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POND BIODIVERSITY AND FUNCTIONS

# Why ponds concentrate nutrients: the roles of internal features, land use, and climate

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**Abstract** Ponds are key freshwater habitats supporting biodiversity and ecosystem services, yet they remain understudied in the context of land use and climate change. We examined 240 ponds across eight countries (seven in Europe and Uruguay) to assess how internal pond characteristics, surrounding land cover and livestock intensity, seasonal climatic variation, and climate influence nutrient concentrations across spatial and temporal scales. Nutrient concentrations were strongly associated with internal features: shallow ponds and short hydroperiods had higher total nitrogen (TN) and total phosphorus (TP) concentrations, while thermal stratification, typically found in deeper ponds, was associated with higher TN, indicating enhanced internal nutrient recycling. Land use also played a significant role with agricultural intensity increasing nutrient concentration (both TN and TP), whereas forest cover reduced TP. Seasonal variation modulated these patterns, with higher TP concentrations observed in summer, and with dilution effects during wetter and cooler periods, particularly for TN in semi-permanent ponds. These findings underscore the combined influence of physical characteristics, landscape context, and climate variability on nutrient concentrations in ponds and highlight the need for integrated, multi-scale approaches

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to anticipate the impacts of global climate change effects on these ecologically valuable ecosystems.

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## Introduction

Rapid human population growth and accelerating economic expansion have driven agricultural intensification and urbanization worldwide (Foley et al., 2005), leading to severe degradation of freshwater ecosystems. Land use change, particularly agricultural intensification, increases nutrient concentrations, especially nitrogen and phosphorus compounds, in water bodies via increases in surface water runoff, erosion, and/or leaching (Albert et al., 2021). Small freshwater ecosystems, such as ponds, are potentially highly vulnerable to increased nutrient loading due to their limited capacity for pollutant dilution, high surface-area-to-volume ratio, and frequent hydrological isolation (Søndergaard et al., 2005; Declerck et al., 2006; Serrano et al., 2017). However, ponds can also maintain high chemical water quality in agricultural settings due to smaller catchment areas, which limit exposure to substantial pollution loads (Biggs & Williams, 2024). Additionally, some biological groups may show resilience to eutrophication, potentially due to the small size of ponds and their proximity to shoreline habitats (Rosset et al., 2014).

Climatic variables such as temperature and precipitation can further intensify eutrophication pressures, as ponds are less buffered against temperature extremes and hydrological fluctuations that alter hydroperiod length and water levels (Gozlan et al., 2019). Warming can accelerate stratification during the day and enhance nighttime mixing (Martinsen et al., 2019), driving internal nutrient release from sediments and increasing ecosystem respiration (Wilhelm & Adrian, 2008; Staehr et al., 2012). These processes may contribute to the high total nitrogen (TN) and total phosphorus (TP) concentrations frequently observed in ponds (Richardson et al., 2022). Changes in precipitation patterns further influence nutrient loading by modifying runoff and water retention (Michalak, 2016). Heavy rainfall events can increase nutrient inflow from the surrounding landscape, while drought conditions reduce water levels, concentrating nutrients and enhancing eutrophication risk through evaporation and reduced dilution capacity (Serrano et al., 2017). In response to these pressures, macrophytes—particularly emergent species—play a key role in modulating nutrient dynamics and sediment chemistry by regulating light availability and assimilating nutrients from the water column (Benelli & Bartoli, 2021), contributing to the observed variability in primary production across pond ecosystems (Richardson et al., 2022).

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Ponds play a critical role in supporting both aquatic (Davies et al., 2008) and terrestrial biodiversity (Lewis-Phillips et al., 2019; Walton et al., 2021) and can contribute to a range of ecosystem services, including water provision, flood mitigation, groundwater recharge, pollution amelioration, recreation, and tourism (Biggs et al., 2017), particularly when implemented as nature-based solutions to maximize these benefits (Bartrons et al., 2024). However, ponds have been historically overlooked in ecological research and conservation management, which often tend to prioritize rivers and larger lakes (Downing, 2010; Sayer, 2014; Hill et al., 2021).

While the number of studies on the impact of land use and climate on ponds is increasing (Usio et al., 2017; Jarosiewicz et al., 2018; Kuranchie et al., 2022), significant challenges remain in understanding the interactive effects between land use and climate across different spatial and temporal scales. Additionally, there is a need to better incorporate pond physical characteristics into these studies. Shallow ponds tend to have high nutrient levels, independent of external inputs, making it important to understand the underlying mechanisms behind this phenomenon (Serrano et al., 2017). The present study uses an extensive, highly standardized dataset spanning 240 ponds across Europe and Uruguay to evaluate the main drivers of physical and chemical variables in ponds across different spatial and temporal scales, with a particular emphasis on nutrient concentrations.

We first identified key gradients in physical and chemical variables across our study ponds and subsequently examined how variation in nutrient concentrations (i.e., TN and TP) was related to local pond characteristics, surrounding land cover, livestock intensity, climate factors (i.e., temperature and precipitation), year (2021 and 2022), and season (spring, summer and autumn). This analysis incorporated multiple spatial scales: local (pond and pondscape), regional (country), and continental. We hypothesized that pond nutrient concentrations would be primarily influenced by pond-specific characteristics and surrounding land use (e.g., cropland cover and livestock intensity). Furthermore, we posited that these effects would be particularly pronounced in regions and seasons with warmer temperatures, or in regions and seasons with high rainfall, where nutrient dynamics may be amplified by climatic extremes or increased runoff from adjacent land.

## Materials and methods

### Study sites

This study encompassed 240 ponds located in eight countries: seven European countries (Belgium, Denmark, Germany, Spain, Switzerland, United Kingdom, Türkiye (Turkey)) and one South American country (Uruguay) (Fig. 1). The selected countries cover a latitudinal gradient across the Western Palearctic spanning different biogeographical, and human land management settings, with Uruguay included to broaden climatic context.

Ponds were sampled within 4 to 6 distinct pondscapes in each country. In this study, the term 'pondscape' refers to a landscape that includes multiple ponds within a broader matrix, considering factors such as pond connectivity and their relationship with surrounding environmental features (Boothby, 1997). Each pondscape covered an area of approximately 7 $km^2$ (with a radius of ~ 3 km) and was separated by, at least, 20 km from other local pondscapes—most often without excessive numbers of intervening ponds—to reduce potential spatial autocorrelation. Within each pondscape, ponds were selected across a gradient of land use intensity and were located at altitudes below 800 m.

Individual ponds ranged from glacial-origin ponds (e.g., kettle holes in northeastern Germany) to man-made ponds created for agriculture and livestock use (e.g., Belgium, United Kingdom and Uruguay), being at least 10 years old at the time of the study if of artificial origin. Pond sizes varied from a few square meters to ca. 1 ha, with maximum depths on the sampling date reaching up to 5.3 m. Selected ponds had no surface hydrological connections with other water bodies and were either permanent (year-round water presence), semi-permanent (permanent but dries out once every several years) or temporary (seasonally dry). None were highly shaded or heavily influenced by woody terrestrial vegetation, and none had been subjected to major artificial modifications such as recent alterations to shoreline structure and hydrology. The ponds were characterized by contrasting levels of anthropogenic pressure, as related to agricultural and livestock activities in their immediate surroundings.

