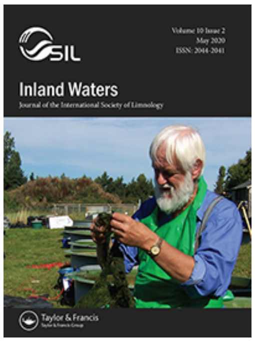

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Influences of climate and nutrient enrichment on the multiple trophic levels of Turkish shallow lakes

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ABSTRACT

Climate warming threatens the structure and function of shallow lakes, not least those in the Mediterranean climate. We used a space-for-time substitution approach to assess the response of trophic and community structures as well as the richness and evenness of multiple trophic levels to temperature, hydrological, and nutrient constraints. We selected 41 lakes covering wide climatic, hydrological, and nutrient gradients within a short distance for reducing the effect of biogeographical factors in the western Anatolian plateau of Turkey. Generalized linear model analyses revealed that temperature was overall the most important driving variable, followed by total nitrogen (TN) and salinity. The chlorophyll *a*:total phosphorus ratio, the cyanobacteria:total phytoplankton biovolume ratio, the fish:zooplankton biomass ratio, the proportion of small fish, and fish richness increased with increasing temperature, whereas macrophyte plant volume inhabited (PVI, %), richness, and evenness decreased. Grazing pressure, macrophyte coverage, piscivore biomass, phytoplankton richness, and evenness decreased significantly with both increasing TN and temperature. Temperature and nutrients also separated the northern highland lakes from other lakes in a non-metric multidimensional scaling analysis. Additionally, salinity reduced richness and evenness of phytoplankton and zooplankton. Our results indicate major changes in lake structure and functioning with warming and eutrophication, and highlight the need for strict control of nutrients and water use.

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Introduction

Global temperature and precipitation patterns have changed markedly in recent decades and are predicted to change even more with more frequent extreme events (e.g., heatwaves, drought, flooding; Meehl et al. 2007, Hao et al. 2018). Shallow lakes are the most widespread type of inland waterbody in the world (Downing et al. 2006) They are sensitive to external perturbations, including land use, human population rise, and climate change (Jeppesen et al. 2009, 2015, Moss et al. 2011, Gozlan et al. 2019), and are already heavily exploited for the provision of "goods and services" (Dudgeon et al. 2006, Woodward 2009). Shallow lakes are furthermore highly sensitive to the balance between evaporation and precipitation because of their large surface:volume ratio (Coops et al. 2003), a sensitivity particularly marked in the Mediterranean climate owing to the strong linkages between climate and the hydrological cycle of the lakes (Bucak et al. 2017). Water abstraction, mostly for the purpose of irrigation, a major water use, has led to a significant decrease in surface and groundwater levels and even loss of lakes and streams in the Mediterranean region (Durduran 2010, Sanz et al. 2011, Graveline et al. 2012, Sabater et al. 2018, Gozlan et al. 2019), a development that may be further exacerbated through the impact of future climate change (Bucak et al. 2017). For Turkey, climate models predict dramatic summer drought episodes across the western and southern parts due to a >30% decrease in winter

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precipitation and enhanced summer evaporation (Lelieveld et al. 2012, Turunçoğlu et al. 2013). These drought conditions may lead to an even stronger reduction in runoff waters, projected to be as large as 30–40% in Turkey (Pachauri et al. 2014), which may have serious consequences for the ecology of shallow lakes in this region and ultimately may lead to complete drying out of the lakes (Beklioğlu et al. 2007, Bucak et al. 2017, 2018).

Moreover, higher evaporation in summer from extreme droughts, often combined with water abstraction, results in reduced water levels, higher sediment resuspension unless macrophytes growth is stimulated by better light conditions, and prolonged retention time, often resulting in enhanced eutrophication and salinisation (Talling 2001, Beklioğlu et al. 2007, 2017, Özen et al. 2010, Coppens et al. 2016). In the Mediterranean region, enhanced nutrient loading during wet periods may not lead to a major increase in lake nutrient concentrations because it can be counteracted by the dilution effect through enhanced flushing (Coppens et al. 2016, Beklioğlu et al. 2017). Concentrations may, however, increase in drought periods because of evaporative water loss, prolonged retention, and internal loading (Jeppesen et al. 2009, 2011, Özen et al. 2010, Coppens et al. 2016). Such conditions are anticipated to become even more pronounced in the future because of expected droughts and heat waves with higher frequency and intensity.

Increased temperatures, salinity, and eutrophication substantially influence lake food web structure and community composition (Carpenter et al. 2001, Jeppesen et al. 2007, Meerhoff et al. 2007, Moss 2010, Brucet et al. 2012, Gutierrez et al. 2018). Warmer lakes tend to have higher densities of small fish (Blanck and Lamouroux 2007, Meerhoff et al. 2007, Jeppesen et al. 2012, Brucet et al. 2013, Boll et al. 2016) and small-sized zooplankton (e.g., Gyllström et al. 2005, Tavşanoğlu et al. 2015, 2017) and are thus more sensitive to nutrient addition because grazer control of phytoplankton is weaker (Meerhoff et al. 2007, 2012, Lemmens et al. 2018). Consequently, higher frequency and longer duration of cyanobacteria blooms have been observed (Havens et al. 2019). Changes in salinity may have more profound consequences than an increase in temperature per se for the diversity and community structure of organisms as a consequence of osmotic stress and reduced top-down control (Brucet et al. 2009, Bezirci et al. 2012, Gutierrez et al. 2018) and may negatively affect the resilience of lakes (Jeppesen et al. 2007, 2015, Meerhoff et al. 2012, Brucet et al. 2010, 2012).

