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The relative importance of dispersal and local factors in structuring phytoplankton communities in high mountain lakes in the Pyrenees

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ABSTRACT

Evaluating the relative contributions of local environmental versus regional spatial descriptors to the shaping of phytoplankton communities provides an understanding of the community dynamics of high mountain lakes. The present study elucidated the role of lake morphometric, physicochemical, biological, and spatial descriptors in determining the patterns in phytoplankton diversity and community composition based on taxonomic and morphologically based functional groups. We collected samples of phytoplankton, zooplankton, and abiotic variables from 24 Pyrenean lakes. The influence of environmental factors on alpha diversity was analyzed using generalized linear models, and the influence on beta diversity was analyzed using linear regressions. To detect biogeographical patterns, we performed Mantel correlation tests, and to identify the environmental drivers of the phytoplankton community composition, we performed redundancy analysis. We found that only local environmental factors significantly contributed to the phytoplankton community structure in high mountain lakes, with nutrient- and light-associated variables being the major drivers of local and regional diversity and compositional variations. Our results suggested that total phosphorus significantly affects alpha and beta diversity patterns. This study highlighted that niche-related local factors are the main drivers to explain phytoplankton composition, and that dispersal limitation is not notably influential in high mountain lakes within the Pyrenean Lake district.

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alpha and beta diversity; environmental filtering; functional classification; lakes; phytoplankton; Pyrenees

Introduction

Elucidating the factors that shape the structure of natural communities is a primary goal in ecology. Environmental factors and niche differences between species primarily determine communities in local areas, and evolutionary, historical, and climatic drivers affect regional patterns of biota (Jenkins and Ricklefs 2011). The metacommunity theory offers a comprehensive framework for understanding local (e.g., environmental filtering) and regional (e.g., dispersal) influences on species composition (Leibold et al. 2004). While this theory underscores the importance of dispersal in connecting local communities, it also acknowledges that certain organisms, such as phytoplankton, may exhibit minimal dispersal limitations due to their microscopic size (Finlay 2002, Huszar et al. 2015, Rusanov et al. 2022, Buchaca and Catalan 2024). Because the relative role of local environmental versus regional factors vary with several determinants, such as spatial scale, habitat type, and dispersal capabilities, it is crucial to recognize that local and regional mechanisms act together in the structuring of natural communities by quantifying their relative contributions within a landscape (Cottenie 2005, Heino et al. 2015).

High mountain lakes provide good natural systems for investigating the macroecological effects of local and regional factors on assemblage composition because these lakes exhibit distinctive characteristics in terms of physical, chemical, and biological factors despite their similar locality and origin (Catalan et al. 2006, Moser et al. 2019). Because high mountain lakes tend to appear in groups that form lake districts (e.g., the Pyrenees), the accumulation of similar ecosystems within relatively short distances should necessarily affect metapopulation dynamics (Catalan et al. 2009, Catalan and Donato Rondon 2016). High mountain lakes are usually embedded in areas of high natural value, and the responses of their aquatic communities to various factors are thus indicative of the response of these ecosystems to anthropogenic pressures and climate change (Camarero et al.

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2004, Miró and Ventura 2013). Although these systems have been the focus of global change research as mostly pristine systems in remote areas (Ventura et al. 2000, Catalan et al. 2006), the specific ecological drivers (e.g., environmental versus spatial factors) that are more important in structuring their community species composition are understudied (Felip et al. 1999, Tolotti et al. 2003).

Taxonomic composition has been used to describe community properties and environmental variation (Lehtinen et al. 2017, Rozema et al. 2017). However, the picoplankton components generally observed in high mountain lakes are difficult to distinguish and measure via microscopy because of their small size. As alternatives to taxonomic classification, trait-based approaches make environmental investigations comparable and facilitate evaluation of environmental responses to varied conditions (Kruk et al. 2002, Naselli-Flores et al. 2003, Weithoff 2003). Classifying phytoplankton into functional groups has been used as a powerful and complementary tool to describe the dynamics of phytoplankton community assemblages and their ecological functions (Reynolds et al. 2002, Salmaso and Padisák 2007, Padisák et al. 2009, Kruk et al. 2010). The morphologically based functional classification developed by Kruk et al. (2010) is based solely on morphological characteristics such as cell volume and surface area, the presence of flagella, and colony length. This approach defined 7 morphology-based functional groups (referred to as functional groups throughout the manuscript) that are easier to identify and more effective for comparisons of many lakes and for monitoring aquatic systems using multiple temporal scales (Salmaso 2010, Izaguirre et al. 2012, Allende et al. 2019).

