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Research Paper

Land use and environmental drivers of nutrients and primary production in 49 inland and coastal saline lakes of semi-arid Türkiye*

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Abstract Saline lakes are increasingly threatened by climate and anthropogenic pressures, yet comparative assessments of nutrients and primary production in inland and coastal saline lakes remain scarce. We assessed 49 saline lakes across semi-arid Türkiye (21 inland, 28 coastal) to identify the main environmental and anthropogenic drivers of physicochemical variables, including nutrients, primary production, and macrophyte percent volume infested (PVI%). Inland lakes exhibited significantly higher nutrient concentrations, particularly total phosphorus (TP) and total nitrogen (TN), with mean values several-fold higher than those in coastal lakes (Wilcoxon test, P<0.001). Inland lakes also tended to have sparse submerged vegetation, likely reflecting more intensive agriculture-dominated catchments, higher evaporative potential and salinization, and lack of hydrological outflow. In contrast, coastal lakes

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maintained lower nutrient concentrations and higher macrophyte PVI%, associated with more heterogeneous land cover and periodic marine connectivity, the latter likely modulating salinity effects and diluting nutrients. Random forest analyses identified land use as the dominant driver of water nutrient concentrations, followed by meteorological variables, and salinity, while water clarity was mainly explained by in-lake nutrient concentrations (TP, TN, and silicate), temperature, and salinity. Across our inland-lake samples, submerged macrophytes were observed only up to a salinity of 3.5 g/L and absent at salinities ≥22.4 g/L (no inland lakes had salinities in between). In coastal lakes, macrophytes persisted up to 43.5 g/L (*Ruppia cirrhosa* (Petagna) Grande), reflecting this species' strong osmoregulatory capacity compared to inland taxa. Our findings underline the divergent ecological trajectories of inland and coastal saline lakes and highlight the need for differentiated management. Conservation strategies should focus on reducing catchment nutrient inputs and water use in inland lakes, as well as on maintaining natural hydrological connectivity and catchment integrity in coastal lakes.

Keyword: climate change; eutrophication; hydrology; macrophyte; water abstraction; salinization

1 INTRODUCTION

Climate change is projected to increase global temperatures and alter precipitation patterns, thereby affecting the hydrological and ecological characteristics of lakes (Core Writing Team et al., 2023). Arid and semi-arid areas, particularly those within the Mediterranean climate zone, are expected to be strongly affected, with predicted precipitation decreases of 25%–40% and temperature increases of 4–5 °C during this century (Carvalho et al., 2022; Zittis et al., 2022). These dryland areas are often subjected to human-induced pressures, such as intensive agriculture with increased water abstraction for irrigation and urbanization purposes, whose adverse ecological consequences are further exacerbated by climate change (Yılmaz et al., 2021; Çolak et al., 2022). Due to increased water abstraction and evaporation, dryland lakes may become more saline or even dry out completely (Jeppesen et al., 2020; Cunillera-Montcusí et al., 2022). Saline lakes account for 44% of the global water volume of large lakes (Messager et al., 2016). They support high biological and environmental diversity due to a wide range of salinities, spanning from oligohaline to saturated brine, that exceed those of seawater (Jolly et al., 2008). Many inland saline lakes have closed basins with little or no surface outflow (Waiser and Robarts, 2009) and consequently experience large seasonal and interannual fluctuations in salinity and water levels, directly impacting their ecosystem structure, productivity, and biodiversity (Jolly et al., 2008; Song et al., 2022).

Coastal saline lakes play a crucial role in land-sea interactions, providing important habitats for various plant and animal species, including migratory birds, fish, and shellfish (Newton et al., 2014). Their structure and functioning are strongly determined by the interplay between water inflows from the basin and exchanges with the sea. Alterations to these fluxes, due to damming, water diversion, changes in groundwater levels, and manipulation of the lake-sea connection, represent significant pressures that affect natural hydrological characteristics, nutrient and sediment transport, and ultimately ecosystem structure and functioning (Newton et al., 2014).

Recent studies have shown that nutrient dynamics in inland and coastal saline systems are shaped by different but partly overlapping hydrological and biogeochemical mechanisms. In Mediterranean inland saline wetlands, catchment nitrogen budgets have highlighted livestock and agricultural pressures as key sources of external nutrient inputs (Tierra et al., 2025). In an endorheic saline lake, salinity-structured denitrifier communities and the denitrification potential indicate salinity-sensitive nitrogen removal (Jiang et al., 2022). In a large shallow hypersaline coastal lagoon, coupled hydrodynamic-biogeochemical modeling revealed that limited connectivity and high evapo-concentration led to persistent nutrient accumulation, underscoring hydrologic flushing as a key regulator of nutrient retention (Huang et al., 2024). In Türkiye, phosphorus mass-balance modeling of the brackish Köyceğiz-Dalyan lake-lagoon system showed eutrophic conditions, sensitivity to external phosphorus loading and reduced freshwater inflow (Aytış et al., 2023), while field observations in Akyatan Lagoon linked hypereutrophic conditions to contaminated riverine nutrient and organic matter inputs (Börekçi et al., 2025). These findings indicate that catchment land use, water abstraction, salinization, and marine

connectivity may interact to shape nutrient dynamics, primary producers, and water clarity in inland and coastal saline lakes.

These recent findings complement earlier studies describing ecological differences between freshwater and brackish shallow lakes along nutrient and salinity-related gradients (e.g., Jeppesen et al., 1994; Moss, 1994; Pfister et al., 2002), but such comparisons remain scarce for inland and coastal saline lakes in semi-arid landscapes, particularly regarding joint effects of salinity, land use, and hydrological connectivity on nutrients and primary producers. Our study addresses this gap by providing a standardized, cross-system comparison of inland and coastal saline lakes, which jointly evaluates the roles of salinity, land use, and hydrological connectivity. Inland saline lakes are highly susceptible to the cumulative impacts of reduced precipitation, increasing temperature, and intensive land use (e.g., agriculture, livestock grazing, irrigation) (Williams, 2002; Yılmaz et al., 2021; Çolak et al., 2022). Such impacts are likely to be partially buffered in coastal saline lakes due to their hydrological connectivity with marine systems, creating comparatively better ecological conditions (Obolewski and Glińska-Lewczuk, 2020). Coastal lakes are often less eutrophic than inland lakes (Newton et al., 2014; Obolewski and Glińska-Lewczuk, 2020). However, there are notable exceptions, such as some delta-associated coastal lakes that receive high nutrient loading primarily from agricultural catchments, resulting in eutrophication (Jeppesen et al., 2007; Christensen et al., 2023). Both inland and coastal saline lakes are increasingly exposed to environmental challenges from climate change, water diversion, pollution, and resource extraction, all of which threaten their biodiversity and ecological integrity. Protecting these vulnerable ecosystems requires urgent, multidisciplinary, ecosystem-based strategies, as they serve not only as biodiversity hotspots but also as environmental sentinels of climate change, as well as providers of socio-economic ecosystem services in a rapidly changing world (Newton et al., 2014; Saccò et al., 2021).

Here, using similar methods, we studied the physicochemical and biological characteristics of 49 saline lakes, comprising 21 inland and 28 coastal lakes across the Mediterranean to the cold semi-arid zone of Türkiye. Climatic projections for this region predict an increase of up to 6.5 °C in average temperatures during the coming decades (Özturk et al., 2015), with potential adverse effects on the ecological status and functioning of the lakes. We assessed key environmental variables, including water transparency, chlorophyll *a*, nutrient concentrations (e.g., total nitrogen, total phosphorus, and silicate), and macrophyte cover (as percent volume infested, PVI%) to obtain an integrated understanding of lake productivity, trophic state, and habitat complexity. Our aim was to assess the primary ecological differences between inland and coastal saline lakes and to identify their key environmental drivers using climatic, morphometric, hydrological-connectivity, and land-use data as explanatory variables. We hypothesized that (1) inland saline lakes, characterized by hydrological closure, stronger evaporative concentrations, and agriculture-dominated catchments, would exhibit higher nutrient concentrations, and lower submerged macrophyte cover than coastal lakes; and that (2) coastal saline lakes would show comparatively lower nutrient concentrations and greater macrophyte persistence because intermittent seawater connectivity and more heterogeneous catchment land cover can partly buffer salinization and eutrophication through enhanced renewal and dilution.