Surveys of lakes over broad geographical areas can contribute to the understanding of ecosystem control mechanisms. Space-for-time substitution involving sampling along latitudinal or altitudinal gradients has been used to provide proxies of thermal or hydrological gradients (Woodward et al. 2010, Meerhoff et al. 2012, Jeppesen et al. 2014). Although this method is limited by underlying confounding gradients in geology, geography, biogeography, land use, and human population rise (e.g., Jeppesen et al. 2014), it is, if interpreted carefully, a plausible way to forecast future changes (Gyllström et al. 2005, Meerhoff et al. 2012, Jeppesen et al. 2014, Mantzouki et al. 2018).

Today, unprecedented rates of climate change are occurring, involving extreme events such as heatwaves, drought, or flooding that threaten the current structure and functioning of lakes when combined with additional multiple stressors (Yang et al. 2008, Malmquist et al. 2009, Richardson et al. 2019). Climate change itself also exacerbates the effects of stressors, especially eutrophication, thereby potentially preventing detection of signals of change (Moss et al. 2011). The current study, encompassing shallow lakes located in areas displaying a wide array of climatic features and land use intensity, uses a space-for-time substitution approach to document the responses of trophic and community structures, richness, and evenness at multiple trophic levels to variations in effects of hydrological constraints, land use, and temperature. Our ultimate aim was to increase the knowledge of how climate change and eutrophication affect shallow lakes in semiarid Mediterranean climatic regions already declared as some of the most sensitive in the world (Gozlan et al. 2019).

Materials and methods

Study sites

Turkey is bounded by 2 continents (36°–42°N; 26°–45°E) and has several high mountain ranges that create a continental-scale variety of climates. It encompasses warm to hot temperate zones with/without dry summers, including the Mediterranean climate zone and arid cold steppe with/without dry summers according to the Köppen-Geiger climate classification (Peel et al. 2007). These large variations have led to the presence of numerous ecosystem types and habitats exhibiting exceptionally high biodiversity and extensive endemism within a relatively limited area (Şekercioğlu et al. 2011). Furthermore, the 41 lakes selected in the current study are located within nearly 5° of latitude (41°52′N–37°06′N) and elevations ranging from 0 to 1423 m in the Western Anatolian Plateau (Fig. 1). The average elevation of the Anatolian Plateau is 1100 m a.s.l., and high elevation lakes were found at all latitudes; however, the study lakes were lumped into 2 elevation groups, 0–50 and

700–1328 m a.s.l., respectively, and regarded as lowland and highland lakes, respectively. Thus, the lakes studied covered distinct climates, from the cold steppe to Mediterranean climate in mid to southwest Turkey and from the warm temperate to the subhumid climate in northwest Turkey (Peel et al. 2007).

Sampling and analysis

We sampled 41 lakes during the peak of the growing season between July and August 2007–2013 following a snapshot sampling protocol described and standardised by Moss et al. (2003). Salinity was measured in situ using a YSI 556 MPS multi-probe (YSI, Yellow Springs, OH, USA), and Secchi disk transparency was measured with a 20 cm diameter disk. We used a visibility index, calculated as Secchi disk depth to maximum depth ratio, because Secchi depth is not sufficiently informative for exceptionally clear-water lakes where the Secchi depth is greater than the water depth (here the visibility index was set to 1). Water samples for chemical and plankton analyses were taken from depth-integrated mixed samples (40 L) at the deepest point of each lake. The water samples were kept frozen and analysed for total phosphorus (TP; Mackereth et al. 1978) and total nitrogen (TN) using a Scalar Auto-analyzer, San++ Automated Wet Chemistry Analyzer (Skalar Analytical, B.V. Breda, The Netherlands), and chlorophyll *a* (Chl-*a*; Jespersen and Christoffersen 1987).

A 50 mL water sample from each lake was fixed using a 2% Lugol's solution for phytoplankton species determination; counting (Utermöhl 1958) and biovolume calculation (Hillebrand et al. 1999, Sun and Liu 2003) were based on the mean length and geometric shapes of at least 10 individuals of each species. We used cyanobacteria and total phytoplankton biovolumes for the statistical analysis. For zooplankton, 20 L water samples were filtered through a 20 μm filter and preserved in 4% Lugol's solution. Samples were counted until 50–100 individuals of the most abundant taxa and the body size of 25 individuals of each taxon were measured, when possible. Dry weight of zooplankton was estimated from the allometric relationship between weight and body length (Dumont et al. 1975, Bottrell et al. 1976, Ruttner-Kolisko 1977, McCauley 1984). For rotifers, biomass was estimated from measurements of the principal diameters of the organisms, and dry weight was calculated based on Dumont et al. (1975) and Ruttner-Kolisko (1977). Biomasses of total zooplankton, large zooplankton (>0.7 mm), cladocerans, and rotifers were used for statistical analyses.

The composition and relative abundance of fish were determined using multiple mesh-sized Lundgren gill nets (mesh sizes 5–55 mm, randomly lined). The number of nets used per lake increased with lake area, with a maximum of 8 (Moss et al. 2003, Boll et al. 2016). We used average catch per unit effort (CPUE), number per unit effort (NPUE), or biomass per unit effort (BPUE), and the ratio of fish <10 cm to total fish numbers as an indicator of the proportion of small fish. We used the proportions of small fish and piscivores biomass (BPUE) and total fish density (NPUE) for statistical analysis.