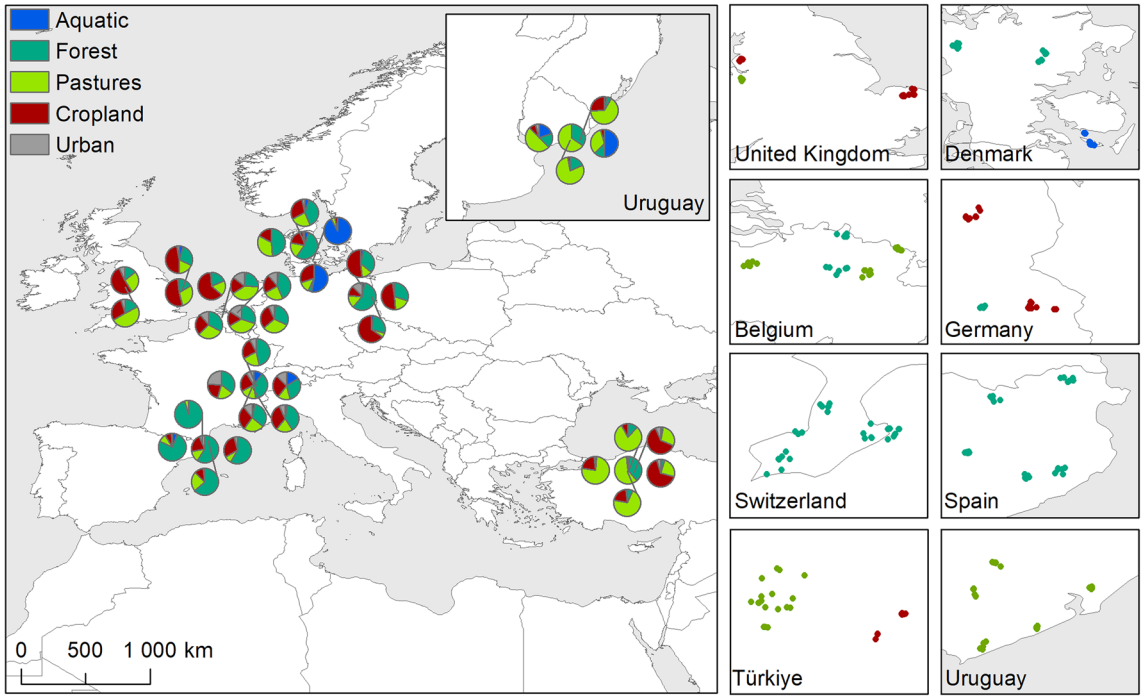


**Fig. 1** Location of 41 pondscapes (left panel) and 240 ponds (right panel). The pie charts on the left depict the percentage composition of the main land-cover types within a 500 m radius within each pondscape, while the panels on the right show detailed clusters of ponds within each pondscape (not drawn to scale). Each pond is color-coded according to the dominant land-cover type of its pondscape

## Sampling and data collection

Data collection took place in 2021 for Switzerland, Germany, Belgium, Denmark, United Kingdom, and Uruguay. In Spain, sampling took place in both 2021 and 2022, with 12 ponds sampled in 2022 due to near-dry conditions in 2021. In Türkiye, sampling was delayed until 2022 due to COVID-19-related mobility restrictions. All ponds were sampled three times per year: in spring, summer, and autumn. Additionally, 12 ponds from each country (excluding Türkiye) were resampled in the following year using the exact same sampling protocol, selecting a single time for the sampling (i.e., spring or summer). All sampling procedures followed standardized protocols developed under the H2020 PONDERFUL project.

### *Morphological, physical, and chemical pond variables*

A depth-integrated water sample (~10 L) for the quantification of suspended matter and multiple chemical variables was collected using a tube sampler at a central point in each pond (or the largest open water area in macrophyte-covered ponds). Water was sampled from different 1 m depth sections of the water column and then mixed to provide a representative sample. In very shallow ponds (< 0.2 m), the same tube sampler was used but filled partially to avoid sediment resuspension. Conductivity, pH, oxygen concentration, and water temperature were measured in situ at 20 cm below the water surface using standard electrodes. Temperature, along with pH, conductivity, and oxygen concentration, was recorded at multiple depths during each pond visit to assess stratification at the time of water chemistry sampling. Depth profiles were measured at the deepest point of the pond, with five sampling intervals determined based on the pond's depth. A pond was considered thermally stratified if there was a difference of 1 °C or greater between the surface and bottom water, which has been used to define thermal stratification in lakes (Woolway et al., 2022).

TN and TP concentrations were determined from unfiltered water samples (250 mL), stored at − 20 °C until analysis. Analyses followed the methods of Sen Gupta & Koroleff (1973), as adapted by Seal Analytical for continuous flow analysis with integrated digestion, in accordance with American Public Health Association (APHA) standards. Alkalinity was measured using the Gran titration method on filtered water samples immediately after collection. Total suspended solids (TSS) were quantified by filtering a known volume of water through pre-weighed glass fiber filters (Whatman GF/C), which were dried at 105 °C for 24 h, and weighted to determine the dry mass of solids retained in the filter. Dissolved organic matter (DOM) was assessed as dissolved organic carbon (DOC) using a Shimadzu TOC-L analyzer, after filtration through pre-combusted GF/F filters (0.7 µm pore size) to remove particulate organic matter. Quality control was maintained using certified reference materials and blanks for each analysis.

Water depth and sediment thickness were measured at the end of the sampling process to prevent sediment disturbance. Maximum pond depth was determined from multiple depth measurements taken along two perpendicular transects, spaced approximately 2 m apart. Sediment thickness was measured at three locations at the deepest point using a measuring stick, which was lowered into the water until it reached the soft sediment and then the hard substrate. Sediment thickness was then calculated as the difference between these two measurements. The proportion of emergent vegetation present within each pond was assessed visually to the nearest 5%.

*Land-cover assessment*

Land cover around each pond was defined for three different spatial scales: 5 m, 500 m, and 5000 m, each serving distinct purposes. To evaluate the effect of the 5 m buffer strip on the physical and chemical characteristics of the ponds, land-cover fractions within this buffer were visually classified into seven categories: forest, pasture, open natural areas, aquatic environments, arable, urban areas, and intensively managed grasslands. For analysis, arable land, urban areas, and intensively managed grasslands were excluded, and the remaining categories were combined into a new variable, termed 'Buffer Strip' which represented the percentage of natural land cover in the buffer zone.