2 MATERIAL AND METHOD

2.1 Study area

Our study encompassed 10 of Türkiye's 25 river basins, thereby providing an extensive environmental gradient in terms of climate, hydrology, and topography, from the semi-arid Anatolian plateau to the Mediterranean coast. We sampled 21 inland (27 stations) and 28 coastal (36 stations) saline lakes (Fig.1). The 21 inland lakes were mainly located within 2 basins: (i) the Konya Closed Basin (KCB), which includes 11 sampled lakes, is the largest endorheic basin of Türkiye (~54 000 km^2, mean elevation 900–1 100 m). It is a wide intramontane depression on the semi-arid Central Anatolian Plateau and mainly consists of Quaternary marl and limestone deposits (Yılmaz et al., 2021; Güz et al., 2025); (ii) the Burdur Closed Basin (BCB), which includes 6 sampled lakes, is a mountainous graben system (6 296 km^2; mean elevation ~1 200 m) formed by Miocene-Pliocene tectonic activity (Çolak et al., 2022). The remaining inland lakes were located in south and west Anatolia (Fig.1), including 3 lakes in the Küçük Menderes River Basin, where intensive agriculture and water abstraction dominate, and 1 lake on Gökçeada



Fig.1 Location of the 28 coastal (yellow circles) and 21 inland (blue circles) study lakes in Türkiye

Major watersheds and drainage basins are also indicated. Lake numbers correspond to the list provided below the map.

Island with a limited catchment and restricted hydrological connectivity, justifying their classification as inland systems despite their proximity to the coast. Significant environmental stressors have been identified in these basins, particularly intensive groundwater and surface water extraction for agricultural irrigation. In KCB, groundwater abstraction for irrigation has increased markedly since the 1970s, with agriculture accounting for over 90% of the total water use, leading to groundwater level declines exceeding 1 m/a, in some areas up to 2 m/a (Yılmaz et al., 2021). In BCB, the irrigation demand reached approximately 253 hm^3/a in 2018, with more than half supplied by groundwater (Çolak et al., 2022). These unsustainable withdrawals have resulted in substantial groundwater depletion, lake shrinkage, or, in some cases, complete drying out of shallow lakes. Both KCB and BCB constitute biodiversity hotspots in Central Anatolia, supporting more than 10% of Türkiye's freshwater fish species, many of which are endemic to this region and highly threatened by habitat loss, groundwater abstraction, eutrophication, and climate change (Korkmaz et al., 2023a). These basins also provide vital habitats for migratory birds, emphasizing their international conservation importance (Özgencil et al., 2025).

The 28 sampled coastal lakes spanned 8 river basins along the Mediterranean and Aegean coasts of Türkiye. Most were located in the Batı Akdeniz River Basin (~21 000 km^2, with 9 sampled lakes), which contains barrier-lagoon complexes characterized by seasonal marine inlets that create pronounced temporal and spatial salinity gradients. Others were located in the Kuzey Ege River Basin (~9 800 km^2, with 7 sampled lakes), which borders the Gulf of Edremit and the Çanakkale Peninsula and consists of lagoons formed by mixed river-deltaic and marine processes. These coastal systems are characterized by dynamic marine-freshwater interactions and diverse biological communities. They provide critical breeding, feeding, and resting habitats for many migratory and resident bird species, including threatened waterbirds (Şekercioğlu et al., 2011; Aslan et al., 2021). Two lakes on Gökçeada Island, Türkiye's largest island in the northern Aegean Sea, were also sampled.

Sampling was conducted during 3 expeditions targeting different geographic subsets of lakes. The first field expedition (5–28 July 2021) focused on the inland lakes of KCB and BCB. The second expedition (18 May–18 June 2022) revisited inland sites, as well as coastal lakes in the Seyhan, Ceyhan, and Göksu river basins. The third field expedition (2–21 May 2023) focused exclusively on coastal lakes in the Batı Akdeniz, Büyük Menderes, Küçük Menderes, Gediz, and Kuzey Ege river basins and the two lakes on Gökçeada Island.

2.2 Catchment delineation and land use analysis

Lake catchments were determined using a 30-m resolution Digital Elevation Model (SRTM). Catchments and sub-basins were delineated in SWAT (Soil and Water Assessment Tool; Arnold et al., 1998) based on topography and stream network analysis. Stream outlets were defined, and flow direction and accumulation were calculated using the D8 algorithm. Each subbasin represented the drainage area to a specific point in the stream network.

Land-use data were derived from the ESA WorldCover product, with 10-m resolution for 2020–2021, based on combined Sentinel-1 and Sentinel-2 satellite data (Global Land Cover Maps; Zanaga et al., 2022). This global dataset has been widely validated and provides reliable land-cover classifications across diverse regions and environmental contexts (Duarte et al., 2023; Lang et al., 2023), and its spatial resolution, thematic accuracy, and land-cover class definitions are considered appropriate for catchment-scale analyses. The 2020–2021 land cover data were selected to provide a representative catchment-scale characterization of land cover for the sampling period. Although a minor temporal mismatch existed because field sampling extended to 2023, catchment-scale land-cover proportions were assumed to remain relatively stable over this short time period. NDVI-based analyses were used to capture interannual variability in vegetation dynamics. Changes in vegetation cover were assessed using the Landsat Collection 2 Tier 1 Level 2 8-day NDVI (Normalized Difference Vegetation Index) composite dataset for 2023, accessed using Google Earth Engine (Gorelick et al., 2017). Landsat-based NDVI products offer a well-established balance between spatial resolution and temporal frequency, making them particularly suitable for basin- and catchment-scale ecological analyses. Lake surface areas were explicitly accounted for in catchment-scale overlay analyses. All spatial overlay and zonal analyses were performed using the Google Earth Engine platform.

2.3 Population

Information on settlement locations within each lake catchment was derived from OpenStreetMap administrative and place layers from Geofabrik shapefiles (Geofabrik, 2025) and then intersected with the delineated catchment polygons to identify districts, neighborhoods, villages, and other administrative units within each catchment. Population data for 2023 were obtained from nufusune.com, which aggregates official settlement-level statistics published by the Turkish Statistical Institute (TÜİK, 2023). Each settlement record was matched to the corresponding spatial unit on an individual basis to avoid duplicates and inconsistencies. For catchments intersecting multiple provinces and administrative units, population information was aggregated following hydrological boundaries: administrative units fully contained within a catchment were included in their entirety, whereas for partially intersecting units, only the settlements located within the catchment boundary were retained based on the spatial overlay. The resulting total population per catchment was used as an indicator of human pressure at the catchment scale.

2.4 Connectivity to the sea

The degree of hydrological connection between the lakes and the sea was assessed using satellite imagery and field observations, employing a semi-quantitative classification approach based on visual interpretation of water exchange features. For each coastal lake, recent satellite images from Google Earth were examined to identify the presence, permanence, and width of surface connections to the sea, including inlets, channels, and seasonal overflow pathways. Based on these observations, the lakes were assigned a connectivity score along a categorical scale ranging from 0 to 4: (0) no visible connection to the sea (includes all inland lakes); (1) connection only during seasonal overflow at high water levels; (2) weak connection with narrow or intermittent channels (<30 m wide, not permanently open); (3) strong connection with clearly defined channels regularly allowing water exchange (>30 m wide, permanent); and (4) fully connected lagoons functioning as extensions of marine waters. This classification enabled us to estimate the relative hydrological connectivity of the study lakes.

2.5 Climate data

Precipitation, air temperature, and total evaporation were obtained from the ERA5-Land reanalysis dataset produced by the Copernicus Climate Change Service (Muñoz Sabater, 2019). ERA5-Land provides high-resolution and internally consistent land-surface climate variables and has been widely applied in regional-scale hydrological and climatological studies (Ekinci and Fıstıkoğlu,

2023; Karaman and Akyürek, 2023). Climate variables were extracted for the same period as the field observations and aggregated at the catchment scale. For each lake, precipitation, temperature, and total evaporation were calculated as area-weighted mean values across the entire catchment using spatial zonal statistics. Total evaporation refers to the ERA5-Land variable integrating evaporation from soil, vegetation, and open water surfaces.

2.6 Lake sampling

The sampling followed the standardized snapshot sampling protocol described by Moss et al. (2003). Sampling was conducted at 63 stations: 27 across 21 inland lakes and 36 across 28 coastal lakes, to capture variability in physicochemical conditions. In small, shallow lakes, sampling was conducted at a single central station.