For macrophytes, both plant coverage and percent plant volume inhabited (PVI%), calculated using the equation plant coverage × average plant height/water depth (sensu Canfield et al. 1984, Levi et al. 2014), were used for the analyses.

Mean summer air temperature and precipitation seasonality (PS, coefficient of variation [CV], a measure of the variation in monthly precipitation totals over the year) data at 30-arc seconds spatial resolution (equivalent to ~0.86 km^2 at the equator and less elsewhere, commonly referred to as "1 km" resolution) were assembled from the WorldClim database using the sampling location coordinates for each study lake (Hijmans et al. 2005, WorldClim 2013). Net evaporation (precipitation–evaporation difference) data were compiled from Turkish Meteorological Office (2013). PS represents annual trends in seasonality (e.g., maritime effects), and net evaporation represents severity of summer conditions or drought. These variables likely capture differences in the study lakes better than weather-specific temperature and precipitation data (WorldClim 2013).

Data on fertiliser use and livestock density across the landscape were compiled from the Turkish Statistical Institute based on the Turkish Ministry of Food, Agriculture and Livestock (Turkish Statistical Institute 2013) and used to estimate the effects of land use in the lake catchments. Because land use data were not available at catchment scale, data from the nearest province of each study lake were used, including information on cattle and sheep per hectare and the quantity of fertiliser used per hectare of arable land. Livestock numbers were standardised based on the mean weight ratio of the groups (cow and sheep), with 1 cow being equal to 5 sheep.

Statistical analyses

We used a generalized linear model (GLM) with Gaussian error distribution and a logarithmic link function to assess the effects of environmental variables on lake trophic and community structures, and also on the richness and evenness of the different community members. We excluded collinear (Pearson $r > 0.6$) predictors. Small sample size precluded model selection using all environmental variables; thus, mean air temperature, salinity, and TN were used because they have been regarded as primary drivers

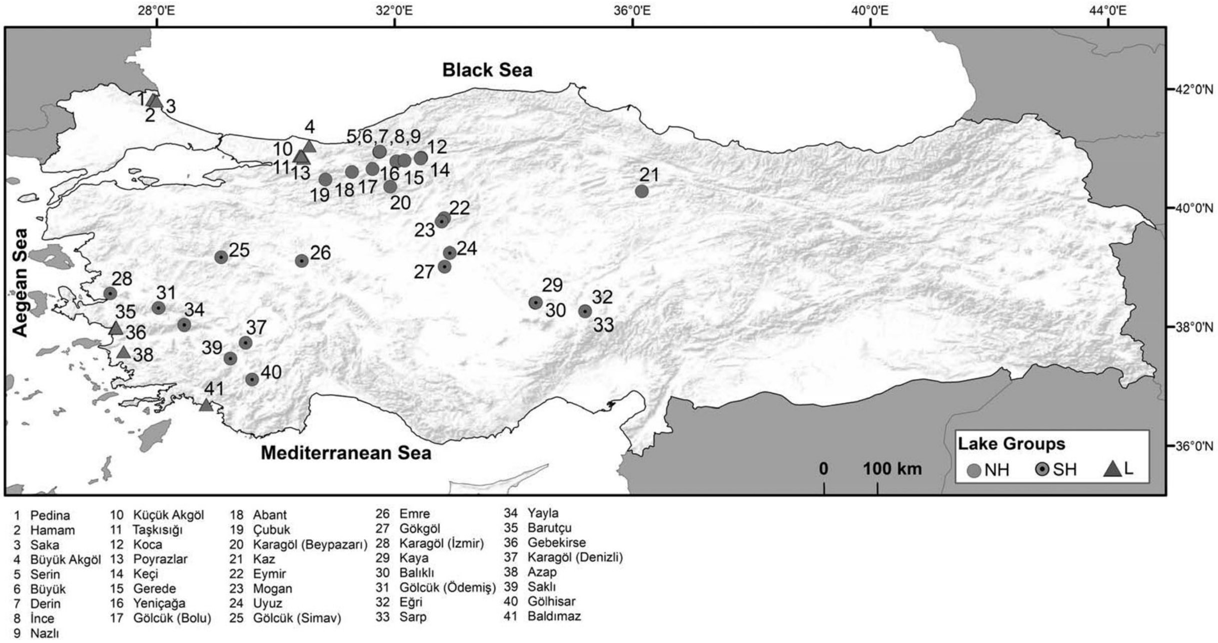

Figure 1. Names and locations of the 41 study lakes in Turkey. H = Highland, L = Lowland, N = Northern, S = Southern.

of lake functioning and community structure and are the most relevant variables for testing our hypothesis. We used TN instead of TP because TN had stronger predictive power for Chl-*a*. The best model was selected using a forward stepwise procedure based on Akaike's information criteria. For each lake, species evenness was calculated as the Pielou's evenness, and species richness was determined as the total number of different species.

Non-metric multidimensional scaling (NMDS) ordination was used to determine how the study lakes were associated according to bioclimatic, biological, and environmental variables, including mean summer air temperature, PS, net evaporation, latitude, elevation, visibility index, salinity, TN, livestock number, fertiliser use, Chl-*a*, macrophyte coverage, large zooplankton biomass, proportion of small fish, and piscivorous fish biomass using pairwise Euclidean dissimilarities (Legendre and Legendre 1998). Subsequently, permutational multivariate analysis of variance using distance matrices (ADONIS) was used to test the significance of differences across identified lake groups (Anderson 2001).