The present study collected phytoplankton data from 24 lakes located in the central Pyrenees (northeast Iberian Peninsula) to examine diversity indices and the community structure of taxonomic and functional groups. Our objectives were to identify which factors were more important in explaining phytoplankton community diversity and the main drivers shaping diversity patterns and compositional variations. This study considered spatial variables (e.g., latitude and longitude) and numerous environmental variables encompassing the geographic setting, the lake biotic environment (e.g., zooplankton and fish), the physical environment (e.g., lake area and light), and water chemistry (e.g., nutrients, conductivity, and pH). Our hypothesis posits that local environmental factors play a more significant role than lake morphometric or regional spatial factors in shaping phytoplankton composition, stemming from the observation that Pyrenean lakes exhibit relatively similar morphometric characteristics and that the high dispersal capabilities of phytoplankton suggest minimal distributional constraints at the scale of the Pyrenean Lake district. Additionally, we aimed to assess the applicability of morphologically based functional classification in elucidating the relationships between local environmental conditions and phytoplankton composition.

Materials and methods

Study sites and sampling

We selected 24 Pyrenean lakes in 3 protected areas of the Natura 2000 network of the European Union (Supplemental Table S1, Fig. 1): 13 located in Alt Pirineu Natural Park, 10 in Aigüestortes i Estany de Sant Maurici National Park, and 1 shallow lake in the Aran Valley, Estanho de Vilac. These Pyrenean lakes have a glacial origin and high elevation with a median value of 2266 m a.s.l. (range 1638–2445). The median surface area is 2.03 ha (0.2–6.8 ha), and the median lake depth is 7.1 m (2.4–33.6 m). These lakes are primarily polymictic lakes covered by ice and snow for 5–6 months annually. Although Pyrenean lakes are regarded as natural and pristine because of their remote location, various anthropogenic perturbations, such as the introduction of alien fish species and the presence of livestock and tourists, have been observed. As a result, increases in the phytoplankton biomass and decreases in the water column transparency were observed in some lakes.

The lakes were sampled once between July and August in 2014 (12 lakes), 2016 (10 lakes), and 2017 (2 lakes). Samples for nutrients (total phosphorus [TP] and dissolved inorganic nitrogen [DIN]), conductivity, and pH were collected at the lake outlet when available or from the lake surface at the center of the lake. Samples for the study of phytoplankton were collected by boat from the deepest point of the lake using a water sampler (USB 50015, UWITEC GmbH, Austria). To facilitate the lake comparison, we standardized sampling by collecting water at an iso-irradiance depth in the deepest part of each lake at 1.5 times the Secchi disk depth. At this depth, 1–10% subsurface irradiance penetrates in summer, usually coinciding with a typical deep chlorophyll maximum (DCM; Catalan et al. 2002, Callieri et al. 2007) resulting from a phytoplankton growth optimum at a depth balancing nutrient and light availability (Pechlaner 1971). In shallow lakes with >10% surface irradiance reaching the bottom and weak stratification, a DCM develops near the lake bottom, as observed by previous studies (Rodhe et al. 1966); therefore, samples were collected 1–2 m above

