP5–RCP8.5, the energy-intensive lifestyle and associated greenhouse gas emissions lead to strong climate changes (Siabi et al., 2023), which affect hydrological conditions and nutrient flows. Generally, this scenario envisions a future marked by urbanization, low-ambition nitrogen policies, improved sewage connections with limited advancements in treatment, high water withdrawal, and inadequate climate mitigation efforts (M. Wang et al., 2024). This high emissions scenario provides insights into the potential scale of impacts on ecosystems under extreme pressure from both climate change and socio-economic drivers. This makes it particularly relevant for identifying nutrient pollution hotspots and assessing resulting threats to freshwater fish species, thereby highlighting the urgency for management and policy actions in the region.

IMAGE-GNM nutrient simulations were performed at a spatial resolution of 0.5° whereas the SWAT+ nutrient simulations were initially performed at HRU level and then aggregated from the sub-basin scale to a 0.5° for comparative analysis. An overview of the major assumptions and implementations for both IMAGE-GNM and SWAT+ models is provided in Tables S1 and S2, supplementary material.

2.3 Thresholds for TN and TP

Numerous nutrient concentration thresholds for TN and TP have been established across various regions and water bodies to protect biodiversity, maintain good ecological conditions and mitigate eutrophication. These efforts aim to preserve water quality and prevent ecological damage caused by nutrient pollution. Table S3 (supplementary material) summarizes nutrient thresholds linked to fish fauna, benthic macroinvertebrates, harmful algal blooms, excessive cyanobacterial growth, and unwanted periphyton blooms in aquatic systems. For our study, we selected thresholds based on the ecological effects of nutrients on river systems, particularly concentrations beyond which fish assemblages are likely to experience significant degradation. Therefore, we adopted thresholds derived from fish-related metrics. In the absence of Africa-specific thresholds, we relied on general freshwater thresholds as a reasonable starting point for the risk assessment.

Several studies have identified nutrient thresholds based on their effects on fish communities. For example, Azevedo et al. (2013) proposed a TP threshold of 0.07 mg P/L for freshwater fish species richness in sub(tropical) streams globally while L. Wang et al. (2007) identified mean thresholds where fish metrics change most dramatically at 0.07 mg/L TP and 0.9 mg/L TN. Robertson (2006) reported breakpoints in fish indices at 0.06 mg/L TP and 0.54 mg/L TN in Wisconsin rivers whereas Miltner & Rankin (1998) proposed a similar threshold of 0.06 mg/L TP and 0.61 mg/L total inorganic nitrogen (TIN), beyond which fish community structure is significantly degraded based on the Index of Biotic Integrity. These fall within relatively narrow ranges of 0.54–0.90 mg/L TN and 0.06–0.07 mg/L for TP reported for fish fauna. Based on the above previous studies, we adopted TN and TP thresholds of 0.7 mg N/L and 0.07 mg P/L, respectively for our study. These values align with trophic transitions for streams, such as the mesotrophic–eutrophic boundary for TP (0.075 mg/L) and the oligotrophic–mesotrophic boundary for TN (0.700 mg/L) (Dodds et al., 1998) and are also broadly consistent with values protecting ecosystems from eutrophication where most studies indicate TP threshold of 0.03–0.06 mg P/L and a

TN threshold of 0.5–2.0 mg N/L, beyond which algal biomass can reach nuisance levels, and diatom composition undergoes significant changes (Poikane et al., 2021). These values are also comparable to those derived in previous studies using other ecological indicators (see Table S3, supplementary material) and provide meaningful endpoints for protecting aquatic life in large rivers.

2.4 Model intercomparison

We compared annual IMAGE-GNM and SWAT+ total nitrogen and total phosphorus simulations using two approaches: (1) analysing the projected percentage changes in TN and TP concentrations across Africa from 2010 to 2050 and (2) evaluating the percentage agreement between the models in classifying grid cells as critical or non-critical based on the ecological thresholds adopted in this study (0.7 mg N L⁻¹ for TN and 0.07 mg P L⁻¹ for TP). Click or tap here to enter text.

2.5 Assessing threat to freshwater fishes

Freshwater fish occurrence data was sourced from the Global Biodiversity Information Facility (GBIF) which hosts the Royal Museum for Central Africa's collection, one of the largest repositories of African freshwater fish in the world (Snoeks & Theeten, 2025). Initially, we retrieved 2,719 freshwater fish species with 86,415 occurrence records. After data cleaning, which involved removing records lacking species names or geographic information and eliminating duplicates, our final dataset comprised 2,624 freshwater fish species with 74,025 occurrence records dating from 1896 to 2023. Lentic species were excluded from the study, as the models used are optimized solely for river systems. The complete dataset is available in the supporting information.

Organisms generally adapt to climate change by migrating to more suitable habitats (Loarie et al., 2009). However, predicting such movements for freshwater fish is challenging due to uncertainties and data gaps related to current and future barriers, such as dams and weirs (McManamay et al., 2018). Additionally, reliable data on dispersal abilities are unavailable for most species (Radinger et al., 2017). To address these limitations, we adopted the "no dispersal" assumption, restricting fish species to their current geographical ranges within the grid cells where they are presently located (Barbarossa et al., 2021). Due to limited data on fish population decline rates, our assessments relied on presence/absence of data over time, assuming uniform abundance within species ranges and linear rates of decline. While we acknowledge the importance of lower thresholds to prevent nutrient deficiency in fish species, this study focused on high nutrient pollution extremes. We assume that fish species can tolerate nutrient-induced hypoxia or toxicity up to the specified TN and TP thresholds of 0.7 mg N/L for TN and 0.07 mg P/L for TP explained above, with uniform tolerance across species within each ecoregion or habitat.