Land-cover fractions within a 500 m perimeter of each pond were analyzed to assess the immediate land cover surrounding each pond and to relate it to pond nutrient concentrations. In contrast, land-cover fractions within a 5000 m perimeter were used to determine the dominant land cover for each pondscape. This was achieved by summing the land-cover fractions across all ponds in each pondscape. While some fractions may have been counted multiple times for closely spaced ponds, the approach emphasized the overall influence of land cover on individual ponds within the pondscape. Land-cover fractions within 500 m and 5000 m of each pond's perimeter were calculated using the ESA World Cover 10 m 2021 v200 map (Zanaga et al., 2022). Land-cover classes were consolidated into five categories to ensure data consistency: Aquatic—encompassing all water bodies such as ponds, lakes, rivers, streams, reservoirs, coastal waters, wetlands and flooded areas—, Cropland, Forest, Pastures/Open Nature, and Urban.

*Livestock intensity*

The density of large animals interacting with the ponds was quantified through on-site assessments of the presence and activity of both livestock and wild animals (especially wild boar, deer, and foxes) during the sampling periods and from direct information provided by farmers, where available. Animal presence was classified into four intensity levels (none, low, moderate, high). Livestock and wild animals were combined into a single 'Livestock' variable, with seven levels (0 to 6), derived by summing the level of both categories and indicating increasing frequency and intensity of animal visits and hence animal-associated disturbance. This variable represents increasing frequency and intensity of animal visits, and thus the potential for disturbance; however, we acknowledge that this method is subject to observer biases and seasonal variation, which may influence the accuracy of animal presence and activity estimates.

*Hydroperiod classification*

Pond hydroperiod was categorized as permanent, semi-permanent (permanent but dries out once every several years) or temporary. Permanent ponds retained water year-round, while temporary ponds dried out annually for several months. Hydroperiod

classifications were based on periodic observations conducted both during and prior to the sampling year, in combination with data from temperature and/or water-level loggers (Hobo U2OL-0x, Onset Brands). A temperature logger was placed in the deepest part of each pond, while another logger, designed to measure air temperature, was positioned in the shade near the pond but outside of the water. A pond was considered dry when the temperature readings from both loggers differed by less than 5 ºC for more than two consecutive days. Although the 5 ºC threshold was not empirically tested, visual examination of the temperature plots confirmed that this criterion reliably indicated the occurrence of pond desiccation.

*Climatic data*

Bioclimatic data for each pond were obtained from the Copernicus Global Land Service dataset, which provides historical reconstructions of bioclimatic indicators at a resolution of 1 × 1 km for Europe and ~ 55 × 55 km for Uruguay (where no regional data were available) for the period 1979–2018 (Wouters, 2021). Using the nearest-neighbor method, we extracted the daily values of the nearest cell for each pond location (Pebesma & Bivand, 2023). We considered a range of climatic variables, based on a 40-year average (1979–2018): annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, annual precipitation, precipitation seasonality, and precipitation of the driest quarter. Additionally, to better reflect the conditions during the study period, we used seasonal (spring, summer, and autumn) mean temperature and accumulated precipitation data from 2021 and 2022.

## Statistical analysis

All statistical analyses were conducted using R version 4.4.1 (R Development Core Team, 2024).

*Data preparation and transformation*

All ponds were sampled three times per year—during spring, summer, and autumn—across one or two years. Data were subsequently analyzed by both season and year to assess temporal variation in nutrient concentrations. Data distributions were assessed for normality using the *fitdistrplus R* package (Delignette-Muller & Dutang, 2015) and established methods for identifying distributions (Cullen & Frey, 1999). Variables were considered highly skewed based on the visual inspection of distribution plots (e.g., Cullen–Frey plots and histograms, Fig. SM1) and quantitative metrics such as skewness and kurtosis. To standardize data for downstream analyses, variables were normalized using the *bestNormalize R* package, with quantile normalization applied specifically to those identified as highly skewed. Finally, z-scores were applied to standardize all predictor variables for modeling purposes.

*Principal component analysis (PCA)*

PCA was conducted to separately visualize the variation among ponds for three groups of variables: (i) physical and chemical, (ii) climate, and (iii) land-cover types. The analysis was performed using *prcomp* function from the base stats R package. To visualize the results, a PCA biplot was created using the *fviz_pca_biplot* function.

*Boosted regression tree (BRT) modeling*

To identify the key factors driving eutrophication, as represented by the physical and chemical PC2 (see Results section for further details), we used Boosted Regression Trees (BRTs) and Generalized Linear Mixed Models (GLMM).

BRTs were implemented using the *gbm* R package (Ridgeway & GBM Developers, 2024) and functions from Elith et al. (2008) to identify the most informative drivers of TN and TP in ponds with non-linear interactions between predictors. The model was calibrated with a bag fraction of 0.75, a learning rate of 0.001, and a tree complexity of 3. TN and TP were the response variables, modeled using Gaussian error distribution and log10-transformed values to improve residual distribution and model stability. Predictor variables in the BRT models were left untransformed, as BRTs inherently handle non-linear relationships (Elith et al., 2008), and included i) pond characteristics: pond area, maximum depth, presence of thermal stratification, hydroperiod (as categorical variable) and percentage of emersed vegetation; ii) land-cover/use categories: proportion of aquatic habitat, cropland, forest, pastures and open nature, urban

area within a 500 m radius, natural area within 5 m buffer strip, and a livestock intensity index; iii) climatic variables: mean seasonal temperature and total of seasonal precipitation; and iv) temporal factors: season and year (both included as categorical variables) (Table 1). Cross-validation via *gbm.step* determined the optimal number of trees (5000). Variable importance was determined based on predictor selection frequency, weighted by variance reduction, and expressed as a percentage. Partial dependence plots were used to visualize the marginal predictor effects.

*Generalized linear mixed models (GLMM)*

To complement the flexible, non-parametric inference from the BRT models, GLMM (Bolker et al., 2008; Harrison et al., 2018) were employed to quantify the statistical significance of individual predictors and account for the spatial structure of our dataset (ponds and pondscapes within countries). This approach mitigates the confounding effects of country-level differences in management practices, land cover (e.g., higher forest cover in Switzerland and Spain), and climate (since we did not select sites with strong climatic gradients within countries). By controlling for these countrywide differences, we ensured that any remaining patterns reflected robust, generalized relationships rather than country-specific influences, even when the climatic signal is weakened. The inclusion of random effects and interaction terms further refined our exploration of how local factors, such as land cover and pond characteristics, shaped nutrient concentrations (TN, TP).