In deeper, larger lakes, multiple stations were established to represent different lake basins and habitats, with at least one station consistently located at the deepest point of the lake. However, in Lakes Salda and Burdur, full-depth sampling was not feasible due to their extreme depths (196 and 110 m, respectively), consequently, the deepest sampling stations were located at 45 m in Lake Salda and 40 m in Lake Burdur. At each sampling station, physicochemical variables were measured using a YSI 650 MDS multiparameter probe. Water transparency was determined using a 20-cm Secchi disc. Depth-integrated composite water samples were collected at the deepest sampling point in each lake, except for Lakes Salda and Burdur, by combining subsamples from multiple depths at equidistant intervals along the water column at the epilimnion layer, measured based on vertical profiles of temperature, oxygen, and salinity. A Ruttner water sampler was used in deep lakes, whereas a pipe sampler was applied in shallow lakes. The number and spacing of depth samples were adjusted based on lake depth to ensure that the composite sample accurately represented the full vertical profile.

Subsamples of lake water were taken and stored frozen to determine total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), nitrate and nitrite (NO_3+NO_2), and silicate (Si). Silicate was included because, together with nitrogen and phosphorus, it helps to interpret nutrient stoichiometry and variation in primary producers across inland and coastal saline lakes. Another subsample was filtered through GF/C filters to determine chlorophyll *a*. TP and SRP were measured using the ammonium molybdate-ascorbic acid reduction method (Mackereth et al., 1978). TN and NO_3+NO_2 concentrations were determined by persulfate digestion using a Skalar San++ Automated Wet Chemistry Analyzer (Skalar Analytical B. V., Breda, The Netherlands) and a Seal Analytical AA3 autoanalyzer (Norderstedt, Germany) (Kroon, 1993; Grasshoff et al., 1999), producing comparable results (validated in Özkan et al., 2023). Total dissolved silicate was analyzed spectrophotometrically using the molybdate formation method (Golterman et al., 1978). Chlorophyll-*a* concentrations were measured after pigment extraction with absolute ethanol, using absorbance at 663 nm and turbidity correction at 750 nm with a spectrophotometer (Jespersen and Christoffersen, 1987).

The percent volume infested by submerged macrophytes (PVI%) was estimated based on multiple transects distributed across each lake or representative areas surrounding the sampling stations. In most small lakes ($<9\times10^7$ m^2), the entire lake surface was surveyed. Macrophyte cover and canopy height were assessed using a bathyscope in shallow, clear waters or by grapnel sampling under deeper or more turbid conditions.

2.7 Statistical analysis

All statistical analyses were conducted using the statistical software R 4.5.1, with significance defined as $P<0.05$. Land-use and climate variables from the entire catchment area were used for all the analyses. Significant differences between inland and coastal lakes in key response and predictor variables were assessed using the Wilcoxon rank-sum test. The influence of connectivity to the sea on key variables was estimated using generalized linear models (GLM). Non-linear impacts of salinization (i.e., log-transformed salinity) on response variables, such as water transparency, chlorophyll *a*, oxygen saturation, macrophyte PVI%, and nutrient concentrations, were analyzed using generalized additive models (GAM, package "mgcv"), with a Gamma (log link) or a Gaussian distribution for log-transformed data (Wood, 2017).

To identify the main environmental predictors of the response variables, we used random forest (RF) regression models ("randomForest" package). The model included in-lake (salinity, TN, TP, and Si), climate (temperature, evaporation, and precipitation), and land-use variables (population, tree cover, cropland, and built-up). Sea connection was included

in the models to evaluate the potential distinction between inland and coastal lakes; however, it was not selected as a relevant variable in any model. Other variables were excluded from the models due to autocorrelation (variance inflation factor, VIF> 10). Data were randomly split into training and test sets (80% training, 20% test). The value for mtry was selected using 5-fold cross-validation, in which the dataset was partitioned into 5 subsets in a random and stratified way, with 4 subsets used for model training and 1 subset for testing in each iteration. This procedure was repeated 5 times, averaging the models of a total of 2 500 trees. K-fold stratified cross-validation prevents overfitting and enhances the stability of results by partitioning data into training and testing sets, balancing the bias-variance trade-off (Kohavi, 1995; Lumumba et al., 2024). Model fit was validated by comparing the root mean squared error (RMSE) and the mean absolute error (MAE) between the predicted and observed values in the test dataset.

Predictor importance was quantified using the increase in node purity (variables with higher node purity than the average among all variables were considered relevant). Predictor importance was also expressed as a percentage of the total node purity for each variable and for each set of variables. Random forest variable importance reflects both main effects and interactions captured through hierarchical tree splits (e.g., if salinity is the second most important variable after another variable split, this indicates that these two variables have a significant interaction) (Breiman, 2001). The linear and non-linear interactions of the most important variables with salinity are shown in 2D heatmap partial dependence plots ("pdp" package). Importance plots also display explained variance, RMSE, R^2, and MAE.

3 RESULT

3.1 Characterization of inland and coastal lakes

Both inland and coastal lakes showed considerable variations in salinity, ranging from freshwater to hypersaline conditions for inland lakes (Lake Bakı, 0.25 g/L–Lake Tuz, 260 g/L) and from subsaline to hypersaline for coastal lakes (Lake Aliağa, 1.3 g/L–Lake Kalpli, 135 g/L) (Fig.2a; Supplementary Table S1). Inland lakes were significantly larger than coastal lakes (median area: 226 km^2, mean±SD: 1 811± 3 012 km^2 vs. 26.8 km^2, 179±315 km^2; Wilcoxon rank-sum test, P=0.012) and were located at higher altitudes (P<0.001), while depth did not differ across lake types. Coastal lakes exhibited higher temperatures, precipitation, and evaporation compared with inland lakes. Land use in the lake catchments differed markedly among lake types. The percentages of cropland, grassland, and bare vegetation areas were higher for inland lakes (P<0.05), while tree cover, shrubland, herbaceous wetlands, and NDVI were higher for coastal lakes (P<0.01). In contrast, the percentages of built-up areas and population in the catchments did not differ significantly between the two lake types (Figs.2b, 3; Supplementary Table S1).

Among the physicochemical and biological variables analyzed, only key nutrient variables and the PVI% of submerged macrophytes differed between lake types. Inland lakes were generally dominated by the submerged macrophytes *Ceratophyllum* spp., *Myriophyllum* spp., and *Stuckenia* spp., whereas in coastal lakes, *Ruppia cirrhosa* (Petagna) Grande was abundant and occurred at salinities up to 43.5 g/L. Inland lakes exhibited mean TP, NO_3+NO_2, and TN concentrations that were 13.9-, 9.5-, and 3.4-fold higher (P<0.001) than those in coastal lakes, respectively. SRP and Si concentrations were, on average, 32.3 and 1.8 times higher in inland lakes than in coastal lakes, respectively; however, these differences were not statistically significant. Submerged macrophytes PVI% was 2.7-fold higher in coastal lakes (P<0.01, interquartile range: 0.005%–32.22%, median: 3.09%, mean±SD: 21.15%±27.7%) compared to inland lakes (interquartile range: 0–7.75%, median: 0%, mean±SD: 7.9%±18.6%), while water transparency, chlorophyll-*a* concentrations, and oxygen saturation did not vary between the two lake types (Fig.4; Supplementary Table S1).

3.2 Change in biological and nutrient variables along connectivity to the sea and salinity gradients

Most response variables were significantly and negatively associated with the degree of connectivity with the sea (except submerged macrophytes PVI%) (GLM, P<0.05). The higher connectivity was significantly related to lower water transparency, chlorophyll-*a*, and nutrient concentrations (TP, TN, SRP, and NO_3+NO_2). In contrast, submerged macrophyte PVI% was positively correlated with connectivity (P<0.05), while oxygen saturation and Si concentrations showed no significant correlation (Fig.5).