To evaluate the potential threat of nutrient pollution to freshwater fish species, we first identified and mapped grid cells where annual TN and TP concentrations from the two water quality models exceeded the critical thresholds. We then created a combined exceedance map for each model indicating areas where at least one of the two nutrients surpassed its critical threshold. Following methodology from Barbarossa et al. (2021), for each species, we quantified the proportion of its geographical range exposed to nutrient pollution by flagging grid cells as "threatened" if either TN and/or TP exceeded their respective thresholds. The percentage of geographical range threatened (PGT) for each species (x) was calculated as:

$$PGT_x = \frac{AT_x}{A_x} \times 100$$

Where AT_x is the total number of grid cells where species x is present and at least TN and/or TP threshold is exceeded, and A_x is the total number of grid cells where species x is present.

To assess the proportion of species threatened by nutrient pollution in each ecoregion, we computed the potentially affected fraction (PAF) of freshwater species in 2010 and 2050. A freshwater ecoregion is a large area encompassing one or more freshwater systems that contains a distinct assemblage of natural freshwater communities and species, where the freshwater species, dynamics, and environmental conditions within the ecoregion are more similar to each other than to those of surrounding ecoregions, forming a conservation unit (FEOW, 2025). The PAF for each ecoregion was determined as follows,

$$PAF_{ecoregion} = \frac{ST_{ecoregion}}{S_{ecoregion}}$$

Where $PAF_{ecoregion}$ represents the potentially affected fraction of freshwater fish species in an ecoregion, $ST_{ecoregion}$, represents the number of unique species in grid cells within the ecoregion where at least one critical threshold (TN and/or TP) is exceeded, and $S_{ecoregion}$ represents the total number of unique species in the ecoregion. The computation carefully avoids repetition if the same species appear in more than one threatened grid cell. A similar analysis was also done for the major river basins in Africa.

3. Results

3.1 Model intercomparison for nutrient hotspots

Projected changes in nutrient concentrations showed strong spatial variability across Africa, with both IMAGE-GNM and SWAT+ projecting widespread increases in TN and TP concentrations by 2050 under SSP5–RCP8.5 (Figure 1). IMAGE-GNM projected that over 80% of Africa’s rivers will experience higher TN and TP concentrations in 2050 relative to 2010, although localized decreases were observed in parts of southern and central Africa. Similarly, SWAT+ projected increases in TN concentrations across approximately 80% of rivers and increases in TP concentrations across about 95% of rivers. Compared to IMAGE-GNM, SWAT+ showed less extensive areas with decreasing nutrient concentrations. Similar patterns are observed at the river basin scale (Figure S1), where several basins in eastern, western, and southern Africa consistently showed increasing TN and TP concentrations.

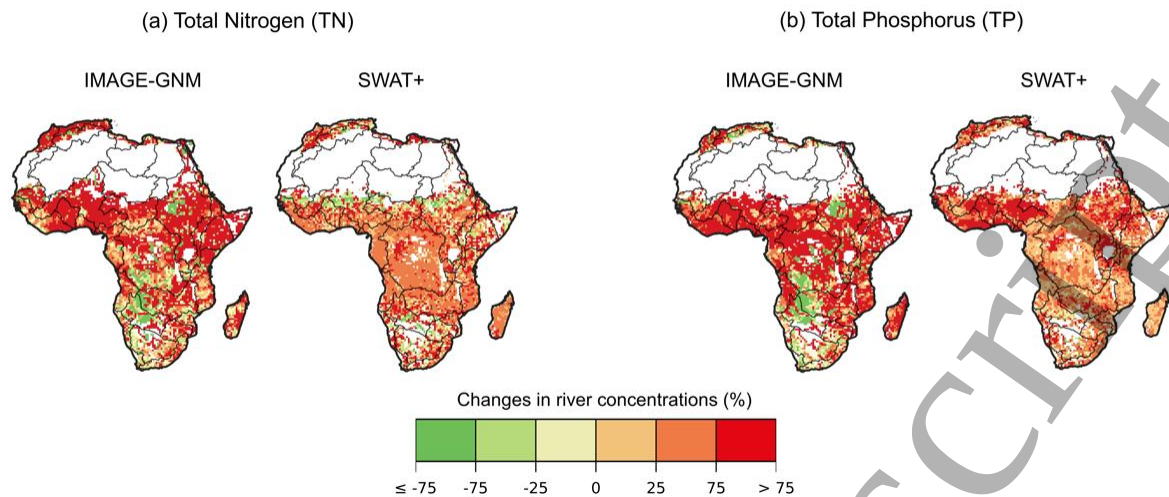


Figure 1: Relative percentage change in (a) total nitrogen (TN) and (b) total phosphorus (TP) river concentrations between 2010 and 2050 based on the SSP5-RCP8.5 scenario for the IMAGE-GNM and SWAT+ model. Polygons represent river basins and white areas represent regions with no available model data (e.g., non-river cells or cells excluded during masking).

Spatial agreement between IMAGE-GNM and SWAT+ in classifying critical and non-critical nutrient pollution areas shows clear spatial and temporal variability across Africa (Figure 2). For TN, overall model agreement decreases from 66% in 2010 to 52% in 2050. Areas consistently classified as critical, exceeding nutrient thresholds by both models, particularly in eastern and southern Africa, increased from 10% to 27%, while robust non-critical areas declined from 56% to 25%. Model disagreement also increased from 34% to 48%, indicating greater uncertainty in the future spatial distribution of nitrogen hotspots. For TP, overall agreement increased slightly from 64% in 2010 to 68% in 2050. Agreement on critical hotspot areas increased from 18% to 32%, suggesting an expansion of regions consistently identified as phosphorus hotspots by both models. In contrast, robust non-critical areas declined from 46% to 36%, while model disagreement decreased slightly from 36% to 32%. Overall, both models project an expansion of nutrient pollution hotspots by 2050, although future TP projections show slightly stronger consistency between models than TN projections. Similar patterns are observed at the river basin scale (Figure S1), where both models consistently classify several major basins in eastern and southern Africa as critical, particularly for TP. In contrast, several basins in western and central Africa remained non-critical or showed disagreement between the models, especially for TN.