**Table 1** Summary of morphometric (mean annual values), physical and chemical parameters (mean annual values), climatic factors, and land cover percentages within a 500 m perimeter around each pond, and livestock intensity of the studied ponds

| Variable | Units | Mean (SD) | Median (Q1/Q3) | Minimum | Maximum |
|---|---|---|---|---|---|
| Pond area | m2 | 1771 (4206) | 646 (286/2000) | 13 | 55,792 |
| Pond depth | cm | 105 (87) | 84 (52/130) | 9 | 510 |
| pH | | 7.4 (0.7) | 7.5 (7.0/7.8) | 2.9 | 9.0 |
| Dissolved oxygen concentration | mg/L | 5.8 (3.1) | 5.6 (3.5/8.0) | 0.2 | 19.0 |
| Dissolved oxygen saturation | % | 62 (34) | 60 (37/83) | 2 | 220 |
| Sediment thickness | cm | 19 (24) | 11 (4/24) | 0 | 145 |
| Conductivity | µS/cm | 457 (436) | 327 (176/571 | 21 | 2795 |
| Alkalinity | meq/L | 7.4 (13.3) | 2.9 (1.6/5.3) | 0.1 | 73.7 |
| Total suspended solids (TSS) | mg/L | 49 (154) | 17 (8/33) | 0 | 1924 |
| Total nitrogen (TN) | mg/L | 1.95 (1.29) | 1.62 (0.95/2.58) | 0.30 | 7.97 |
| Total phosphorus (TP) | mg/L | 0.36 (0.52) | 0.19 (0.08/0.37) | 0.02 | 3.71 |
| Dissolved organic matter (DOC) | mg/L | 17.3 (14.0) | 13.3 (9.4/20.9) | 1.1 | 109.5 |
| Annual Mean Temperature | ºC | 11.4 (2.5) | 10.6 (9.6/12.4) | 7.9 | 16.7 |
| Max Temperature of Warmest Month | ºC | 24.7 (3.5) | 24.5 (21.55/26.6) | 18.8 | 32.2 |
| Temperature Annual Range | ºC | 16.9 (4.1) | 16.8 (13.3/18.8) | 8.0 | 25.9 |
| Annual Precipitation | mm | 925 (320) | 823 (699/1139) | 435 | 1615 |
| Hydroperiod | 0: permanent, 1: semi-permanent, 2: temporary | 0.3 (0.4) | 0 (0/1) | 0 | 2 |
| Thermal stratification | 0: no, 1: yes | 0.4 (0.3) | 0.3 (0/0.7) | 0 | 1 |
| Emersed vegetation | % | 32 (27) | 22 (10/42) | 0 | 100 |
| Aquatic | % | 1.6 (5) | 0 (0/0.3) | 0 | 39 |
| Pastures and open nature | % | 36 (28) | 29 (13/52) | 1 | 99 |
| Forest | % | 31 (28) | 19 (9/46) | 0 | 98 |
| Urban | % | 0.02 (0.05) | 0 (0/0.02) | 0 | 0.5 |
| Cropland | % | 29 (27) | 22 (4/52) | 0 | 96 |
| Livestock intensity | 0: none, 6: high | 1.6 (1.4) | 1 (0/2) | 0 | 6 |

GLMM provide a flexible approach by allowing the response variable to follow different distributions from the exponential family, linking its mean ($\mu$) to the explanatory variables via a linear predictor, and partitioning variance in nutrient concentrations. This framework allowed us to examine how factors at different spatial scales (ponds, pondscapes, and countries) affect nutrient concentrations.

$$g\left(E\left(y_{ij}\right)\right) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \cdots + \beta_k x_{kij} + b_i$$

where $g(\cdot)$ is the link function, $E\left(y_{ij}\right)$ is the expected value of the response variable for observation $j$ in group $i$, $\beta_0$ is the intercept, $\beta_k$ are the fixed effect coefficients for predictors $x_{1ij}, x_{2ij}, \cdots x_{kij}$, and $b_i$ represent random effect for group $i$. For the nutrient's models, we used Gaussian distribution with an identity function and log-10 transformation. The same set of predictors used in the BRT models was applied in this analysis, but continuous variables were first transformed to approximate normality and then standardized to z-scores to enable comparison of their relative contributions to the response variables. Multicollinearity among the predictors was assessed to ensure robust model estimation (Graham, 2003; Vatcheva et al., 2016). Pairwise Pearson's correlation coefficients were calculated for predictors (Fig. SM2). Fixed effects included the interaction between season and each of the following variables: depth, hydroperiod, land cover, thermal stratification, and emersed vegetation. Random effects were specified by country, pondscape, and pond. The GLMM were conducted using the *lmer* functions in the *lme4* R package (Bates et al., 2015).

Variance Inflation Factors (VIFs) were computed for all predictors. Variables with VIFs greater than 5 were iteratively removed to reduce multicollinearity while also preserving key explanatory variables.

The total variance $\mathrm{Var}\left(y_{ij}\right)$ is partitioned as

$$\mathrm{Var}\left(y_{ij}\right) \approx \mathrm{Var}_{\mathrm{fixed}} + \mathrm{Var}_{\mathrm{random}} + \mathrm{Var}_{\mathrm{residual}}$$

where $\mathrm{Var}_{\mathrm{fixed}}$ is the variance explained by the fixed effects $\beta_k$, $\mathrm{Var}_{\mathrm{random}}$ is due to the random effect, and $\mathrm{Var}_{\mathrm{residual}}$ is due to residual variance.

*Model selection and interpretation*

To determine the best-performing models, we used stepwise model selection (*step* in the *lmerTest* R package, Kuznetsova et al., 2017), based on the Satterthwaite method for degrees of freedom estimation, which ensures more accurate p value calculations for mixed-effects models by accounting for the random effects structure. Additional evaluation criteria included adjusted R-squared and explained variance. For each model, the significance of factors was assessed using *F*-statistics and *p* values. The significance level was set at $p < 0.05$ for all statistical analyses. The performance of the models was further evaluated through fivefold cross-validation using the *cv* function from the cv *R* package (Fox & Monette, 2025). For models with the Gaussian family, residual normality was tested using the Shapiro–Wilk test, where a $p > 0.05$ indicates that the residuals do not significantly deviate from normality, thus satisfying the assumption of normality. No overdispersion was detected (threshold set as 1). Due to the limited sample size for sediment thickness (164 ponds), this variable was modeled separately using the same model structure to assess its effect on TN and TP.

*Simple linear regression analysis*

To further explore the influence of cropland on pond nutrient concentrations, we examined the relationship between TN and TP (log10-transformed) relative to the percentage of cropland within a 500 m radius around each pond. These relationships were examined for different dominant pondscape land-cover types, including cropland, pastures and open natural areas, forest, and aquatic habitats. The dominant land-cover type in each pondscape was determined based on land-cover proportions within a 5000 m radius. By examining these relationships, we aimed to elucidate the potential impact of agricultural activities on pond water quality across different landscape contexts.