Water transparency decreased with salinity in

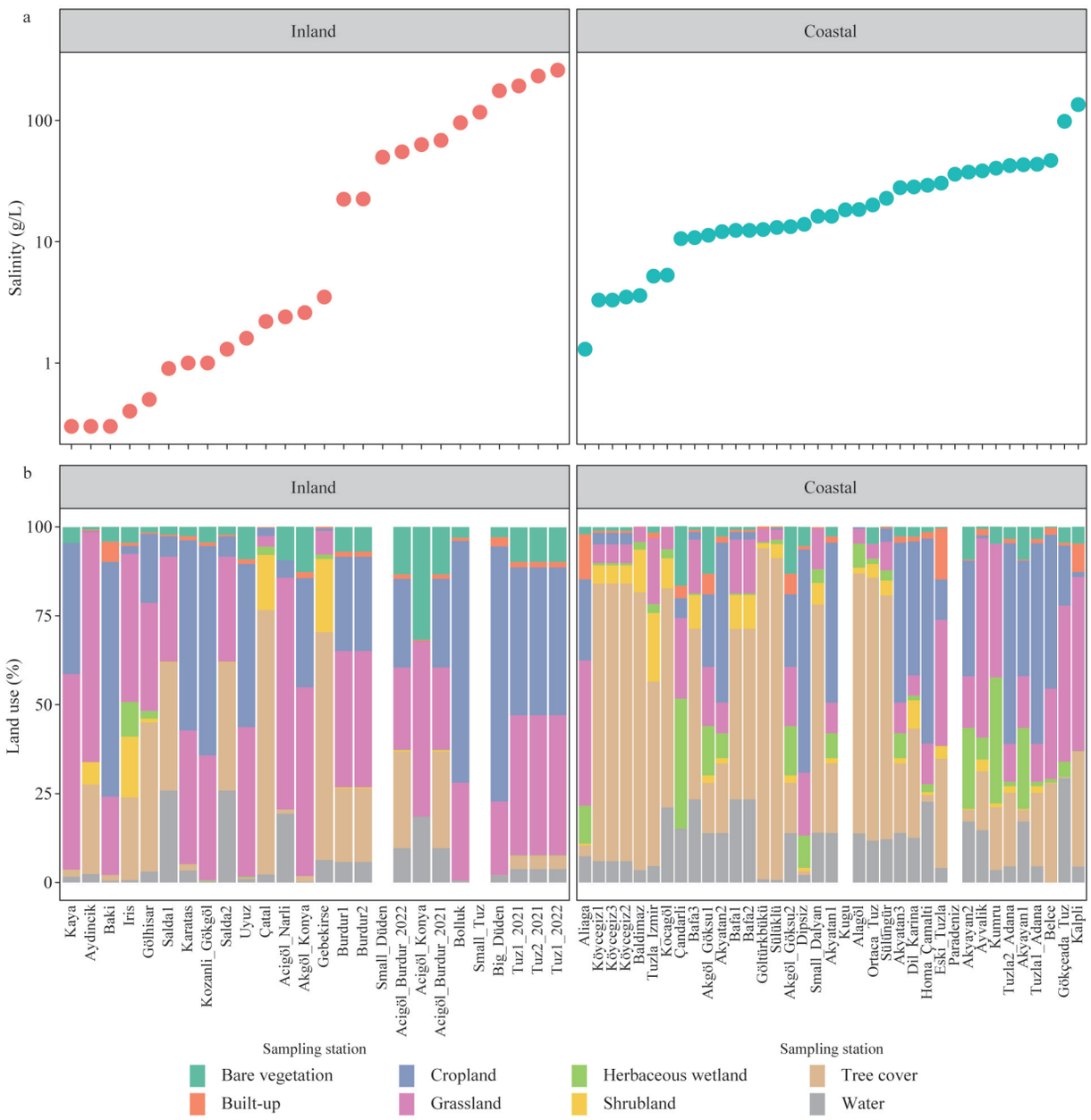


Fig.2 Salinity (a) and percentage of land-use types in the catchments (b) of the inland (red) and coastal (blue) study lakes

both inland and coastal lakes (GAM, $P<0.05$), most pronouncedly in coastal lakes. Similarly, oxygen saturation declined with salinity in both inland and coastal lakes ($P<0.01$). Chlorophyll-*a* concentrations were not affected by salinity in inland lakes but declined sharply with increasing salinity in coastal lakes ($P<0.05$). TP and TN concentrations increased linearly with salinity in inland lakes ($P<0.05$) but exhibited a unimodal response to salinity in coastal lakes, decreasing up to approximately 20 g/L, followed by an increase ($P<0.01$). NO_3+NO_2 responded differently to salinity, rising in inland lakes ($P<0.05$) but declining in coastal lakes ($P<0.01$). In contrast, SRP and Si did not respond significantly to salinity in either inland or coastal lakes. PVI% exhibited distinct threshold responses to salinity that differed between lake types. In inland lakes, PVI% was observed at salinities up to 3.5 g/L but was absent at the next observed salinity level (22.4 g/L and above), indicating macrophyte loss at high salinities; however, intermediate salinities were not represented in the dataset ($P<0.001$). In coastal lakes, macrophytes were well-established at salinities ranging from 5 to 43.5 g/L but were absent above this threshold and occurred at<8% PVI% at salinities<5 g/L ($P<0.001$)

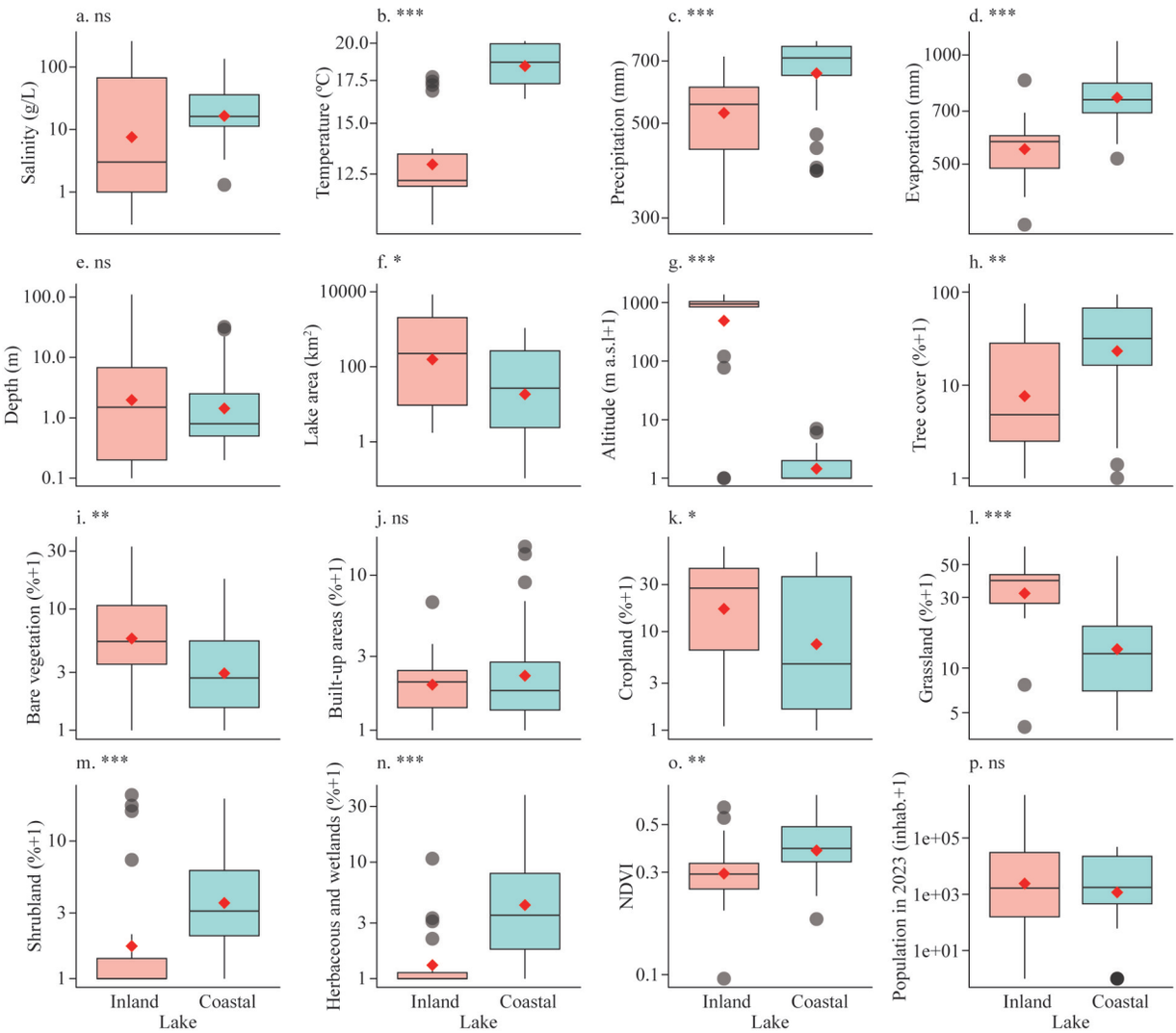


Fig.3 Differences in predictor variables between the inland (red) and coastal (blue) study lakes

Significant differences across lake types were assessed using Wilcoxon rank-sum tests and marked with asterisks: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: non-significant. Red diamonds represent average values. Depth was measured at the sampling station.