The analyses were conducted with R software using the *vegan* package (R Development Core Team 2019).

Results

The 41 study lakes were largely shallow and small with wide variations in TN concentrations as well as notable differences in visibility and Chl-*a* concentrations (Table 1). Mean summer air temperature of the lakes varied between 16 and 26 °C, salinity between 0.1‰ and 4.8‰, and TP and TN between ~15–633 µg L^{-1} and 239–2340 µg L^{-1}, respectively. Of the lakes, 32 had macrophytes, with macrophyte PVI% and coverage averaging 17.4% and 26.4%, respectively. Piscivores were caught in only a limited number of lakes. The proportion of small fish to total fish varied between 0 and 1 with a mean of 0.3 (Table 1).

We used GLM to analyse the responses of trophic structure and community composition as well as the richness and evenness of organisms related to the explanatory variables of temperature, TN, and salinity (indicators of the climate, nutrient enrichment, and hydrology, respectively). Of the 3 explanatory variables selected, temperature was overall the most important driving variable, followed by TN and salinity (Table 2). The Chl-*a*:TP ratio representing the yield, the cyanobacteria to total phytoplankton biovolume ratio, the predation pressure of fish on zooplankton (fish to zooplankton biomass ratio), the proportion of small fish, and fish richness increased with increasing temperatures, whereas macrophyte PVI, richness, and evenness decreased (Table 2). The visibility index (Secchi disk to maximum depth ratio) and zooplankton evenness decreased with increasing TN concentrations, whereas total phytoplankton biovolume increased. Chl-*a* concentrations, cyanobacteria biovolume, biomasses of zooplankton and rotifers, and total fish density (NPUE) increased with temperature and TN (Table 2). Additionally, zooplankton biomass and fish (NPUE) were negatively affected by salinity. The biomass of cladocerans

Table 1. Range, mean, and median of some of the physical, chemical, and biological characteristics of the study lakes. Macrophyte PVI is the macrophyte percent volume inhabited.

Variables	Range	Mean	Median
Mean summer air temperature (°C)	16–26	20	21
Precipitation seasonality (mm)	29–98	47	40
Net evaporation (mm)	276–839	481	461
Elevation (m)	0–1423	777	975
Lake area (ha)	0.1–714	60	9
Mean depth (cm)	22–474	167	152
Salinity (‰)	0.1–4.8	0.6	0.2
Visibility index	0.1–1.0	0.4	0.3
Total phosphorus (µg L^{-1})	15–633	131	79
Total nitrogen (µg L^{-1})	239–2340	1091	955
Chlorophyll *a* (µg L^{-1})	1.8–100.4	24.2	12.7
Macrophyte PVI (%)	0–77.5	17.4	7
Macrophyte coverage (%)	0–89	26.4	20.0
Piscivorous fish (g fish per net per night)	0–2923	339	0
Proportion of small fish to total fish (g fish per net per night)	0–1	0.3	0.2

and large zooplankton increased with increasing TN but decreased with temperature and salinity. Grazing pressure (zooplankton:phytoplankton ratio), macrophyte coverage, piscivore biomass, phytoplankton richness, and evenness decreased significantly with both increasing TN and temperature (Table 2). Phytoplankton richness and evenness were additionally decreased with increasing salinity. While zooplankton richness and evenness were negatively related to salinity, the evenness was also negatively affected by TN (Table 2).

Lake area and mean depth were separately tested as additional explanatory variables together with temperature, TN, and salinity. Lake area had a significant negative relationship with Chl-*a*:TP concentrations ($p < 0.01$) and the fish:zooplankton biomass ratio ($p < 0.05$), whereas mean depth had a negative relationship with macrophyte coverage ($p < 0.001$) and PVI ($p < 0.01$). Additionally, lake area had a significant positive relationship with cyanobacteria biovolume ($p = 0.03$) as well as total zooplankton ($p < 0.05$) and cladoceran biomass ($p < 0.05$). We further tested the effects of area and latitude together with temperature, TN, and salinity on richness and evenness at the different trophic levels. Lake area and latitude had significant positive effects on zooplankton richness ($p < 0.01$) and fish richness ($p < 0.001$), respectively. The effect of fish density (NPUE) as an additional explanatory variable together with temperature, TN, and salinity was also tested to reveal top-down effects. Fish density contributed significantly and positively to the variation in Chl-*a* concentrations, the cyanobacteria:phytoplankton biomass ratio, and rotifer biomass ($p = 0.021$, $p = 0.03$, and $p = 0.049$, respectively). To explore the role of macrophyte coverage and PVI for zooplankton biomass, we included these separately into GLM with temperature, TN, and salinity, but no significant effects of the 2 variables were captured. To explore the effect of zooplankton on Chl-*a* concentrations and Chl-*a*:TP, we conducted further GLM analyses using large zooplankton biomass as an explanatory variable with temperature, TN, and salinity. We found a significant negative effect of biomass of large zooplankton on the Chl-*a* concentration ($p = 0.02$) but no significant effect on Chl *a*:TP.

We used NMDS to analyze how the study lakes were associated relative to the climatic, environmental, and biological variables. Two clusters of lakes were identified

Table 2. Parameter estimates from a generalised linear model of multiple regression. Independent variables include total nitrogen, mean summer air temperature (given as temperature), and salinity. Dependent variables are chlorophyll *a* (Chl-*a*); Chl-*a*:TP; NPUE = number per unit effort (individual fish per net per night); BPUE = biomass per unit effort (g fish per net per night); proportion of small fish NPUE = small fish NPUE to total fish NPUE ratio, PVI = macrophyte percent volume inhabited (%).