## Results

General description of the ponds

The studied ponds exhibited diverse physical and chemical characteristics (Table 1, Fig. SM3-5), revealing two principal gradients (Fig. 2). The first (PC1, 28.6% explained variance) largely reflected a eutrophication gradient, with negative values associated with increased TN, TP, and DOC, and

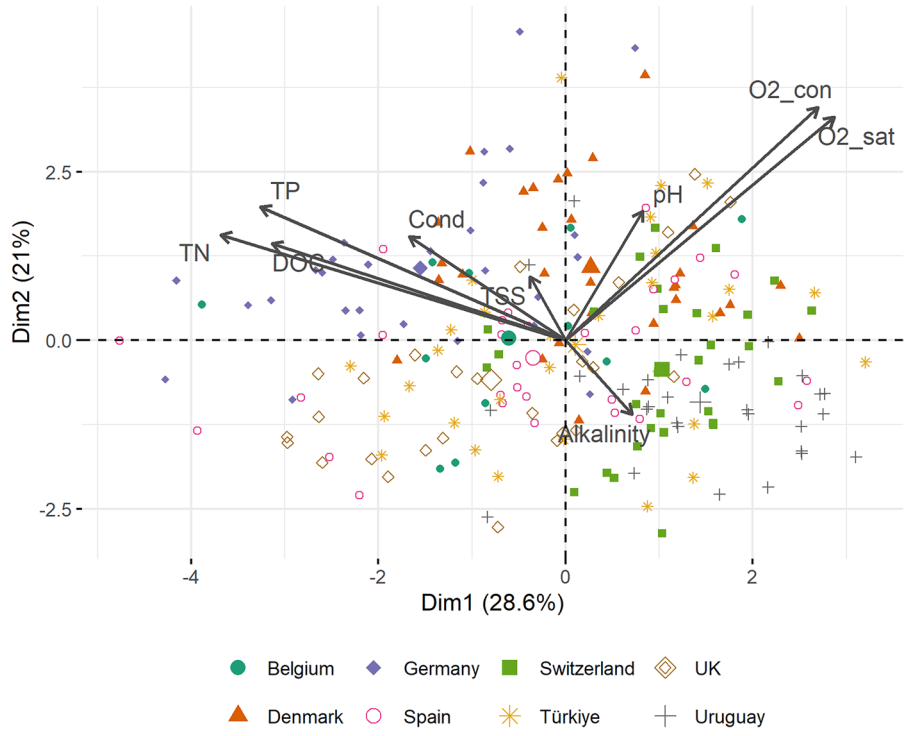


**Fig. 2** The first two ordination axes of a Principal Component Analysis (PCA) based on standardized mean annual physical and chemical variables in the ponds (points). The larger symbols in the plot represent the centroids (group means) for each country, indicating the central tendency of that group in the ordination space. For abbreviations, see Table 1

positive values associated with oxygen concentration. The second (PC1, 21.0% explained variance) represented a water chemistry gradient, primarily driven by conductivity and alkalinity, with potential influences from geological factors and climatic conditions.

The PCA ordination based on land cover within a 500 m perimeter around the ponds identified two major gradients (Fig. SM6-7). PC1 (30.7% explained variance) and separated ponds surrounded by forest (dominant in Spain and Switzerland) from those in more open landscapes, such as pastures and natural areas (dominant in Türkiye and Uruguay). PC2 (28.2% explained variance) was strongly associated with cropland and urban land cover. Livestock intensity varied latitudinally, being highest in Uruguay and Türkiye and lowest in Denmark and the UK (Fig. SM7B).

Climatic variables effectively differentiated the ponds by country (Fig. SM8). PC1 (48%) captured differences in temperature and precipitation across regions, with Türkiye characterized by pronounced seasonal extremes, while the UK and Denmark exhibited moderate annual mean temperature and higher precipitation. PC2 (29%) was driven by annual mean temperature, with Denmark the coolest and Uruguay and Spain the warmest climates.

## Relation between TN and TP, and pond characteristics, land cover, and climate

Modeling TN with the BRT explained 62% of the variance among ponds, with cropland cover (22% of relative explained variance) and pond depth (13%) as the stronger predictors (Fig. 3 & SM9). For TP, the model explained 59% of the variance being primarily driven by forest cover (21%), cropland cover (12%), and pond water depth (11%) (Fig. 3 & SM10). The TN and TP models showed a cross-validated variance of 0.052 (±0.004 SE) and 0.141 (±0.007 SE) and cross-validated correlations of 0.669 (±0.025 SE) and 0.643 (±0.024 SE), respectively. Partial dependence plots revealed that, for both TN and TP, concentrations were highest in ponds shallower than 1 m. Cropland impact peaked around 50% coverage, with a stronger effect on TN than on TP, while inflection points for other variables were less distinct. TN concentrations were highest in summer, and both semi-permanent and temporary ponds exhibited higher TN and TP levels than permanent ponds.

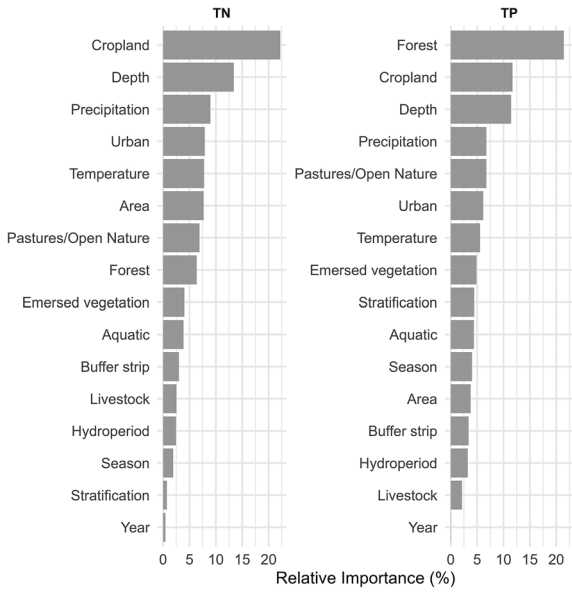


**Fig. 3** Relative importance of predictor variables in Boosted Regression Tree (BRT) models for total nitrogen (TN) and total phosphorus (TP) across ponds. Variable importance is based on the frequency and improvement of splits across all trees in the BRT model. The order of variables is independent for each panel and reflects their importance in the respective nutrient model. Partial dependence plots for these variables are shown in Figs. SM9-10

To further quantify the statistical significance of predictors and account for data hierarchy, we used GLMM (Table 2, Fig. 4). For TN, cropland proportion within 500 m, livestock intensity, and thermal stratification had positive effects, while pond depth and precipitation had negative effects. For TP, positive influences were found for cropland and livestock intensity, with pond depth negatively affecting TP concentrations. Seasonal interactions indicated that TN concentrations were lowest in spring in semi-permanent ponds, while TP peaked in summer, particularly in larger ponds. Random effects for pond, pondscape, and country accounted for spatial structure. Local factors (pond and pondscape) explained 37.5% (25% + 12.5%) of TN and 35% (25% + 10%) of TP variance, while country-level effects explained 12.5% of TN and 20% of TP variance. Incorporating country-level random effects accounted for differences in management practices among countries, which were confounded in the BRT models. However, they also accounted for climatic and land cover variability (e.g., temperature and forest cover), which was difficult to distinguish within countries due to weak climatic gradients, ultimately leading to their exclusion from the GLMM. $R^2$ values were 0.13 (marginal) and 0.60 (conditional) for TN, and 0.12 (marginal) and 0.62 (conditional) for TP.