(Fig.6). Besides salinity, the occurrence of submerged macrophytes was strongly associated with depth and temperature. PVI% declined linearly with lake depth in coastal lakes ($P<0.01$) and showed a unimodal response in inland lakes ($P<0.01$), where they were completely absent in lakes with depths <0.5 m or >45 m. PVI% responded negatively to temperature in inland lakes but positively in coastal lakes ($P<0.05$), while it was not significantly associated with TP or TN (Supplementary Fig.S1).

3.3 Driver of nutrient and biological variables across inland and coastal lakes

Random forest models indicated that TP was the most important predictor of water transparency across all lakes, followed by TN, temperature, Si, and salinity (45% of total variance), with negative relationships with these variables. All those variables interacted with salinity to affect transparency, with clearer waters predicted only at a combination of low salinity (<1.6 g/L) and low values of TP, TN, temperature, and Si. Chlorophyll *a* was positively affected mostly by TP, TN, and cropland areas, and negatively by salinity (23%). Sharp declines in predicted chlorophyll *a* were observed at salinities >16 g/L, especially at low TP (<25 μg/L) and TN (<900 μg/L) levels, and in lakes with lower cropland areas (<50%). Temperature, evaporation, and built-up areas explained the highest proportion of variance in PVI% (19%), with positive relationships; population negatively affected PVI%, while tree cover displayed a U-shaped relationship, negatively affecting PVI%

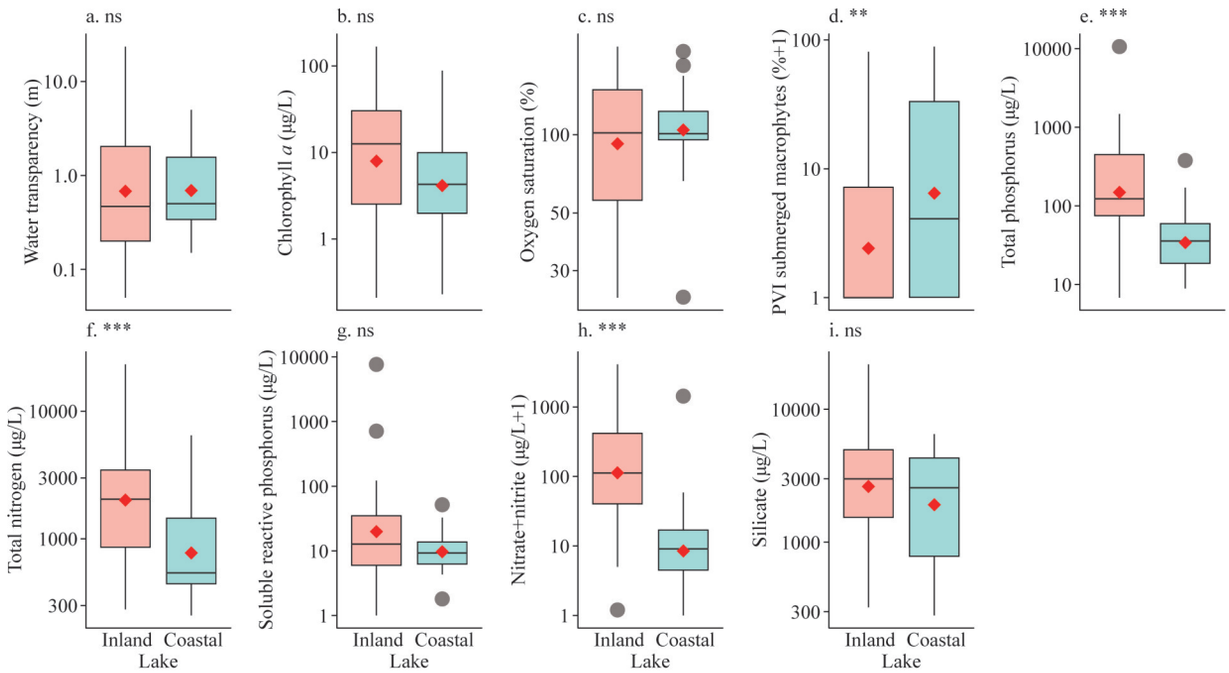


Fig.4 Differences in response variables between the inland (red) and coastal (blue) study lakes

a. water transparency; b. chlorophyll *a*; c. oxygen saturation; d. submerged macrophyte PVI%; e. total phosphorus; f. total nitrogen; g. soluble reactive phosphorus; h. nitrate+nitrite; i. silicate. Significant differences across lake types were assessed through Wilcoxon rank-sum tests and marked with asterisks: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: non-significant. Red diamonds represent average values.

up to ~30% tree cover, and positively after this threshold. Higher PVI% values were observed at combinations of intermediate salinities (~5–16 g/L), higher evaporation levels (>700 mm), and built-up areas (>2%). The explained variance in oxygen saturation was insignificant (negative explanation) (Fig.7; Supplementary Fig.S2).

TP variance was mostly explained by evaporation, followed by cropland and tree cover (57%), with negative effects from evaporation and tree cover and positive effects from cropland. TN variance was mainly explained by cropland, precipitation, evaporation, built-up, and salinity (31%), with negative effects of evaporation, positive effects of cropland, built-up areas, and salinity, and unimodal effect of precipitation, positive at values <500 mm and negative at >500 mm. All those variables exhibited pronounced non-linear interactions with salinity that influenced TN, with higher concentrations in hypersaline lakes (>60 g/L), combined with higher cropland areas (>60%), intermediate precipitation (400–600 mm), low evaporation (<600 mm), and a low percentage of built-up areas (2%–5%). Variance in SRP was primarily mediated by the positive influence of cropland areas and salinity, and the negative influence of temperature and tree cover (8%). Higher SRP was predicted under brine conditions (>116 g/L), combined with a higher percentage of cropland (>70%), low temperatures (<12 °C), and tree cover (<5%). NO_3+NO_2 concentrations were mainly explained by the negative influence of temperature and evaporation, and the positive effect of salinity (31% of explained variance). Higher salinities (>116 g/L), combined with lower temperatures (<12 °C) and evaporation (<600 mm), resulted in markedly higher predicted NO_3+NO_2 concentrations. Among the variables explaining the greatest proportion of variance in Si (30%), tree cover (<25%), salinity, precipitation (<600 mm), and temperature showed negative correlations, whereas tree cover (>40%) and precipitation (>600 mm) also exhibited positive correlations. Those variables had little to no interactions with salinity (Fig.7; Supplementary Fig.S2).

4 DISCUSSION

We found marked differences in physicochemical and biological variables between the inland and coastal saline lakes studied in Türkiye, primarily driven by variations in nutrient concentrations, salinity, climate, connection to the sea, and catchment land use. Inland lakes had notably higher