Variables	Total nitrogen	Temperature	Salinity
Trophic structure			
Visibility index	−0.020*	—	—
Chl-*a*	<0.001***	0.029*	—
Chl-*a*:TP	—	0.049*	—
Cyanobacteria:phytoplankton	—	0.004**	—
Zooplankton:phytoplankton	−0.049*	−0.023*	—
Fish:zooplankton	—	0.023*	—
Community variables			
Phytoplankton	0.004**	—	—
Cyanobacteria	0.025*	0.060	—
Zooplankton	<0.001***	0.053	−0.001**
Large zooplankton	0.010*	−0.010**	—
Cladocera	0.027*	−0.045*	−0.056
Rotifers	0.024*	0.020*	—
Macrophyte coverage	−0.004**	−0.005**	—
Macrophyte PVI	—	−0.052	—
Fish NPUE	0.004**	0.007**	−0.013*
Piscivore BPUE	−0.052	−0.019*	—
Proportion of small fish NPUE	—	0.042*	—
Richness and evenness			
Phytoplankton richness	−0.054	−0.054	−0.028*
Zooplankton richness	—	—	−0.007**
Macrophyte richness	—	−0.040*	—
Fish richness	—	0.038*	—
Phytoplankton evenness	−0.030*	−0.052	−0.045*
Zooplankton evenness	−0.026*	—	−0.040*
Macrophyte evenness	—	−0.030*	—
Fish evenness	—	—	—

Significance level: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

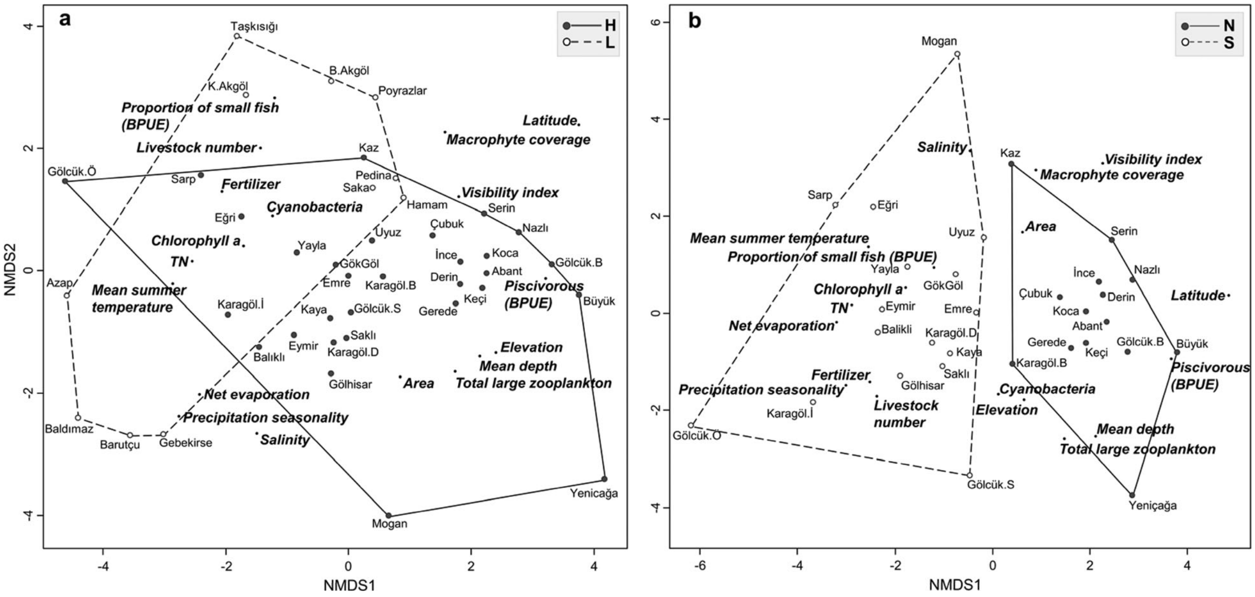

Figure 2. Classification of the 41 study lakes using non-metric multidimensional scaling analysis to compare (a) highland ($n = 30$) and lowland lake ($n = 11$) groups and (b) 2 within-highland groups: the northern ($n = 14$) and southern ($n = 16$) highland lakes. Refer to Fig. 1 for lake locations.

in the first NMDS analysis, differing along an elevation gradient as lowland (L) and highland (H) lakes (Fig. 2a). Although ADONIS showed that these 2 lake groups differed significantly ($p = 0.001$, $R^2 = 0.13$), there was also important overlap. The lowland lakes had high values of mean summer temperature, PS, high net evaporation, salinity, fertiliser use, livestock density, TN, and Chl-*a* concentrations as well as high proportions of small fish, the same characteristics also shared by some of the highland lakes (Fig. 2a).

Because highland lakes were rather widespread along the different gradients, we further analysed the highland lake cluster using NMDS analysis. The lakes from the highlands differed markedly along the latitudinal gradient, divided clearly into northern and southern highland lakes (NH and SH, respectively; Fig. 2b). These 2 groups differed significantly based on a global ADONIS test ($p = 0.001$, $R^2 = 0.26$). The NH lakes were associated with high visibility, macrophyte coverage, piscivorous fish biomass, total large zooplankton biomass, and mean depth, whereas the SH lakes were related to the same variables as the lowland lakes (Fig. 2b).