Linear models showed that cropland consistently increased TN and TP concentrations across most land-cover types, except in forest-dominated landscapes (both for TN and TP) and pastures/open nature (for TP), where no significant effect was observed (Fig. 5). The sediment thickness model was excluded from the full models due to insufficient data, showing no significant relationships with TN or TP when modeled independently (Table SM1).

## Discussion

Our study reveals the complex interplay among land cover, internal pond features, climate, and seasonal dynamics influencing nutrient concentrations in ponds located in contrasting climatic regions. Land use was a key determinant of both TN and TP, with cropland cover and livestock intensity consistently associated with elevated nutrient concentrations, whereas forested land appeared to buffer TP enrichment. Pond-specific characteristics also played a critical role, with shallower ponds showing higher TN and TP, and both hydroperiod and thermal stratification being associated with higher TN. Climatic factors had context-dependent impacts, varying according to country-scale land use patterns and hydrological dynamics. Seasonally, TP concentrations were highest in summer, while TN declined in semi-permanent ponds during spring, likely due to water-level fluctuations and dilution processes.

### Pond depth, hydroperiod, and internal processes as key drivers of TN and TP

Pond depth emerged as a key predictor of variation in TN and TP concentrations, with hydroperiod and thermal stratification providing additional explanatory power for TN. Shallow lakes typically exhibit higher nutrient concentrations than deeper systems due to increased contact between sediments and the water column, promoting internal nutrient release and recycling (Søndergaard et al., 2005; Serrano et al., 2017; Richardson et al., 2022). However, the degree

**Table 2** Best-fit Generalized Linear Mixed Models (GLMM) output for total nitrogen (TN) and total phosphorus (TP), including-pond, pondscape and country as random effects

| Fixed effects | TN | | | TP | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 0.16 | 0.05 – 0.26 | **0.003** | − 0.81 | − 0.96 – − 0.66 | **< 0.001** |
| S. [Spring] | − 0.02 | − 0.06 – 0.03 | 0.534 | − 0.03 | − 0.08 – 0.03 | 0.381 |
| S. [Summer] | 0.01 | − 0.04 – 0.06 | 0.738 | 0.17 | 0.11 – 0.23 | **< 0.001** |
| Cropland | 0.06 | 0.02 – 0.10 | **0.003** | 0.11 | 0.05 – 0.17 | **< 0.001** |
| Hydroperiod [Semi-permanent] | 0.05 | − 0.04 – 0.15 | 0.298 | | | |
| Hydroperiod [Temporary] | 0.05 | − 0.08 – 0.18 | 0.457 | | | |
| Pond Depth | − 0.04 | − 0.08 – − 0.01 | **0.015** | − 0.10 | − 0.15 – − 0.06 | **< 0.001** |
| Pond Area | | | | − 0.00 | − 0.06 – 0.06 | 0.939 |
| Precipitation | − 0.04 | − 0.07 – − 0.01 | **0.006** | | | |
| Thermal stratification[Existence] | 0.04 | 0.01 – 0.08 | **0.022** | | | |
| Livestock | 0.06 | 0.02 – 0.10 | **0.003** | 0.08 | 0.02 – 0.13 | **0.010** |
| S. [Spring] × Hydroperiod [Semi-permanent] | − 0.09 | − 0.18 – − 0.00 | **0.040** | | | |
| S. [Summer] × Hydroperiod [Semi-permanent] | 0.01 | − 0.08 – 0.10 | 0.822 | | | |
| S. [Spring] × Hydroperiod [Temporary] | − 0.09 | − 0.20 – 0.02 | 0.111 | | | |
| S. [Summer] × Hydroperiod [Temporary] | 0.09 | − 0.04 – 0.22 | 0.159 | | | |
| S. [Spring] × Pond Area | | | | − 0.01 | − 0.06 – 0.05 | 0.834 |
| S. [Summer] × Pond Area | | | | 0.08 | 0.02 – 0.14 | **0.013** |
| Random Effects | | | | | | |
| $\sigma^2$ | 0.04 | | | 0.09 | | |
| $\tau_{00\ Pond}$ | 0.02 | | | 0.05 | | |
| $\tau_{00\ Country:Pondscape}$ | 0.01 | | | 0.02 | | |
| $\tau_{00\ Country}$ | 0.01 | | | 0.04 | | |
| ICC | 0.57 | | | 0.54 | | |
| $N_{Pond}$ | 228 | | | 228 | | |
| $N_{Country}$ | 8 | | | 8 | | |
| $N_{Pondscape}$ | 41 | | | 41 | | |
| Observations | 681 | | | 681 | | |
| Marginal $R^2$/Conditional $R^2$ | 0.116/0.617 | | | 0.132/0.598 | | |

The models used a normal distribution with an identity function and log-10 transformation, with predictors transformed for normality and standardized for direct effect size comparison

The models were trained using data from 228 ponds across all sampled countries and validated using fivefold cross-validation, as described in the Methods section

Statistically significant variables ($p < 0.05$) are highlighted in bold. S. stands for Season

to which this finding applies to small ponds is little understood. While wind-driven mixing of sediments is traditionally considered unlikely due to limited fetch, the open landscapes surrounding our study sites may increase effective fetch, potentially contributing to the area-related increase in summer TP concentrations observed in this study.

Additionally, multiple mechanisms, including water-level fluctuations, thermal stratification, benthic activity, and sediment disturbance by large-bodied fauna, could explain the relationship between water depth and nutrient concentrations in ponds. Semi-permanent ponds showed lower TN concentrations in spring, likely driven by dilution from rising water levels. This aligns with previous findings reporting pronounced seasonal fluctuations in temporary waters (Calzada-Bujak et al., 2001; Badosa et al., 2006; Coppens et al., 2016; Quintana et al., 2018). Despite