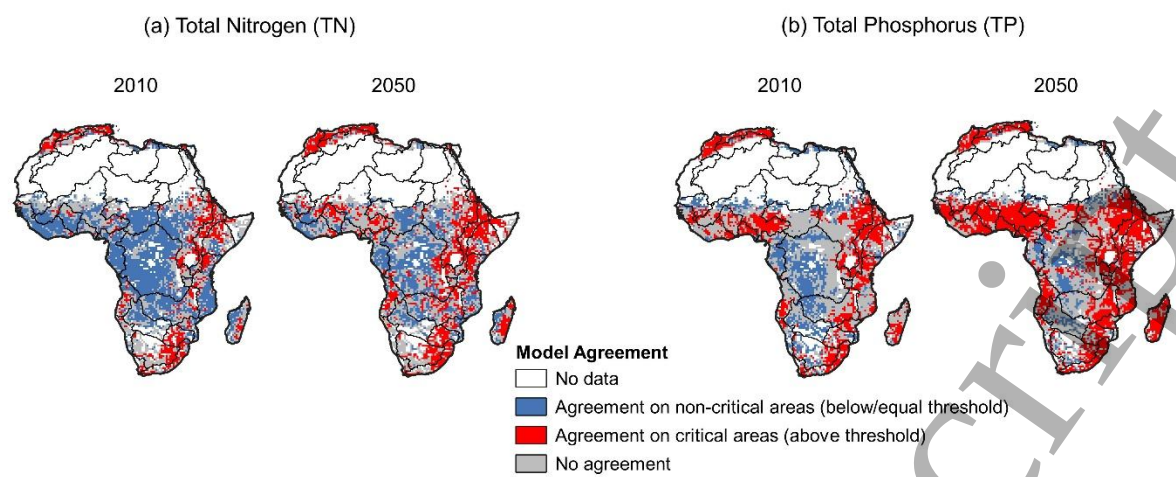


Figure 2: Spatial agreement between IMAGE-GNM and SWAT+ models in classifying nutrient pollution risk across Africa for (a) Total Nitrogen (TN) and (b) Total Phosphorus (TP) in 2010 and 2050 under SSP5-RCP8.5 according to predefined thresholds for freshwater fish species: 0.7 mg N/L for TN and 0.07 mg P/L for TP. Polygons represent river basins and white areas represent regions with no available model data (e.g., non-river cells or cells excluded during masking).

3.2 Threat of species exposure to nutrient pollution

IMAGE-GNM projected that the critical areas with combined TN and/or TP exceedance would increase from 38% in 2010 to 59% in 2050, while non-critical areas reduce from 62% to 41% (Figure 3(a)). In contrast, SWAT+ projected more spatially extensive affected areas, with critical areas already covering about 90% of Africa's river systems in 2010 and increasing slightly to 91% by 2050. Correspondingly, non-critical areas in SWAT+ remained below 10% for both periods. Spatially, both models identified extensive critical areas in eastern, western, and southern Africa, with hotspot regions becoming more widespread by 2050. However, IMAGE-GNM showed larger proportions of non-critical regions, particularly across central Africa, whereas SWAT+ projected more continuous and spatially extensive exceedance patterns. Overall, these differences suggest that SWAT+ projects broader nutrient threshold exceedance across African rivers, while IMAGE-GNM indicates stronger spatial heterogeneity and localized non-critical regions. Similar patterns were also observed at the river basin scale (Figure S3).

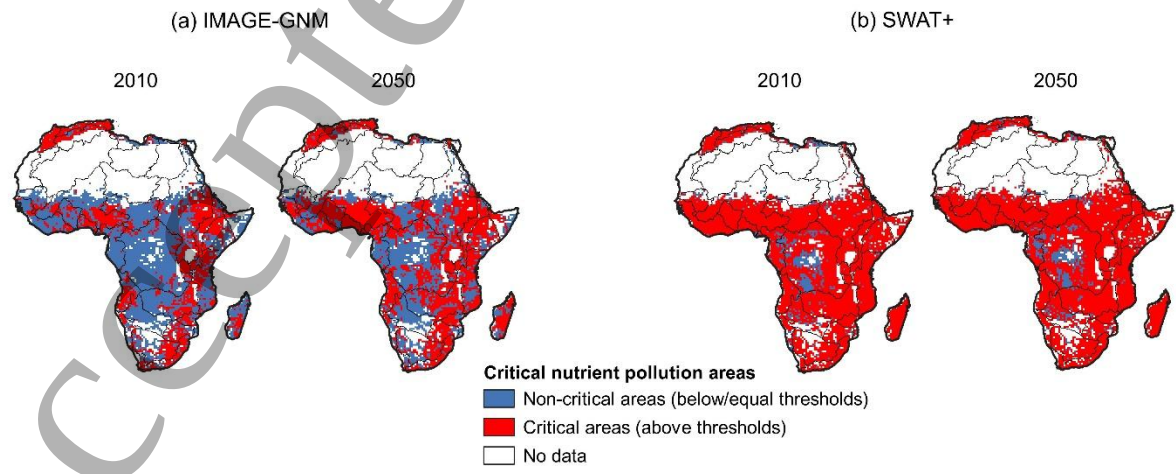


Figure 3: Spatial distribution of critical nutrient pollution areas across Africa for (a) IMAGE-GNM and (b) SWAT+ in 2010 and 2050 under SSP5–RCP8.5, based on combined exceedance of TN and/or TP thresholds for freshwater fish species (0.7 mg N L^{-1} for TN and 0.07 mg P L^{-1} for TP). Red areas indicate grid cells where at least one nutrient threshold was exceeded, while blue areas represent non-critical areas where both nutrient concentrations remained below or equal to the thresholds. Polygons represent river basins and white areas indicate regions with no available model data or non-river cells excluded during masking.