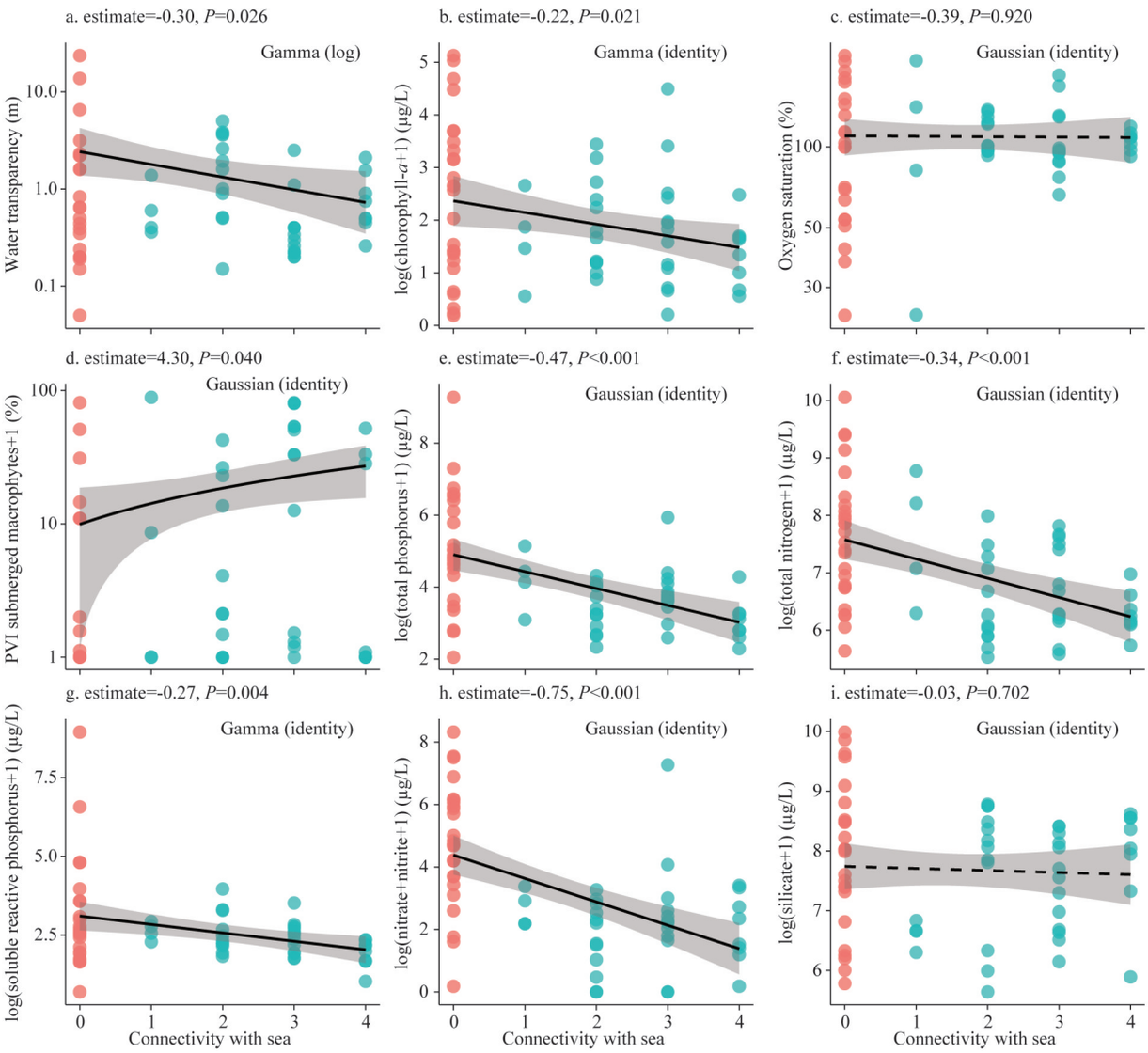


Fig.5 Effects of the degree of connectivity with the sea on the response variables in inland (red) and coastal (blue) study lakes

a. water transparency; b. chlorophyll *a*; c. oxygen saturation; d. submerged macrophytes PVI%; e. total phosphorus; f. total nitrogen; g. soluble reactive phosphorus; h. nitrate+nitrite; i. silicate.

nutrient concentrations, a pattern consistent with extensive farming and human impacts in Central Anatolia's closed basins, including higher cropland, bare vegetation, and grassland areas and lower tree cover, shrubland, herbaceous wetlands, and NDVI in inland lake catchments (Fig.8). Although direct data on fertilizer application rates, irrigation volumes, and drainage inputs were not available for each lake, the higher nutrient concentrations observed in inland lakes align with the extensive cropland cover and irrigation pressures documented in previous studies from the regions (Davraz et al., 2019; Yılmaz et al., 2021; Çolak et al., 2022; Dervişoğlu et al., 2022; Korkmaz et al., 2023b), suggesting that agricultural runoff and groundwater abstraction promote eutrophication and deteriorate water quality in Turkish shallow lakes (Beklioğlu et al., 2020; Yılmaz et al., 2021).

Our findings underscore the vulnerability of inland lakes to combined pressures from nutrient enrichment, climate-driven drying, and salinization. Model projections for Anatolian lakes predict that these stressors will severely impair ecosystem functions, particularly in shallow, endorheic basins (Bucak et al., 2018). Lower nutrient concentrations (TP, TN, NO_3+NO_2) in coastal lakes were associated with lower cropland proportions and higher coverages of tree, shrubland, herbaceous vegetation,

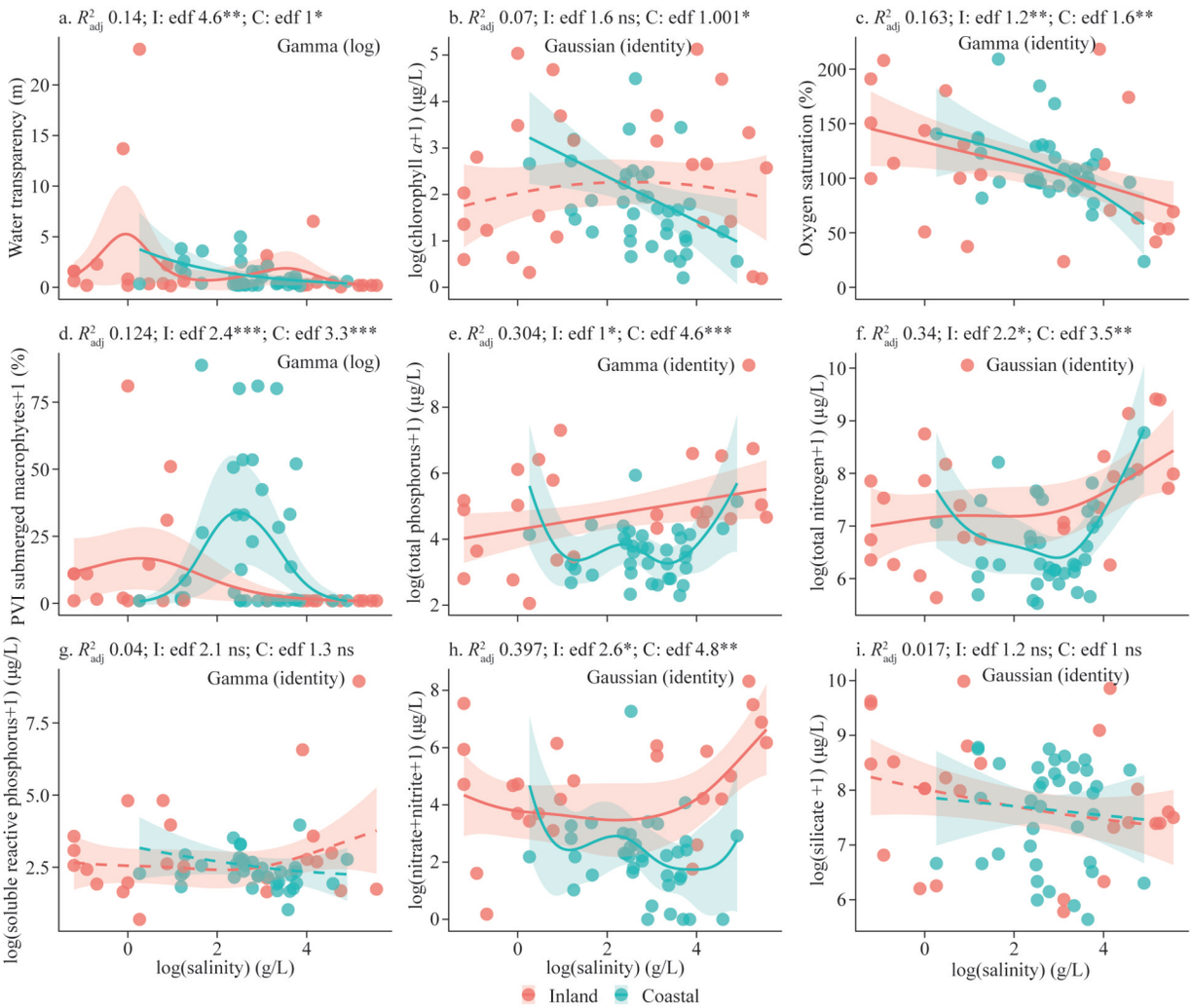


Fig.6 Changes in response variables along the salinity gradient in inland (I, red) and coastal (C, blue) study lakes

a. water transparency; b. chlorophyll *a*; c. oxygen saturation; d. submerged macrophytes PVI%, e. total phosphorus; f. total nitrogen; g. soluble reactive phosphorus; h. nitrate+nitrite; i. silicate. Dashed lines represent non-significant generalized additive models, solid lines represent significant models, and shaded areas indicate 95% confidence intervals. edf: estimated degrees of freedom.

and wetland areas within their catchments, resulting in higher overall NDVI values. Accordingly, the coastal lakes exhibited a higher macrophyte PVI% than the inland lakes. High macrophyte coverage may limit phytoplankton development due to competition for resources and shading, leading to clearer water and higher nutrient retention in sediments in both inland lakes (Jeppesen et al., 2005; Meerhoff and Beklioğlu, 2024; Amorim et al., 2025) and coastal lakes (Hamilton and Mitchell, 1996, 1997). This has also been observed in oligohaline mesocosm experiments (Billah et al., 2025) and may help explain the lower nutrient levels in coastal lakes. Although the higher PVI% observed in coastal lakes is consistent with a regulatory role of submerged macrophytes in nutrient retention and water clarity, this contribution was not quantified independently in our study lakes and should therefore be interpreted cautiously.