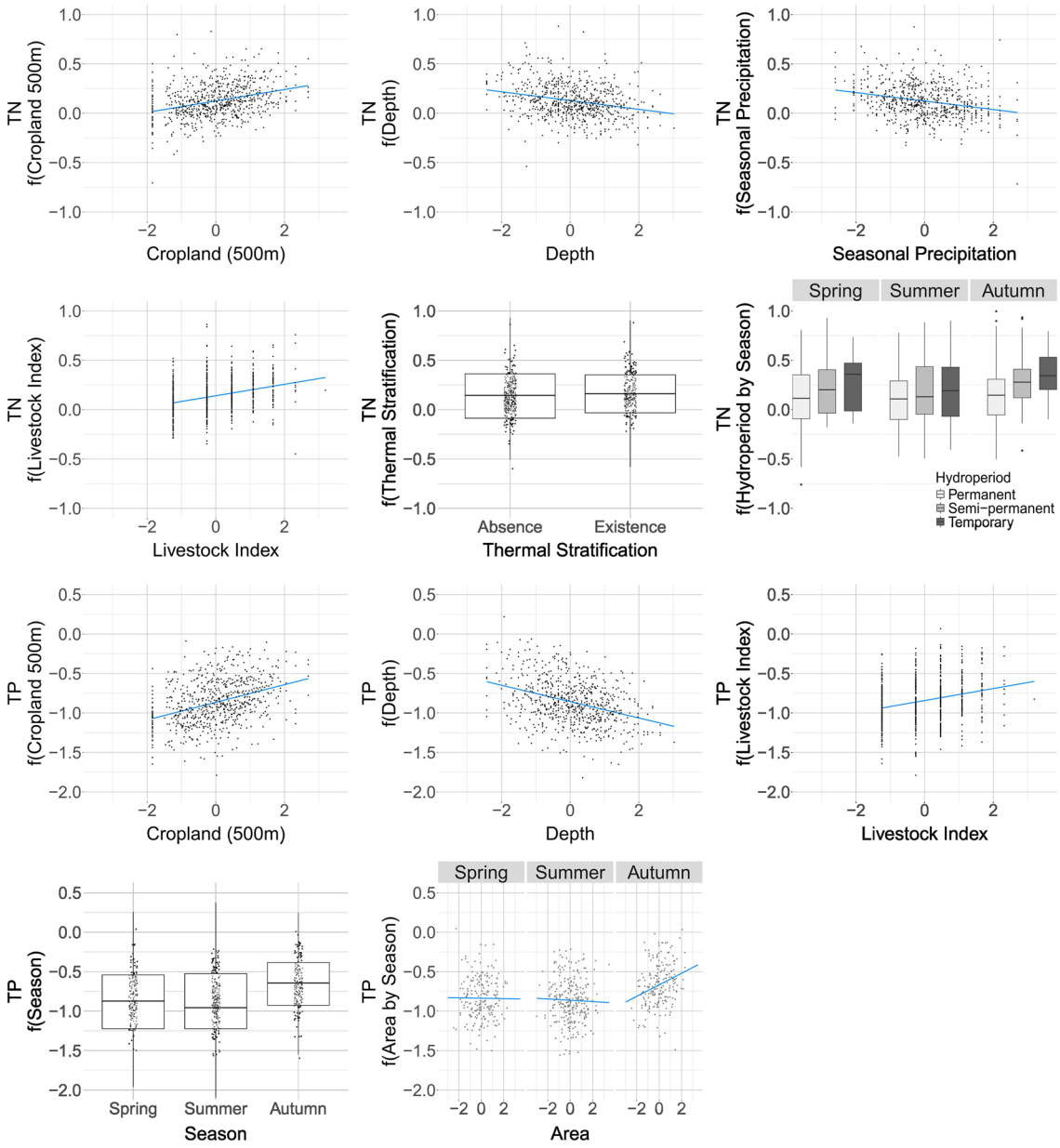


**Fig. 4** Partial residual plots for fixed effect predictors in best-fit generalized linear mixed models (GLMM) ($p < 0.05$) for total nitrogen (TN) and total phosphorus (TP). Partial residuals illustrate the influence of key predictors on nutrient concentrations. The blue lines represent the estimated regression coefficients

potential nutrient losses during dry phases—through processes such as mineralization, ammonia volatilization, and denitrification (Sahuquillo et al., 2012)—such patterns were not evident in our data. This suggests that desiccation may reduce organic matter without preventing nutrient enrichment, particularly when external inputs or internal recycling persist.

Thermal stratification, even in small, shallow systems, was positively associated with TN concentrations, likely due to enhanced sediment nutrient release under anoxic bottom conditions. This interpretation is supported by our PCA results showing a negative relationship between dissolved oxygen and both TN and TP (Fig. 2), consistent with

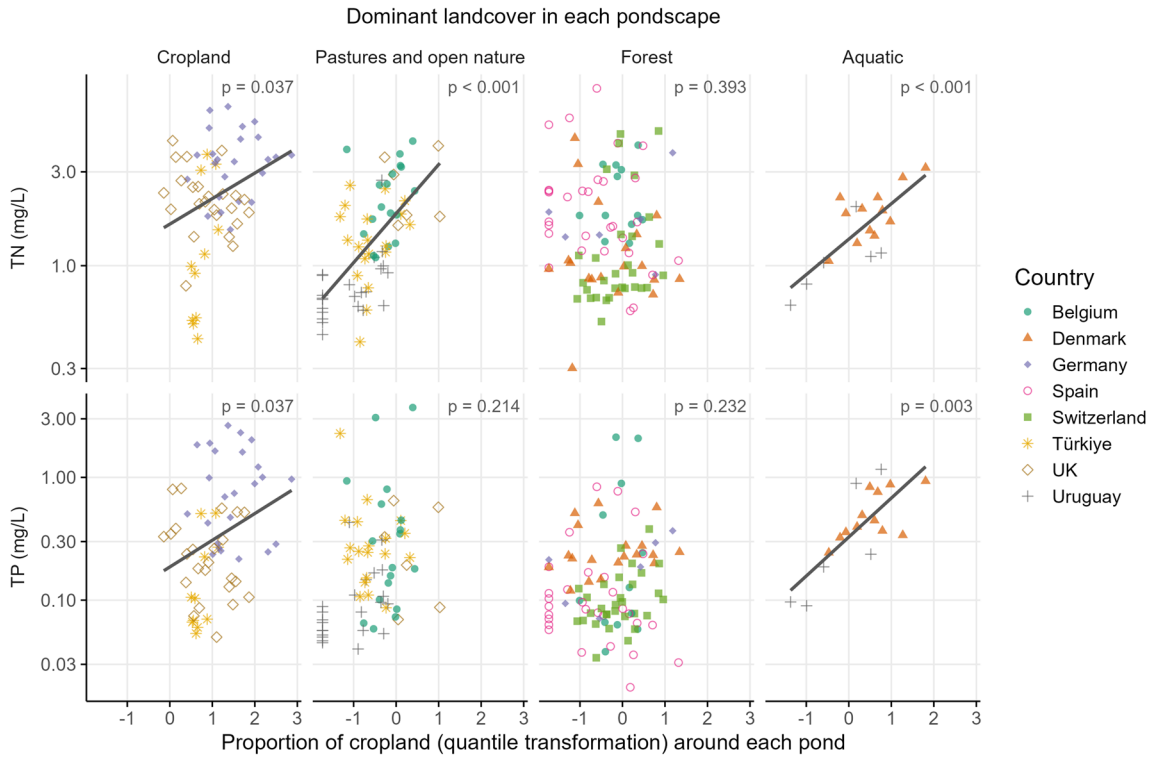


**Fig. 5** Change in total nitrogen (TN) and total phosphorus (TP) concentrations (y-axis is log10-transformed) relative to the percentage of cropland surrounding ponds, shown for different dominant pondscape land-cover types: cropland, pastures and open natural areas, forest, and aquatic habitats. The percentage of cropland was adjusted using quantile transformation and centering

prior observations in small water bodies (Holgerson et al., 2022).