Our results indicate a substantial increase in the proportion of freshwater fish species with their geographical ranges threatened with future nutrient pollution (Figure 4A). Based on IMAGE-GNM projections, the percentage of species with at least half of their geographical range threatened increased from 15% in 2010 to 42% by 2050. On the other hand, species with no threatened range decreased from 60% to 35%, indicating a marked expansion of nutrient pollution prone areas across African freshwater ecosystems. In contrast, SWAT+ projected consistently higher risks of nutrient pollution, with over 70% of fish species having at least half of their geographical range threatened in 2010 and 2050.

Several fish orders, including Synbranchiformes (swamp eels), Clupeiformes (freshwater herrings and sardines e.g. *Limnothrissa*, *Stolothrissa*), Cypriniformes (*Labeo*, *Enteromius*), and Siluriformes (catfishes), showed high vulnerability to nutrient pollution, particularly under the SWAT+ model, where more than 80% of their geographical range was threatened in both 2010 (Figure 4B) and 2050 (Figure 4C). Similarly, Polypteriformes (bichirs) and Characiformes (African tetras and tigerfishes) exhibited substantial increases in threatened range by 2050. In contrast, IMAGE-GNM projected comparatively lower threatened ranges across most fish orders, especially in 2010. Orders such as Gonorynchiformes (kneriids, hingemouths, and sandfishes), Anguilliformes (freshwater eels), and Mugiliformes (mullets) showed relatively lower threatened ranges, generally remaining below 50% under IMAGE-GNM projections. Overall, both models projected an increase in the geographical range threatened by nutrient pollution between 2010 and 2050, although SWAT+ consistently estimated substantially higher impacts than IMAGE-GNM across nearly all fish orders.

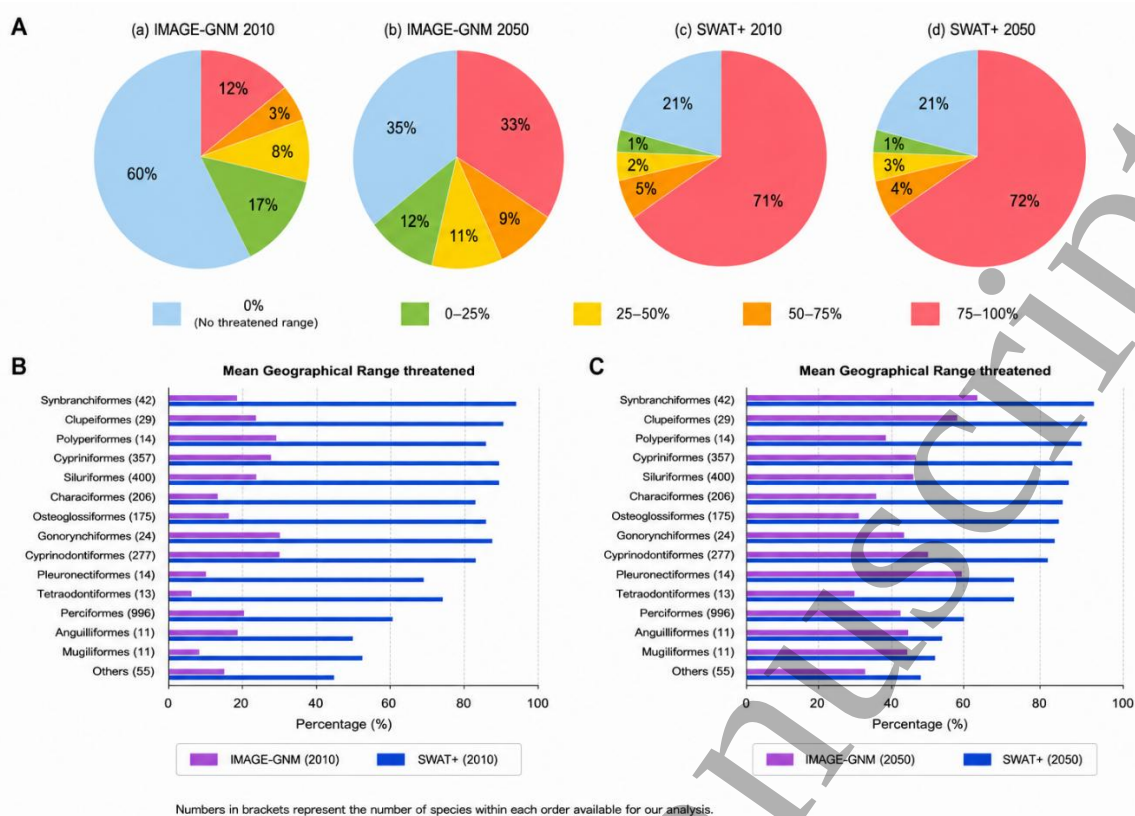


Figure 4: **A.** Total percentage of freshwater fish species (numbers in the pie-chart) that fall within different percentage classes of geographical range threatened by nutrient pollution for IMAGE-GNM in (a) 2010 and (b) 2050 and for SWAT+ in (c) 2010 and (d) 2050. **B.** Percentage of geographical range threatened by nutrient pollution for different riverine fish orders in Africa in 2010 and **(C)** 2050. Numbers in brackets represent the number of species within each order available for our analysis. Fish orders in the group “Others” are those with less than 10 unique species. These can be found in Table S4, supplementary material. Source data is provided as Supplementary information.