Furthermore, connection to the sea was associated with lower nutrient concentrations (TN, TP, SRP, NO_3+NO_2) in coastal lakes, consistent with dilution through increased water exchange. Greater connectivity may enhance water exchange and dilution, often resulting in lower nutrient concentrations and phytoplankton biomass (Coutinho et al., 2012). Such a pattern is also consistent with enhanced hydrologic renewal and reduced nutrient retention in sea-connected coastal systems (Huang et al., 2024). However, the management of sea connections (openings) in coastal wetlands must be approached with caution,

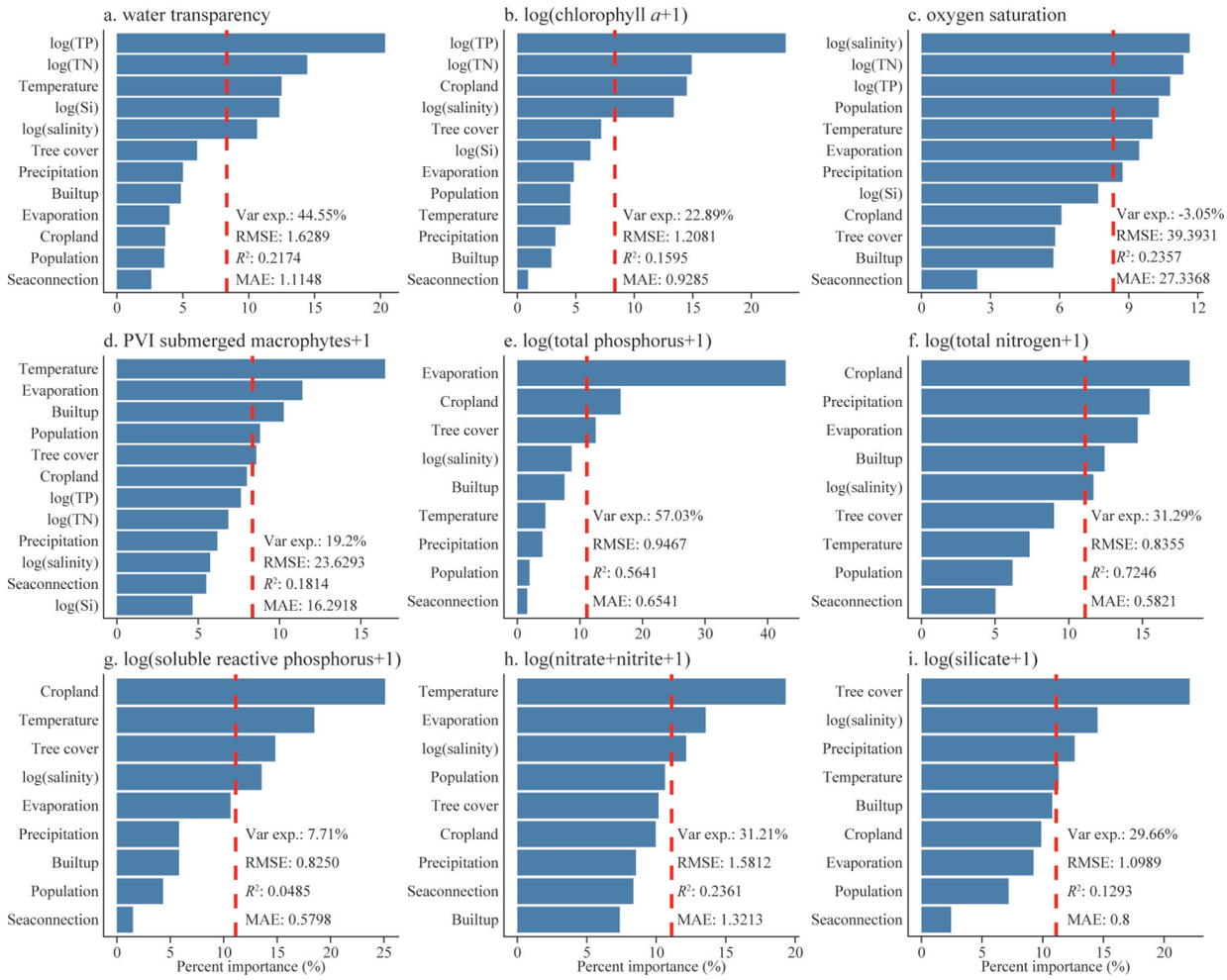


Fig.7 Normalized percentage of importance values (node purity) for the variables included in the random forest models

In each model, the red lines indicate the mean percentage of importance.

as responses are highly site-specific and depend on connection frequency and the types of land use in the catchments. Less frequent artificial openings can trigger nutrient enrichment, macrophyte die-off, phytoplankton blooms, and sediment destabilization because seawater exchange may be limited, and chemical stratification may trap nutrients (Schallenberg et al., 2010), whereas uncontrolled openings may alter coastal wetland water levels and disrupt natural hydrology (Ferreira, 2024).

Macrophyte PVI% decreased significantly with increasing salinity in inland lakes (>3.5 g/L, with no data between 3.5–22.4 g/L), while in coastal lakes, submerged vegetation was present up to 43.5-g/L salinity. The nonlinear decline in macrophyte abundance and transparency with increasing salinity aligns with the results of other studies suggesting that salinity in inland lakes can cause abrupt shifts in plant community structure and function once certain thresholds are crossed (Sim et al., 2006). In addition to salinity, extreme depths limited submerged vegetation in inland lakes, with a complete absence observed in 9 very shallow lakes (maximum depth<0.5 m) and in 4 very deep lakes (maximum depth>45 m). The occurrence of *Ruppia cirrhosa* in coastal lakes with salinities up to 43.5 g/L observed in this study is consistent with its well-documented high salinity tolerance (La Peyre and Rowe, 2003; Tsioli et al., 2019). Among submerged angiosperms, *Ruppia* spp. is recognized as having the broadest salinity tolerance, which can be attributed to its strong osmoregulatory capacity (Kantrud, 1991). By contrast, inland saline lakes were generally dominated by *Ceratophyllum*, *Myriophyllum*, and *Stuckenia* species, which typically thrive in lower salinity environments but are less resilient under highly variable or extreme saline conditions. Coastal lagoons are characterized

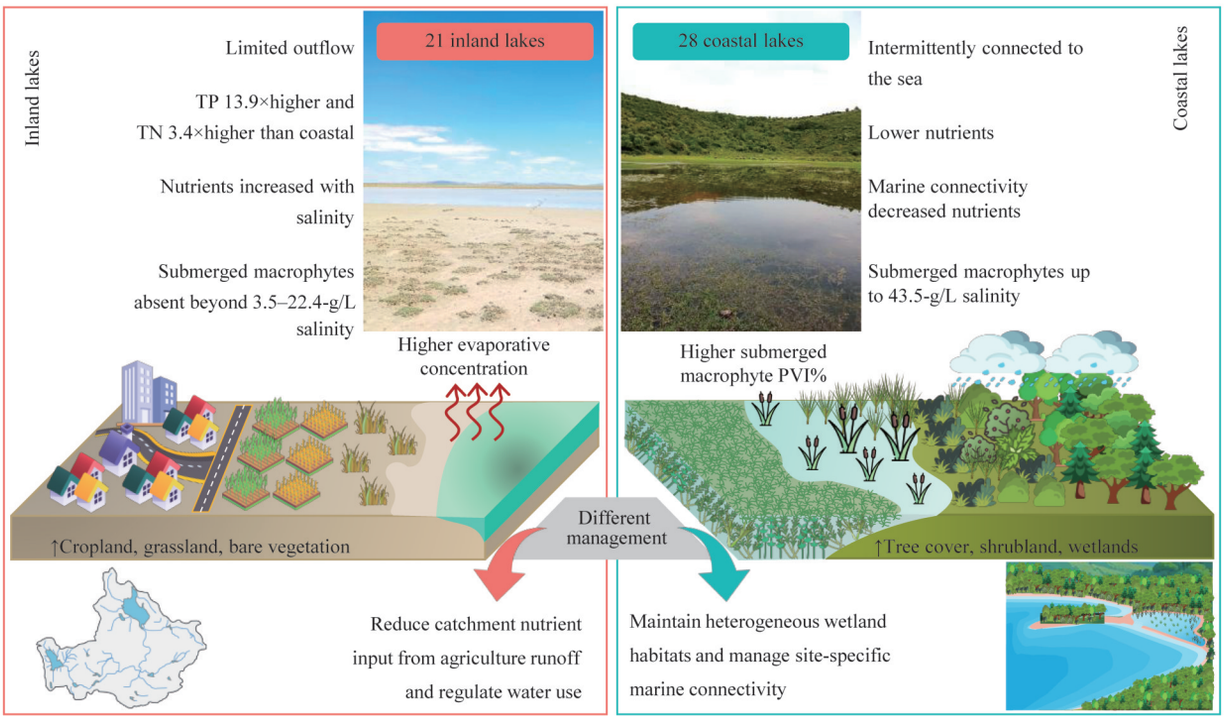


Fig.8 Summary of the main results of the present study highlighting the contrasting environmental drivers, ecological responses, and management priorities in inland and coastal saline lakes of Türkiye