Some of the key bioclimatic and environmental variables, critical for separating the 3 lake groups, were used to compare the lakes pairwise (Fig. 3). Lake area, mean depth, cyanobacteria biomass, and the proportion of small fish significantly differed only between the northern highland and lowland lakes (Fig. 3a, b, f). The lowland lakes were larger, shallower, and had a higher cyanobacteria biomass and proportion of small fish than the highland lakes. Salinity and livestock density in the catchment differed only between the northern and southern highland lakes, being lower in the northern highland lakes (Fig. 3c, k). Pairwise comparisons showed that TN and Chl-*a* concentrations were significantly different between the northern and southern highlands lakes and between the northern highland and lowland lakes (Fig. 3d–e). Piscivore biomass and the amount of fertiliser used in the catchment differed significantly among all the lake groups; piscivore biomass was highest in the northern highland lakes, and fertiliser use was highest in the lowland lakes (Fig. 3h, j). Macrophyte coverage did not differ among the lake groups (Fig. 3) but tended to be slightly higher in the northern highland lakes.

Discussion

The results from our study lakes, representing different elevations and latitudes corresponding to different climatic and hydrological conditions and land uses, indicated that temperature, nutrients, and salinity critically affected the trophic structure, community composition, richness, and evenness of organisms at multiple trophic levels. Temperature was the most influential variable, affecting trophic structure and community composition, followed by nutrients (TN) and salinity, which was most critical for richness and evenness of various trophic groups (Table 2). We also found major differences between the lakes in the northern highlands and the other regions (southern highland lakes and lowland lakes).

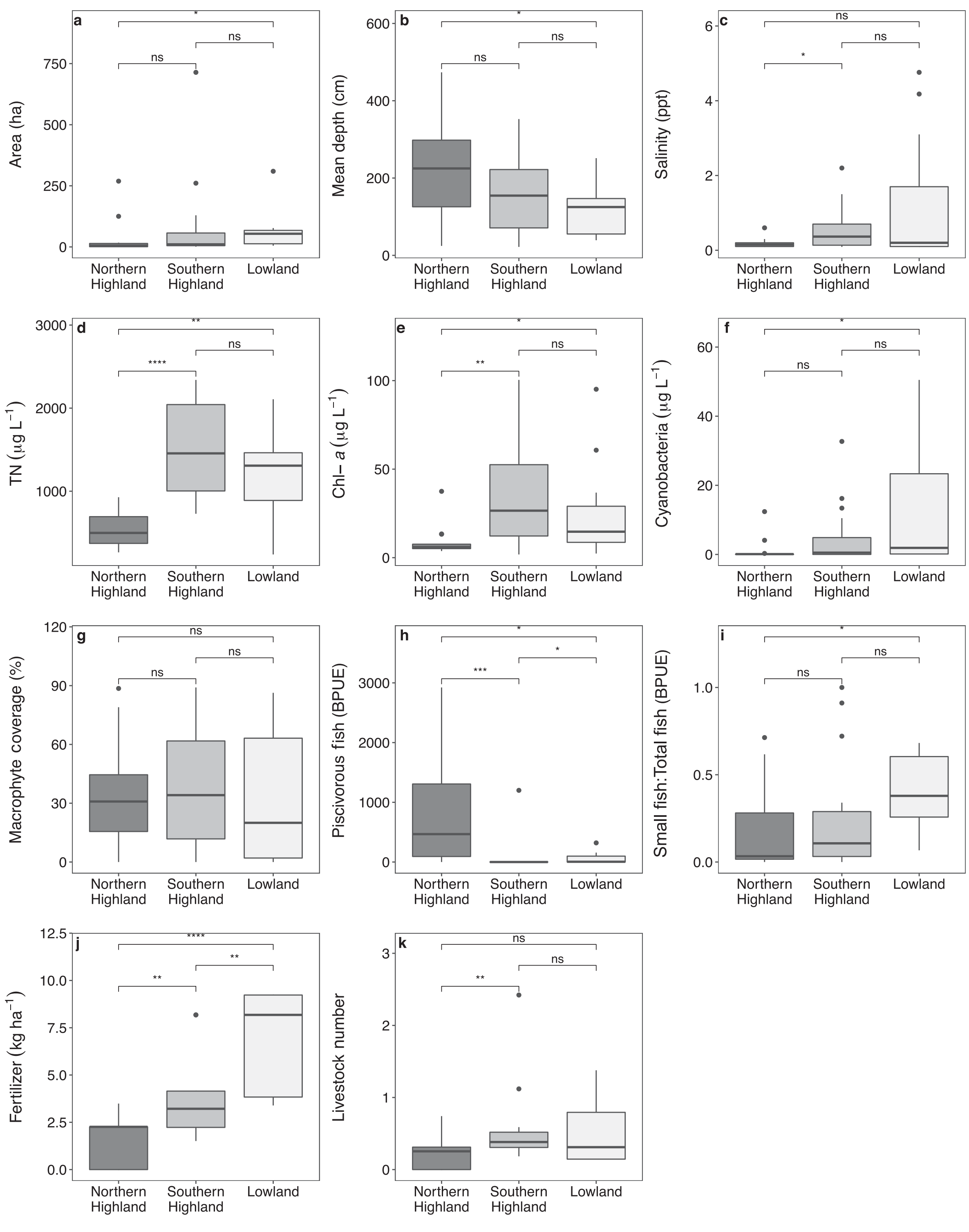

Figure 3. Box and whiskers plots of environmental variables in relation to lake groups. Northern highland ($n = 14$), Southern highland ($n = 16$), and Lowland lakes ($n = 11$): (a) area, (b) mean depth, (c) salinity, (d) TN, (e) Chl-*a*, (f) cyanobacteria, (g) macrophyte coverage, (h) piscivorous fish, (i) proportion of small fish, (j) fertiliser use, and (k) livestock number in the catchments. The box was drawn from the first quartile to the third quartile, the middle is the 50% quartile or median, and the whiskers are from each quartile to the minimum or maximum. For testing the significance between groups, Wilcoxon rank sum test was employed. Significance level: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Influence of temperature (climate)