The ecoregions database indicates that central and western Africa, characterised by (sub)tropical floodplain rivers, coastal rivers and wetlands have the highest freshwater fish species richness. In contrast, southern and northern regions, dominated by xeric freshwaters, closed basins, and montane freshwaters, exhibit the lowest species diversity due to limited water availability (Figure S5,a-b). Both IMAGE-GNM and SWAT+ projected increasing Potentially Affected Fraction (PAF) values for freshwater fish species from 2010 to 2050 across most ecoregions, indicating greater future eutrophication risks (Figure 5). Particularly high values were observed in temperate upland rivers, temperate coastal rivers, and large lake basins, where PAF values approached or reached 1.0 by 2050. In contrast, tropical and subtropical floodplain rivers and xeric freshwaters and endorheic basins showed relatively lower values especially with IMAGE-GNM, although notable increases were still projected.

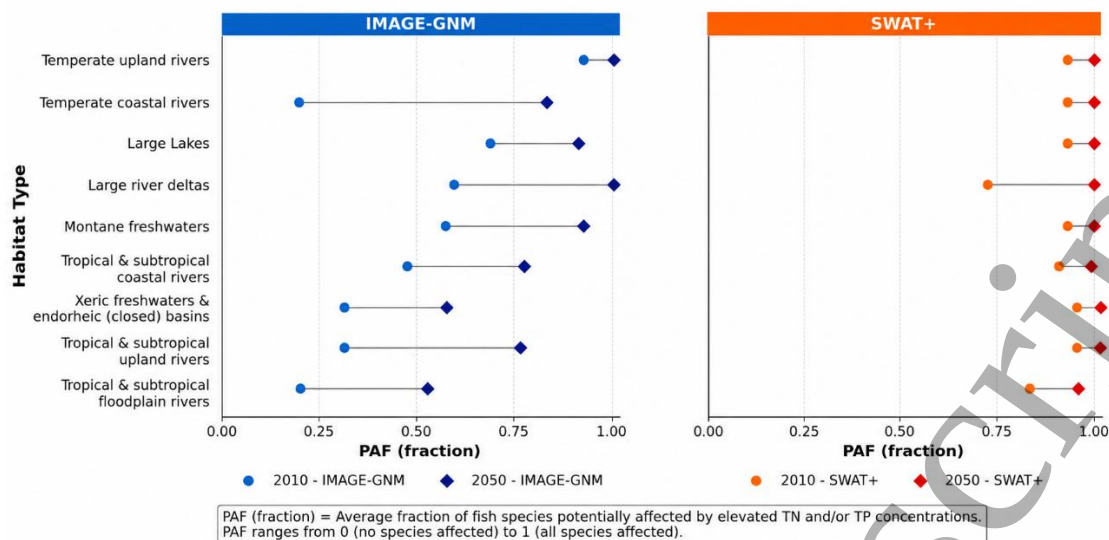


Figure 5: Average potentially affected fraction (PAF) of freshwater fish species across different freshwater habitat types in Africa for 2010 and 2050, comparing results from the IMAGE-GNM and SWAT+ models. Horizontal lines connect the two time periods for each habitat type, illustrating projected changes in biodiversity exposure to nutrient pollution.

At the river basin scale, we calculate that PAF will increase in all river basins (Figure S6). Among the selected basins, the Jubba, Turkana, Nile, and Zambezi basins exhibited particularly high PAF values in both models, with several projections approaching or reaching 1.0 by 2050, suggesting that nearly all freshwater fish species within these basins could potentially be exposed to nutrient concentrations exceeding ecological thresholds (Figure 6). The Congo Basin, despite containing the highest number of freshwater fish species (1131 species), showed moderate PAF values in IMAGE-GNM but substantially higher values in SWAT+, especially in 2050. Relatively lower PAF values were observed in the Limpopo, Okavango, and Senegal basins, although increasing trends were still projected over time. In general, both IMAGE-GNM and SWAT+ projected increasing PAF values from 2010 to 2050 under SSP5–RCP8.5, indicating rising eutrophication risks across major African river systems. SWAT+ generally projected higher PAF values than IMAGE-GNM, particularly in the Niger and Volta basins, where future conditions approached near-complete freshwater fish species exposure to elevated nutrient concentrations.