Photos by C. Amorim. Icons from www.flaticon.com.

by dynamic salinity regimes that can sustain diverse submerged vegetation assemblages, particularly where nutrient inputs enhance plant growth and partially buffer salinity fluctuations (Rodríguez-Gallego et al., 2015). In contrast, the more stable salinization trajectory of inland lakes promote progressive declines in macrophyte communities, reducing biodiversity and ecosystem functioning (Xia et al., 2020; Moreira et al., 2023).

The strong positive correlation between salinity and nutrient concentrations (TN, TP, NO_3+NO_2) in inland lakes is likely driven by evaporative concentrations under arid conditions (Coppens et al., 2016; Beklioğlu et al., 2020). These processes can accelerate nutrient and salt accumulation and destabilize aquatic food webs, particularly when combined with low inflow and outflow and with higher water abstraction (Cunillera-Montcusí et al., 2022). The positive relationships between cropland and chlorophyll *a*, TN, TP, and SRP in the random forest models point to relevant land-water feedback. Intensive agriculture often produces high nutrient loading and groundwater overuse in the semi-arid climate, both of which intensify lake shrinkage, salinization (Jeppesen et al., 2020), and sinkholes. Excessive nutrient runoff due to agricultural practices can lead to eutrophication, degrading aquatic ecosystems and converting marshlands into less productive areas (Pennings, 2012). Policy interventions and sustainable practices, such as managed aquifer recharge and surface-water transfers, can help mitigate the impacts of salinization and over-abstraction (Jasechko et al., 2024).

Water transparency declined with increases in eutrophication indicators (TP, TN, Si), as expected, especially at higher temperatures and salinities. Higher proportions of cropland and built-up areas were associated with elevated TN. In contrast, greater tree cover in the catchments likely contributed to enhanced PVI%, lower TP and SRP concentrations, and higher Si levels in the studied lakes. Urbanization indicators, such as population density, further reinforced the negative impacts on PVI%. Overall, our findings highlight the importance of catchment-scale land-use management to preserve ecological integrity and mitigate eutrophication in inland and coastal saline lakes, particularly by reducing agricultural runoff and conserving shrubland and tree cover. Landscape composition plays an important role in controlling nutrient inputs and supporting lake ecological integrity (Ou et al., 2023).

Although climate variables contributed less to the overall impact than land-use and in-lake variables, they nonetheless influenced PVI% and nutrient concentrations, suggesting that even minor climatic differences can shape key ecological features. Temperature was negatively related to Secchi, SRP, NO_3+NO_2, and Si, but had an opposite effect on submerged macrophyte PVI%. Similar patterns have been observed in other dryland regions, where increased nutrient loading and warming drive shifts from benthic organisms to planktonic taxa, resulting in reduced water clarity (Xiang et al., 2025). Given the projected warming and drying trends for semi-arid Türkiye (Özturk et al., 2015), inland lakes are likely to be increasingly impacted, as surface water losses intensify salinization and eutrophication in shallow closed basins. As warming enhances stratification and evaporation, further increases in nutrient and salinity concentrations may occur, potentially exceeding ecological thresholds and triggering regime shifts. By contrast, coastal lakes may exhibit comparatively buffered responses to climatic changes due to intermittent marine connectivity and greater landscape heterogeneity (Kirwan and Megonigal, 2013; Wang et al., 2015).

Inland lakes may undergo accelerated biotic homogenization (Özgencil et al., 2025) and collapse of aquatic vegetation, reflecting their high sensitivity to combined climatic and hydrological pressures. On top of that, the prevalence of exotic species may contribute to the disruption of native trophic networks and biodiversity loss (Ramírez-García et al., 2026). In contrast, the comparatively buffered responses observed in some coastal saline lakes suggest that hydrological connectivity and habitat heterogeneity (e.g., tree cover, shrublands, NDVI, and wetlands) may partly modulate climate-driven impacts rather than confer intrinsic resilience. While such structural complexity can influence nutrient dynamics and short-term system responses, coastal lakes are simultaneously exposed to multiple interacting pressures, including hydrological alterations, salinization, and increasing human use. As highlighted by Ferrarin et al. (2014), enhanced connectivity and external forcing may also promote hydro-morphological homogenization and the progressive loss of hydro-diversity in Mediterranean lagoon systems. These contrasting processes underline that apparent buffering in coastal lakes should not be interpreted as long-term resilience but rather as context-dependent responses shaped by both connectivity and cumulative pressures. Consequently, conservation strategies should be explicitly tailored to local hydrological structure and disturbance regimes.

Among the potential limitations of our study is that several biotic and abiotic processes and patterns change seasonally and interannually, and our space-for-time approach did not capture these dynamics. Although the present study surveyed 49 lakes in semi-arid Türkiye, this number is still insufficient to represent the entire salinity gradient in inland lakes (e.g., lakes with salinities between 3.5 and 22.4 g/L were not included). This gap limits our ability to identify the precise thresholds of submerged macrophyte loss in inland lakes. Finally, extreme climate and environmental conditions across both lake types, as well as their natural differences, resulted in several outliers in the most important response and predictor variables, thereby limiting the predictive capacity of most statistical and ecological models.

Future research should prioritize high-resolution buffers and connectivity, using remote sensing and process models to better quantify nutrient fluxes. In addition, experimental approaches can be used to investigate responses to interactions like salinity-nutrient-warming-macrophytes. Such approaches, based on observations, experiments, and predictions, are essential for predicting the responses of semi-arid saline lakes challenged by intensifying pressures from climate and land-use change, as demonstrated by previous experiments conducted in cold semi-arid and warm Mediterranean shallow lakes (Özkan et al., 2023; Yilmaz et al., 2026; Zadereev et al., 2026).

5 CONCLUSION

In this study, we provide a detailed comparison of inland and coastal saline lakes in semi-arid Türkiye, a region experiencing pronounced land-use and climate change pressures. The results largely supported our hypotheses that (1) inland lakes exhibit higher nutrient concentrations, lower macrophyte cover, and stronger sensitivity to eutrophication and catchment-scale human pressures (e.g., population, cropland, built-up areas); and (2) coastal lakes sustain submerged vegetation even at high salinities, likely reflecting periodic seawater inflow and more diverse, vegetated catchments. Contrary to our first hypothesis, however, water transparency, chlorophyll *a*, and oxygen saturation

did not differ significantly between the two lake types, indicating that the contrast between inland and coastal saline lakes is expressed primarily through nutrient concentrations and macrophyte cover rather than through bulk water-clarity metrics. By analyzing the roles of salinity, land cover, climate, connectivity to the sea, and morphology, our results suggest that coastal lakes tend to maintain higher resilience to eutrophication pressures because of lower nutrient enrichment and the persistence of high macrophyte PVI. However, this apparent buffering does not imply long-term resilience and remains strongly context-dependent. In contrast, inland lakes, especially those located in closed basins, are highly vulnerable to nutrient accumulation and salinity-driven collapse of macrophyte communities. Our findings provide evidence that landscape context and hydrological connectivity to the sea shape the responses of saline lakes to environmental stressors. Conservation and restoration management strategies for these distinct lake types should therefore adopt differentiated, ecosystem- and watershed-specific approaches, prioritizing reduction of catchment nutrient inputs and water use in inland systems, and safeguarding natural hydrological connectivity, wetland buffers, and catchment integrity in coastal landscapes.

6 DATA AVAILABILITY STATEMENT

The data will be made available from the corresponding authors upon reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Table S1 and Figs.S1–S2) is available in the online version of this article at https://doi.org/10.1007/s00343-026-5243-0.