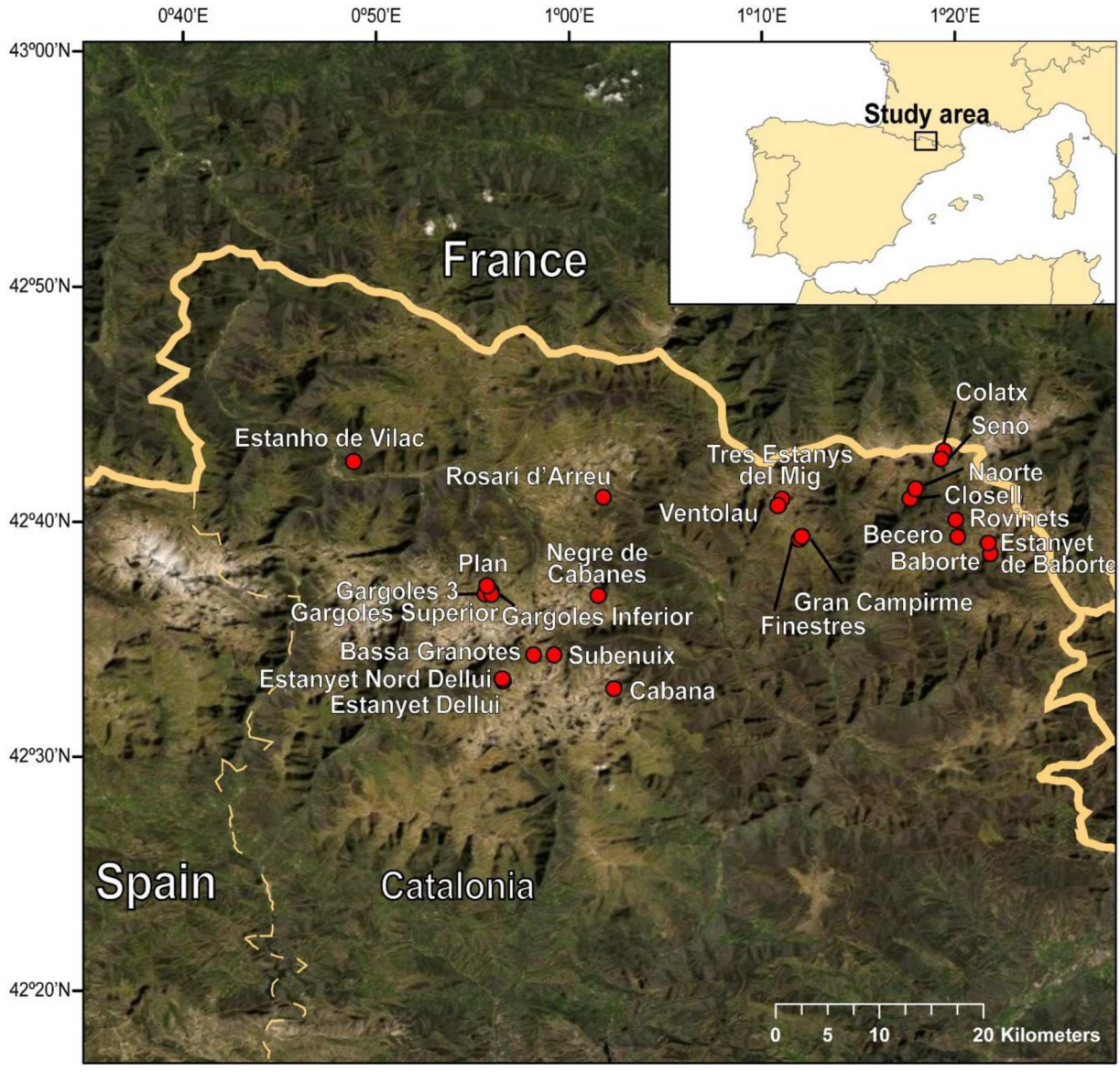


Figure 1. Location of the 24 studied lakes.

the surface sediment in 10 lakes where the Secchi depth reached the sediment surface. To quantify the light availability within the water column, we estimated the light attenuation coefficient in the water column (K_D; m^{-1}) from Secchi disk measurements (Z_{SD}; m) with the relation:

$$K_D = K/Z_{SD},$$

where K = constant = 1.7 (Poole and Atkins 1929). A constant attenuation coefficient of 0.2 m^{-1} was used in lakes where the Secchi disk reached the bottom, following median values obtained for the set of study lakes (Table 1). Conductivity was measured using a WTW PTI-10 conductivity meter (Xylem; https://www.xylemanalytics.com). Nitrate, nitrite, and ammonium were determined using an AA3 HR autoanalyzer (Seal Analytical, Mequon, WI, USA) following Grasshoff et al. (2009). DIN was calculated as the sum of nitrate, nitrite, and ammonium. TP was estimated using an AA3 autoanalyzer after previous digestion with acid persulfate (Koroleff method cited in Grasshoff et al. 2009). Chlorophyll *a* (Chl-*a*) was extracted using 5 mL of 90% acetone via sonication, and the Chl-*a* concentration was calculated using the equations of Jeffrey and Humphrey (1975). To count phytoplankton, 125 mL of water was collected and fixed with Lugol (1% final concentration) for microscopic enumeration of microphytoplankton and ciliates (Utermöhl 1958).

Because single or 2 fish species were observed in each lake, lakes were grouped into 3 categories depending on the fish species present: lakes with trout (*Salmo trutta*,

Table 1. Descriptive statistics of variables indicating lake morphometric, local environment, and geographical characteristics along the Pyrenean lakes.

Variables		Abbreviation	Min	Max	Median
Lake morphometry	Lake area (ha)	Larea	0.194	6.764	2.036
	Lake depth (m)	Ldepth	2.4	33.6	7.1
Local environment	Conductivity (μS cm^{-1})	Cond	3.82	106.90	15.22
	pH	pH	6.12	9.37	7.51
	Total phosphorus (μg L^{-1})	TP	0.2	21.2	6.25
	Dissolved inorganic nitrogen (μg L^{-1})	DIN	1.3	166.5	21.4
	Light attenuation coefficient (m^{-1})	K_D	0.189	2.237	0.204
	Chlorophyll *a* (μg L^{-1})	Chl-*a*	0.2	27.7	1.1
	Macrozooplankton (μg C L^{-1})	MZP	0.007	397.9	20.5
	Rotifera (μg C L^{-1})	Rotifera	0.001	84.17	0.84
Geography	Elevation (m)	Elv	1638	2445	2266
	Longitude (°W)	Lon	0.81401	1.36446	1.03898
	Latitude (°S)	Lat	42.54800	42.71680	42.65387

Min, Max, and Median indicate the minimum, maximum, and median values of the variables, respectively.