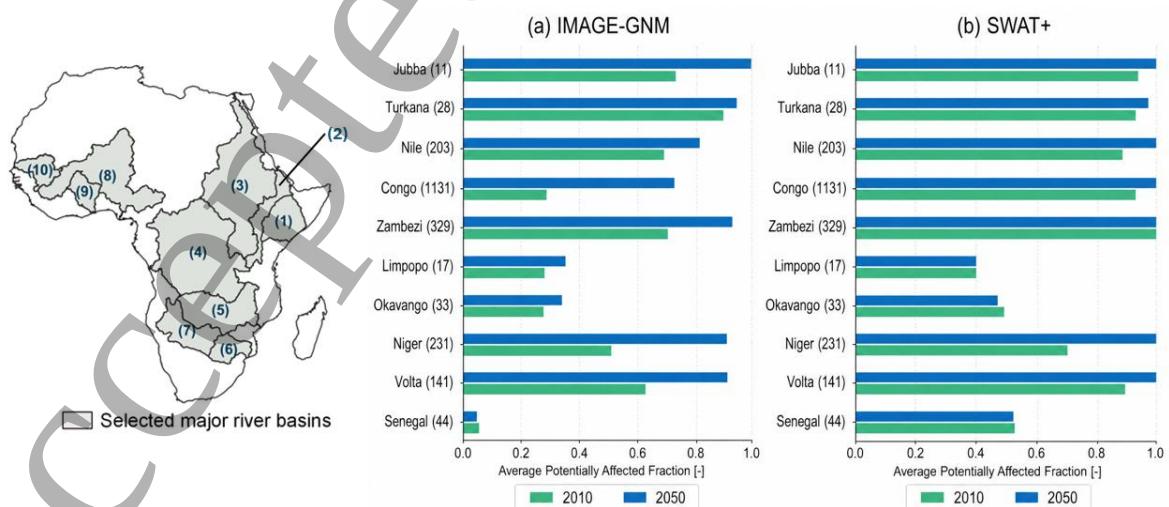


Figure 6: **Left:** Spatial delineation of the selected major African river basins: (1) Jubba, (2) Turkana, (3) Nile, (4) Congo, (5) Zambezi, (6) Limpopo, (7) Okavango, (8) Niger, (9) Volta, and (10) Senegal. **Right:** Average Potentially Affected Fraction (PAF) of freshwater fish species in each selected river basin exposed to elevated TN and/or TP concentrations simulated by (a) IMAGE-GNM and (b) SWAT+ models exceeding the defined ecological thresholds for the years 2010 and 2050 under SSP5–RCP8.5. Numbers in brackets indicate the total number of freshwater fish species included in the analysis for each basin.

4. Discussion

4.1 Model intercomparison on a continental scale

Our results show that both SWAT+ and IMAGE-GNM models consistently project increased TN and TP concentrations in African rivers by 2050 under SSP5-RCP8.5. The models show moderate agreement in identifying pollution hotspots which suggests that they can provide useful insights into eutrophication risks under this scenario. Despite broadly similar spatial patterns of nutrient increases, the magnitude of these changes differs between the models. There are several possible reasons for these differences. Table S1 gives an overview of the main assumptions and implementations of SWAT+ and IMAGE-GNM. IMAGE-GNM projects that ~55 % of rivers will have an increase in TN or TP greater than 75%, which is mainly explained by the dynamic land use change. The expansion of agricultural land and the reduction of natural land cover is causing relative high changes (in percentage). SWAT+ uses a constant land use map of 2010, thus the agricultural increase is more limited (in relative sense). In areas where grassland is playing an important role (for example Europe, but not Africa), the difference between the models could be more significant. Also, IMAGE-GNM explicitly accounts for long-term nutrient legacies from historical groundwater accumulation, whereas SWAT+ simulates groundwater flow and nitrate transport but does not explicitly represent nutrient legacies from historical loads. Additionally, IMAGE-GNM incorporates aquaculture as an anthropogenic nutrient source which is not represented in SWAT+.

Differences in hydrology between the two models influence not only the magnitude of river discharge (Figure S10) and nutrient transport, but also nutrient timing and residence time, contributing to contrasting future projections. For example, IMAGE-GNM is sensitive to structural uncertainties in its underlying hydrological model, PCR-GLOBWB (Sutanudjaja et al., 2018). In our study, SWAT+ is driven by an ensemble of four CMIP5 GCMs (MIROC5, IPSL-CM5A-LR, HadGEM2-ES, and GFDL-ESM2M), with distinct precipitation and temperature biases (Liu et al., 2022; Sierra et al., 2015), whereas IMAGE-GNM uses the HadCM3 model, which tends to overestimate precipitation in some regions (Valdes et al., 2017). Such differences in climate forcing can substantially influence hydrological responses, nutrient leaching, and runoff generation, ultimately leading to contrasting TN and TP projections. In addition, IMAGE-GNM explicitly represents lakes and reservoirs and accounts for nutrient retention during routing (Beusen & Bouwman, 2022), whereas the current SWAT+ setup does not explicitly include reservoir and lake trapping processes (Teran et al., 2026), which may lead to higher downstream nutrient export estimates given that reservoirs can retain approximately 20–25% of continental nitrogen and phosphorus loads (Beusen et al., 2015). Nevertheless, despite these structural differences, the main assumptions that can influence water quality are almost the same for both models hence why both models identify comparable large-scale nutrient pollution hotspots across Africa.

These two models, to our knowledge, are the only existing spatially distributed nutrient models, making them the only suitable option for our study. Both models consistently identify nutrient pollution hotspots such as the Nile and Niger basins and parts of Northern and Southern Africa, offering a foundation for prioritizing regions for

water quality monitoring (Pérez et al., 2017). However, the model discrepancies in hotspot identification emphasize the need for model intercomparison frameworks to better evaluate these models (van Vliet et al., 2019). Reliance on single model predictions can increase susceptibility to uncertainty, therefore using at least two models allows for model intercomparison and increases confidence in identifying robust patterns of nutrient pollution, particularly where both models consistently identify the same hotspot regions and show high spatial agreement in threshold exceedance. The ISIMIP water quality community, for example, established a protocol to harmonize model inputs enabling cross-scale assessments under climate change (Strokal et al., 2024). From this, models can identify pollution hotspots, sources, and trends, particularly in data-scarce regions like Africa with limited monitoring networks.