The GLM analyses including air temperature, TN, and salinity revealed that temperature was of key importance. The Chl-*a*, Chl-*a*:TP ratio, cyanobacteria:phytoplankton ratio, proportion of small fish, fish:zooplankton ratio, and rotifer biomass all increased with temperature, whereas BPUE of piscivores, fish, and the zooplankton: phytoplankton ratio decreased. Together these results concur with those of other multi-trophic level comparative studies from European lakes and experimental investigations (Gyllström et al. 2005, Meerhoff et al. 2012, Jeppesen et al. 2015) as well as with a recent cross-Atlantic comparison of shallow lakes in Florida (USA) and Denmark (Jeppesen et al. 2020). A higher yield (Chl-*a*: TP) in warm lakes has also been recognised in other latitudinal gradient studies (Mazumder and Havens 1998, Flanagan et al. 2003) and may, in part, reflect a decline in the grazing control of zooplankton on phytoplankton because fish predation is higher on large-bodied zooplankton (Jeppesen et al. 2009). This finding is supported by the decrease in the biomasses of large zooplankton and cladocerans and the zooplankton:phytoplankton ratio with increasing temperatures observed in our study. The significant reduction in piscivore biomass with increasing temperature likely reduced the predation control on planktivores. Accordingly, total fish density (NPUE) increased significantly with temperature (Table 2). Similar findings were obtained from 81 shallow European lakes, spanning a wider latitudinal gradient (Sweden to Spain), and (sub)tropical lakes (Gyllström et al. 2005, Meerhoff et al. 2007, Iglesias et al. 2008). Low abundance of piscivores with increasing temperature may reflect that consumption of animals is less appealing at higher temperatures (Moss 2010, González-Bergonzoni et al. 2012). A more detailed study on fish abundance and community structure undertaken in the same study lakes as those used in our investigation suggested that temperature was among the most important factors contributing to fish species richness, especially the proportions of small omnivorous and zooplanktivorous fish (Boll et al. 2016). Similarly, the impact of temperature on fish richness has been evidenced in large-scale comparative cross-latitudinal studies on shallow and deep lakes, where higher contributions of small, fast-growing species were recorded in subtropical and Mediterranean regions than in cold temperate areas (Blanco et al. 2003, Blanck and Lamouroux 2007, Jeppesen et al. 2012, Brucet et al. 2013, Emmrich et al. 2014).

Furthermore, the biomass of cyanobacteria and their share of the total phytoplankton biomass increased with increasing temperature, as expected (Jeppesen et al. 2009, Paerl and Huisman 2009, Moss et al. 2011, Havens et al. 2019).

Macrophyte PVI, richness, and evenness significantly decreased with increasing temperature, possibly an indirect temperature effect because warm lakes are also more nutrient-rich with low water clarity, leading to disappearance of shade-intolerant species (Jeppesen et al. 2000). Evidently, nutrient availability further decreased the macrophyte coverage (Table 2), although this was unimportant for PVI. Analyses of surface sediment remains of aquatic plants from many of the current study lakes revealed nutrients and salinity as the most important environmental variables determining community composition (Levi et al. 2014), although the current study could not fully confirm these findings.

Influence of nutrients (TN)

As expected from numerous previous studies (Carpenter et al. 2001, Jeppesen et al. 2009, 2011, 2020), several of the environmental variables studied were related to nutrients (TN), mostly together with temperature but also alone, and in a few cases with salinity (Table 2). Chl-*a*, phytoplankton biomass, the biomass of cyanobacteria, and various groups of zooplankton and fish (NPUE) all increased, reflecting the higher availability of resources. Moreover, we noted a decrease in the evenness of both zooplankton and phytoplankton. Land use clearly had a significant effect on nutrient concentrations; however, elevated nutrient concentrations may also, in part, reflect drier conditions, leading to a decline in the nutrient retention capacity and to less water to hold nutrients because lake volume is reduced. Supporting this view is a mass balance study undertaken in 2 Turkish lakes over a 20-year period indicating a reduced nitrogen and phosphorus retention capacity during periods with less precipitation and warmer temperatures, leading to higher nutrient availability (Özen et al. 2010, Coppens et al. 2016, Beklioğlu et al. 2017).