Elevated biological activity in shallow ponds may also play a critical role in accelerating nutrient cycling. Temperature fluctuations drive microbial processes (Jeppesen et al., 2021) and benthic infauna activity, enhancing bentho-pelagic coupling and sediment nutrient remineralization (Farrell et al., 2024). Shallow systems are also more prone to sediment disturbance from large-bodied domestic (e.g., cattle, horses) and wild fauna (e.g., wild boar, deer) that may resuspend sediments and release stored nutrients into the water column, hence further amplifying nutrient cycling dynamics. These disturbances, combined with livestock presence, likely amplify nutrient cycling in shallow systems, as reflected in our data. Further, focused studies of pond physical–chemical processes will be required to understand the mechanisms that drive water depth–nutrient relationships for ponds. Given climate change-driven shifts in hydroperiod regimes, pond loss, and depth reductions observed across diverse biomes (Smol & Douglas, 2007; Zacharias & Zamparas, 2010; Yılmaz et al., 2021), the need for further studies in this area is highlighted, with the possibility raised that increased prevalence of drought may have important implications for nutrient dynamics and hence pond ecosystem stability and conservation.

## Effect of land cover and livestock intensity on TN and TP in ponds

Land cover within a 500 m radius was a key factor determining TN and TP concentrations in the investigated ponds, with no consistent seasonal effect observed. This observation is in line with earlier studies of both lakes (Carpenter et al., 1998) and ponds (Novikmec et al., 2016; Jarosiewicz et al., 2018). In our study, ponds surrounded by cropland had median TN concentrations 1.6 times higher, and median TP

concentrations 2 times higher than ponds in pastures, open nature, or forest-dominated landscapes (Fig. SM11). This observation likely results from a combination of fertilizer application and enhanced soil erosion from plowing on agricultural land (Montanarella et al., 2015), which increase nutrient concentrations in surrounding waterbodies, exacerbated by surface and subsurface runoff (Calvo et al., 2024). Sites were selected without inflows (e.g., ditches or field drains), which could have influenced nutrient inputs if present. Additionally, intensive and/or unregulated agricultural uses often lead to the reduction or loss of the natural riparian vegetation that can partially mitigate such inputs (Calvo et al., 2024). Livestock intensity also contributed to elevated TN and TP levels in ponds, despite the challenges in quantifying its impact, given livestock rotation and spatial shifts. Nutrient inputs from livestock arise primarily from manure and soil disturbance (Hooda et al., 2000; Odebiri et al., 2024).

In contrast, forests in the 500 m radius surrounding the ponds mitigated nutrient pollution. Acting as natural buffers, forested areas absorbed and stored nutrients (Vitousek & Reiners, 1975), while forest soils, rich in organic matter and root density, may further reduce nutrient transport by trapping nitrogen and phosphorus and slowing runoff (Binkley & Fisher, 2012; Calvo et al., 2024). However, dense forests can also contribute organic matter from leaf fall, potentially increasing anoxia in ponds (Stoler & Relyea, 2020). This effect was primarily captured by the BRT, as forested areas around ponds were dominant only in certain countries (Fig. SM7), and therefore, the spatially structured GLMM did not detect them.

## Climatic and seasonal modulation of TN and TP in Ponds

Seasonal patterns revealed that TP concentrations peaked consistently in summer, while TN concentrations were lowest in spring, especially in semi-permanent ponds. These patterns are likely driven by higher water levels in spring, resulting from increased precipitation and lower temperatures, which contribute to the dilution of solutes. Supporting this interpretation, TN concentrations were negatively correlated with precipitation. While greater precipitation typically increases nutrient loading via catchment runoff in larger freshwater systems (Michalak, 2016), smaller systems like ponds may respond differently. In regions with consistent and prolonged precipitation (e.g., the UK, Denmark and Switzerland), enhanced flushing and runoff can lead to nutrient dilution (Robotham et al., 2021), particularly where nutrient sources are diffuse or relatively low (Goyenola et al., 2015; Ockenden et al., 2017). Conversely, in dry climates or during summer, reduced precipitation and high evaporation can concentrate nutrients due to reduced water volumes and enhanced internal nutrient cycling (Coppens et al., 2016).

The influence of climatic factors on nutrient dynamics is highly context-dependent, shaped by regional variation in climate, land use, and management practices (Sterly et al., 2018). Climate change may intensify these interactions by increasing temperature and altering precipitation regimes (Birk et al., 2020). These changes are expected to enhance nutrient mobilization, increase runoff intensity and nutrient loads from non-point sources, and prolong thermal stratification in standing waters, thereby exacerbating eutrophication and its associated symptoms (Moss et al., 2011; Sinha et al., 2017; Meerhoff et al., 2022). Higher temperatures can also promote algal blooms, anoxia, and internal nutrient cycling (Woolway et al., 2022). Additionally, freshwater eutrophication may contribute to climate change through feedback loops involving greenhouse gas emissions (Davidson et al., 2018; Meerhoff et al., 2022).

## Multiscale drivers of TN and TP in ponds

The GLMM revealed significant variation in TN and TP concentrations at both local (pond and pondscape) and country scales. Local-scale variance (37.5% of TN and 35% of TP), attributed to pond and pondscape characteristics (e.g., season, depth, dominant land cover), highlight their importance in regulating nutrient concentrations within ponds. Country-level differences explained 12.5% of TN and 20% of TP variance, likely reflecting broader patterns in land cover and climate not captured by within-country variables. For example, the elevated TN concentrations observed in Germany may reflect more intensive agricultural management, while lower TN levels in Switzerland and Spain could be linked to higher forest cover and less intensive land use, which likely reduce nutrient inputs to ponds. The absence of a strong climate signal in the GLMM is consistent with the weak

climatic gradients within countries. Overall, these findings underscore the combined influence of local features and country-specific management regimes on nutrient dynamics in pond ecosystems.

## Conclusions

This study demonstrates that nutrient concentrations (TN and TP) in ponds are shaped by the combined influence of internal pond characteristics and land use. Shallower ponds with shorter hydroperiods and with thermal stratification exhibited higher nutrient concentrations, reflecting the importance of internal biogeochemical processes. Land use—particularly agricultural and forested land cover, and livestock intensity—also influenced nutrient levels, with effects varying by region and likely shaped by underlying land management practices. Seasonal and climatic variability further modulated nutrient concentrations, potentially through precipitation-driven dilution or concentration effects, depending on pond hydrology and regional context. These findings underscore the vulnerability of ponds to ongoing climate change and land use intensification, which are expected to reduce water levels, disrupt stratification regimes, and increase nutrient accumulation, thereby exacerbating nutrient imbalances and disrupting ecosystem dynamics. To better predict and manage nutrient concentrations in ponds and pondscapes, both internal and external drivers must be integrated. Future research should prioritize fine-scale, pond-level studies across broad spatial gradients to capture the ecological variability often masked in coarser-scale analyses, thereby improving our capacity to understand, model, and mitigate nutrient imbalances in these critical freshwater systems.

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**Data availability** The datasets used in this study are available upon reasonable request.

### Declarations

**Conflict of interest** The authors declare no conflict of interest.

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