4.2 Nutrient pollution and its threat to freshwater fish species

Our analysis reveals a significant projected increase in nutrient pollution across African rivers under the SSP5-RCP8.5 scenario by 2050, largely driven by population growth and increasing food demand (M. Wang et al., 2024). The results showed that based on IMAGE-GNM projections, rivers exceeding at least one of the nutrient thresholds increase from 38% in 2010 to 59% in 2050, indicating intensified nutrient loading predominantly from anthropogenic sources (Beusen & Bouwman, 2022). Agricultural intensification with the use of synthetic fertilizers and urbanization are key contributors to this trend (Beusen et al., 2022). For instance, Soro et al., (2023) demonstrated that nutrient enrichment in Côte d'Ivoire's major rivers stems predominantly from agricultural sources, particularly fertilizer use. This pattern is common across Africa, where agricultural lands often lie close to river waters (Thomas & Whittington, 2023). On the other hand, Yasin et al., (2010) reported a shift over time from natural nutrient sources (e.g., soil weathering, atmospheric deposition, biological fixation, and runoff from natural ecosystems) to increasingly anthropogenic sources such as agriculture, livestock production, and wastewater discharge in most African basins between 1970 and 2050. Importantly, Sub-Saharan Africa's projected population growth, potentially doubling to 1.7 billion by 2050 (KC & Lutz, 2014), coupled with urbanization, is likely to exacerbate river pollution, especially without efficient wastewater treatment. Jones et al., (2023) identified hotspots of water quality deterioration coinciding with areas of rapid urban expansion, particularly around major urban centres and along river basins such as the Nile and Orange. Notably, while some basins like Congo, dominated by natural nutrient export (Beusen & Bouwman, 2022), largely maintain concentrations below established thresholds, our models project increases by 2050 due to growing anthropogenic influences under the SSP5-RCP8.5 scenario.

Furthermore, future climate simulations of precipitation indicate increased annual sediment and nutrient (TN and TP) loads (Ockenden et al., 2017; Qiu et al., 2021), likely driven by enhanced runoff and flushing processes that are explicitly represented in both models. However, with the use of annual concentrations, we may miss these flushing events. River flow projections (Figure S11) indicate increased precipitation in most African rivers, with significant increments in basins such as Jubba and the Sahel region. These changes are likely to result in increased surface runoff, potentially leading to higher nutrient loading that could pose a threat to fish populations. The vulnerability of freshwater fish species to climate change was highlighted by Barbarossa et al. (2021), who found that 36% of global freshwater fish species have over half of their present-day geographical range exposed to climate extremes beyond current levels.

The proportion of African freshwater fish species with more than half of their geographical range threatened by nutrient pollution is projected to increase from 15% to 42% under IMAGE-GNM, while SWAT+ projects over 70% of species to remain highly threatened in both 2010 and 2050 (Figure 4) generally indicating an increasing trend in the vulnerability of freshwater fish species to nutrient pollution. Our results confirm previous findings on the alarming threat of extinction on freshwater fish by nutrient pollution (Miranda et al., 2022; Zhou et al., 2024). Elevated nutrient levels promote algal blooms which create harmful conditions for freshwater fish (Camargo & Alonso, 2006; Yan et al., 2021). These effects are corroborated by Heiskary and Markus (2003), who reported significant negative correlations between fish and macroinvertebrate assemblage characteristics and concentrations of TP and TN in nonwadeable rivers in Minnesota. Similarly, L. Wang et al., (2007) observed strong relationships between nutrient concentrations and most fish assemblage measures in wadeable streams in Wisconsin. Most freshwater fish are sensitive to eutrophication, which can lead to hypoxic conditions and changes in plankton communities that affect their food webs (Bertora et al., 2021; Poiesz et al., 2024). Even though Anguilliformes (eels) had the least threatened areas due to nutrient pollution, they remain vulnerable to other environmental stressors such as habitat fragmentation and biological invasions (Bertora et al., 2021), despite some tolerance to eutrophic conditions (Drouineau et al., 2018). Our findings indicate a general increasing trend in the potentially affected fraction (PAF) of freshwater fish species across different ecoregions and river basins from 2010 to 2050. This trend is particularly pronounced in tropical watersheds, aligning with previous studies suggesting large climate change-induced freshwater habitat degradation in the tropics (Barbarossa et al., 2021). Zhou et al., (2024) showed that characterization factors (CFs) for phosphorus and nitrogen impacts on freshwater fish are higher in densely populated regions encompassing either large lakes or the headwaters of large rivers. This is consistent with our observation of PAF values above 0.6 in the African Great Lakes region (Figure 6).

The insights from this study can guide regional or national strategies to: (1) prioritize good practices for nutrient water quality management in rivers, including nature-based solutions such as establishing riparian buffer zones, bed and bank stabilization, as well as developing and enforcing stricter regulations on polluting industries and promoting public education and outreach, (2) implement sustainable agricultural practices to avoid further losses to the streams and rivers and (3) invest in efficient wastewater treatment methodologies and infrastructure for industry and population waste to avoid high loads of point sources to ground and surface water. Given the vulnerability of regions with rapid population growth and inadequate sanitation infrastructure to the adverse impacts of algal blooms (Suresh et al., 2023), effective solutions will require integrated policies that align environmental management with socio-economic strategies. A unified approach in managing transboundary water resources is also important to develop consistent standards for nutrient pollution control, improve data collection and data sharing, and strengthen enforcement efforts to preserve water quality across regions (UNEP, 2010). Consequently, this would contribute to achieving targets of SDG 6 (clean water and sanitation) and SDG 14 (life below water) under the condition that also SDG 2 (no hunger) is achieved.

4.3 Limitations of the study

Because the IMAGE-GNM model operates on a coarse 0.5° (~55 km) grid, our analysis is limited to large catchments ($\geq 3025 \text{ km}^2$). This spatial limitation means that while our study provides a broad assessment of nutrient pollution, finer-scale processes such as storm-driven runoff, localized point-source discharges and riparian nutrient retention in smaller catchments may not be fully captured. Moreover, we used annual mean

nutrient concentrations to assess risk largely because of the temporal resolution of most global/regional models (Strokal et al., 2025). IMAGE-GNM operates at a yearly timestep, while SWAT+ outputs were aggregated to annual averages to enable model comparison. While this approach is suitable for assessing long-term exposure, it does not capture seasonal or short-term peak events, which can strongly influence nutrient export (Blaen et al., 2017). Consequently, our threshold-based assessments should therefore be interpreted as first-order, broad-scale indicators of nutrient pollution risk that identify general hotspot regions rather than precise local exceedances. Future studies using higher temporal resolution models could better capture seasonal variability.