Influence of salinity

For a few variables, salinity also contributed to the variation. Salinity had strong and negative effects on the richness and evenness of phytoplankton and zooplankton. An analysis of surface sediment remains of cladocerans collected from some of the current study lakes also revealed that salinity and nutrients were the most important environmental variables determining community composition, richness, and diversity (Çakıroğlu et al. 2014). A similar response was reported for macrophytes by Levi et al. (2014). Salinity has been identified as an important stressor in other studies as well (for phytoplankton see Larson and Belovsky 2013; for zooplankton see Brucet et al. 2009 and Gutierrez et al. 2018), causing osmotic stress in salt-sensitive zooplankton taxa, which affects survival, reproduction, and growth (Aladin 1991, Aladin and Potts 1995, Jeppesen et al. 2007, Bezirci et al. 2012, Gutierrez et al. 2018). Although salinity had a negative effect on fish biomass, it did not influence fish richness and evenness. Increased salinity can be expected in the future in Mediterranean lakes as a result of precipitation deficiency and enhanced net evaporation induced by climate change (Pachauri et al. 2014). A long-term monitoring study conducted in 2 southern highland shallow lakes in Turkey evidenced that prolonged drought with a duration of 3–4 years resulted in a 3-fold increase in salinity and a shift to a meso-saline state (from 1.2‰ to 3.2‰ and 1.0‰ to 2.8‰, respectively; Beklioğlu and Tan 2008, Beklioğlu et al. 2017).

Influence of additional variables

Morphological factors (e.g., depth, area), such as the large lake area range in our study lakes, sometimes override the effect of environmental drivers. Larger lakes may have more species as more niches are offered, but in our study, lake area emerged as a significant factor only for richness of zooplankton (as found elsewhere, Dodson 1992) and the biomass of zooplankton, especially the large zooplankters including cladocerans. Accordingly, fish predation pressure on zooplankton (as indicated by the fish to zooplankton biomass ratio) and Chl-*a*:TP decreased with the lake area. Moreover, in addition to the effects of temperature, TN, and salinity, fish density (NPUE) contributed significantly to the variation in Chl-*a* and the cyanobacteria:phytoplankton biomass ratio, which was higher when NPUE was higher, typical for lakes with higher fish predation pressure on large-bodied cladocerans (Jeppesen et al. 2009). None of the zooplankton variables was related to either macrophyte cover or PVI, in contrast to the northern lakes in which macrophytes offer reliable refuges against fish predation (Meerhoff et al. 2007, 2012). Our findings of weak or no refuge effects is in line with in situ experiments conducted in some of the current study lakes as well as laboratory experiments (Tavşanoğlu et al. 2012, 2015) and cross-climate experiments with artificial plants (Meerhoff et al. 2007, 2012).

Northern and southern highland and lowland lakes

The NDMS revealed some overlap between highland and lowland lakes, mainly attributed to a relatively high agricultural effect (higher fertilisation) as well as warmer temperatures in some of the southern highland lakes and the lowland lakes. Moreover, the northern highland lakes clearly distinguished themselves from the southern highland lakes. The northern highland lakes were characterised by low agricultural impact (low fertiliser use as well as low livestock density), higher net precipitation, low air temperature, higher water depth, low concentrations of nutrients and low Chl-*a*, clear water conditions, high biomass of large-bodied zooplankton, high proportions of piscivorous fish, and high macrophyte coverage, although the latter was not significantly different (Fig. 2b and 3). The high biomasses of piscivorous fish and large-bodied zooplankton (e.g., cladocerans) and the indication of high zooplankton grazing pressure suggest low top-down control by fish on the zooplankton in the northern highland lakes. Similar conditions are found in north temperate, relatively nutrient-poor lowland lakes (e.g., Jeppesen et al. 2000). A study by Brucet et al. (2017) on the predation effect of size-structured predators (i.e., predation by individuals of different sizes) on prey size structure, using data from some of the current study lakes, revealed that highly size-diverse fish assemblages including large piscivorous fish occurring in the northern highland lakes were associated with highly size-diverse zooplankton assemblages, comprising also large-sized cladocerans, as we found in the highland lakes. Meanwhile many of the characteristics of the lowland lakes were shared with southern highland lakes, being overall larger, more saline, and more eutrophic, with higher TN and Chl-*a* concentrations, cyanobacteria biomass, and a larger proportion of small fish (Fig. 2 and 3).

Conclusions, caveats, and perspectives

Enhanced temperature along with eutrophication and salinity seemed to be the key factors controlling the trophic structure, community composition, and richness and evenness of organisms at different trophic levels in Turkish shallow lakes. However, possible biogeographical effects cannot be fully excluded, although we sought to minimise these in our study by employing a large climate gradient over a short geographical distance. That we found a similar response pattern in the Turkish lakes to other latitude studies covering much larger latitudes and thus biogeographical gradients, however, suggests that the observed responses to temperature, nutrients, and salinity are a real functional response and not strongly influenced by biogeography.

Climate change-induced extreme heat waves and drought events are anticipated to occur more frequently and with higher intensity in semiarid Mediterranean climatic regions in the future (Pachauri et al. 2014).

Moreover, the land affected by drought is expected to double in size from 2000 to 2100 (IPCC 2007), entailing a risk of much higher water temperatures and, in turn, higher salinisation and risk of eutrophication. These conditions will cause extensive phytoplankton growth, probably with frequent cyanobacteria blooms in shallow lakes or, perhaps, complete drying, as already observed for some lakes (Graveline et al. 2012, Bucak et al. 2017, Sabater et al. 2018, Gozlan et al. 2019). To counteract the effect of warming, strict control of nutrients in shallow lakes seems to be a prerequisite to avoid cyanobacteria blooms and turbid water. In addition to nutrient control, restrictions on water use, especially for irrigation purposes, are needed to mitigate the adverse impacts, especially because >80% of the freshwater abstraction in most Mediterranean countries is used for irrigation (Katerji et al. 2008).

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