Another limitation is that our study uses generalized threshold concentrations for nutrient pollution derived from global fish metrics, which may not accurately reflect local conditions in African freshwater ecosystems. Thresholds can vary by water body type and environmental conditions (Poikane et al., 2019), and specific toxicity thresholds for many African freshwater ecosystems remain largely unknown (de Villiers & Thiart, 2007). In addition, fish species adapted to low-nutrient environments may have lower or higher thresholds for nitrogen and phosphorus toxicity. While our study uses nutrient thresholds (0.7 mg N/L for TN and 0.07 mg P/L for TP) tailored to fish metrics, these are higher than thresholds reported for other ecological indicators, such as benthic chlorophyll (Dodds et al., 1998) and periphyton (McDowell et al., 2020). To evaluate the robustness of our findings to threshold selection, we conducted a sensitivity analysis by varying the default thresholds by $\pm 20\%$. The results showed that the overall spatial patterns of nutrient pollution risk remained largely consistent across all threshold scenarios for both TN and TP (Figures S7–S9). While the absolute extent of critical and non-critical areas changed with threshold choice, SWAT+ consistently classified a substantially larger proportion critical areas than IMAGE-GNM across all years and scenarios. Despite differences in magnitude, both models projected increasing eutrophication risk under future climate and socioeconomic conditions, suggesting that the main conclusions of our study are relatively robust to moderate threshold uncertainty. Nevertheless, future research should prioritize establishing region-specific toxicity thresholds based on biological responses of African freshwater fish species to enhance the accuracy of nutrient risk assessments and inform targeted management strategies.

A core assumption in this study is that increases in TN and TP concentrations correlate with declines in fish species richness. This assumption could be refined by increasing species observations, as current limitations may lead to overestimating species sensitivity due to underestimated richness in certain ecoregions. Access to more occurrence records could reduce uncertainty in data-scarce areas (Zhou et al., 2023). Potential sampling bias in our point occurrence dataset presents another source of uncertainty. Many GBIF occurrence records are affected by spatial and taxonomic biases associated with uneven sampling effort, accessibility, and digitization limitations, which may not fully represent actual biodiversity patterns (Ball et al., 2025; Bowler et al., 2025). As a result, data gaps in fish occurrence records, particularly in regions already vulnerable to nutrient pollution, could influence the accuracy of the projected biodiversity risk patterns.

Fish species loss is influenced by a complex interplay of factors beyond nutrient pollution, including freshwater salinization (Ahmed et al., 2022), increasing water temperatures, changing outflow (Reid et al., 2019), and micro/nano plastics pollution (Jaiswal et al., 2022). These factors often interact, potentially exacerbating impacts. Future research should account for additional anthropogenic pressures such as habitat fragmentation, altered river connectivity, water abstraction and overfishing (Sanon et al., 2020). Incorporating these stressors into ecological

risk assessments would provide a more comprehensive understanding of the cumulative threats to freshwater fish biodiversity and help disentangle the effects of nutrient pollution from other interacting pressures (Barbarossa et al., 2020). The contribution of climate change to future nutrient pollution varies across Africa. For example, projected increases in river discharge in the Jubba Basin and parts of the Sahel (Figure S11) may enhance nutrient transport, while hotspots in the Volta, Turkana, and Niger basins likely reflect combined hydrological and anthropogenic pressures (Chawanda et al., 2024). Given the timescale and scope of climate change, it is unlikely that mitigation efforts will prevent all biodiversity losses, particularly in sensitive freshwater ecosystems (Richman et al., 2015), therefore building ecological resilience through the maintenance of habitat connectivity is essential to support species distribution shifts in response to a changing climate. For many freshwater fish, maintaining natural connectivity between habitats will be vital for adapting to environmental changes and reducing species vulnerability to nutrient pollution and eutrophication (Walker et al., 2002).

5. Conclusion

This study highlights the urgency of addressing TN and TP nutrient pollution in Africa's rivers. Using IMAGE-GNM and SWAT+ models, we have identified pollution hotspots and assessed the associated threats to freshwater fish species, providing a framework for understanding the extent and potential impact of river nutrient pollution across the continent. Our analysis shows that by 2050, under the SSP5-RCP8.5 scenario, IMAGE-GNM projects that 42% of African freshwater fish species would have at least half of their geographical range threatened by nutrient pollution, while SWAT+ projected similarly high threats for over 70% of species. Major rivers such as Niger, Volta, and Turkana will see a significant fraction (>0.8) of fish species affected. These threats are concerning as eutrophication not only degrades habitat quality but also intensifies competition, potentially leading to substantial species loss. Addressing these challenges will require a coordinated policy response including stricter regulation of nutrient emissions, sustainable agricultural practices, improved wastewater treatment, and transboundary water management. Ultimately, achieving ambient water quality and protecting fish biodiversity will demand increased public awareness, investments in pollution prevention, and a stronger commitment to cross-sectoral collaboration. Only through such comprehensive efforts can Africa's freshwater resources be preserved for future generations, safeguarding both the ecological integrity of aquatic habitats and the human communities that depend on them.

Data availability: All nutrient simulations used in this study are available under the ISIMIP Water quality sector protocol (<https://www.isimip.org/>). Shapefile for freshwater ecoregions available for download at <https://www.feow.org/download>

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