Salvelinus fontinalis, or *Oncorhynchus mykiss*), lakes with minnows (*Phoxinus* sp.; Miró and Ventura 2013, 2015), and fishless lakes.

Phytoplankton and zooplankton analyses

The abundance of phytoplankton was estimated using the Utermöhl methodology (Soumia 1978). Subsamples of 10 mL (lakes with Chl-*a* > 15 μg L^{-1}) and 50 mL (lakes with Chl-*a* < 15 μg L^{-1}) were transferred to settling chambers. After 24 h of sedimentation, sedimented algae were identified to species or genus and enumerated using an inverted microscope (Zeiss, Model Axioskop 40). We counted large taxa (>20 μm) at 100× magnification, scanning 50% of the chamber. The most common species were counted in >20 randomly selected fields at 400–650× magnification. Smaller taxa were counted at 400–650× magnification on 2–3 perpendicular transects across the chamber. The biovolume was calculated based on approximations of cell shapes by appropriate geometric formulae (Hillebrand et al. 1999).

We obtained 130 species belonging to 77 genera that were subsequently grouped into functional groups (Supplemental Table S2; Kruk et al. 2010). This classification resulted in 7 groups based on the morphological traits of the phytoplankton, including colony formation, the presence of flagella, mucilage, siliceous exoskeletal structures, aerotopes, and heterocysts. The maximum linear dimension was characterized using light microscopy and estimates of volume and surface/volume relationships (classification details in Supplemental Table S3).

Planktonic crustaceans were collected with a Hensen-type net (0.027 m^2 and 200 μm mesh size) from the deepest lake area, including 3 vertical trawls that were pooled in a single sample. The rotifer samples were taken with a water sampler (USB 50015, UWITEC GmbH, Austria) by collecting almost 12 L from different depths integrating the whole water column and were subsequently filtered with a 50 μm width mesh. Samples were fixed with formol or Lugol for posterior analysis. The zooplankton species were identified by separating adult individuals from each species under a binocular magnifying glass. Individuals were identified under a stereomicroscope according to Dussart (1969), Einsle (1992), Keifer (1978) for Copepoda, Alonso (1996) for Cladocera, and Voigt and Koste (1978) for Rotifera. To calculate the biomass, a minimum of 250 individuals per aliquot were counted under an inverted microscope (Olympus IMT-2), or the total sample was counted when the material was scarce. Biomass was converted to carbon following the procedure of Staškrabová et al. (1999).

Statistical analyses

Prior to the following analyses, relative abundance data for the taxonomic and functional groups were double-square rooted to reduce the weight of the more abundant groups (Salmaso 2010). Variables describing morphometric, physicochemical, and biological factors and site coordinates (latitude and longitude) were scaled using min–max normalization after some environmental variables (lake area, conductivity, DIN, Chl-*a*, and K_D) and biological variables (rotifers and macrozooplankton) that showed skewed distributions were log transformed or double-square rooted. The normalization method provides interpretability on the importance of each variable with robustness to outliers when combined with appropriate data preprocessing (Faußß et al. 2021). Linear models were used for unconstrained ordinations (principal component analysis [PCA]; ter Braak and Verdonschot 1995) of environmental variables. Computations were performed using CANOCO 5.0 (Ter Braak and Smilauer 2002).

The phytoplankton community composition was examined via hierarchical clustering based on the

Bray–Curtis distances of the taxonomic group composition and the Sørensen distances of the functional groups across Pyrenean lakes. Given the complexity of plankton taxonomy and extensive variability in species composition across different lakes, aggregating the information at the genus level allowed a more comprehensive and comparative assessment of community structure and function. We applied 2 indexes: Bray-Curtis index considering abundance information to detect differences based on species abundance, and Sørensen index based solely on presence–absence information to provide insights into species turnover between communities. To illustrate the relationships between compositional variations in taxonomic and functional groups and 13 environmental variables (Table 1), we performed distance-based redundancy analysis (db-RDA), a constrained linear ordination method that allows non-Euclidean dissimilarity matrices (e.g., Bray–Curtis and Sørensen distances) in RDA (Borcard et al. 2011). A significance test of db-RDA was performed based on 999 permutations to generate a null distribution under the assumption of no relationship between the phytoplankton composition based on taxonomic and functional groups and the environmental variables (ter Braak and Verdonschot 1995). The backward stepwise selection was performed by first including all variables and then removing step-wise the variables that did not significantly explain beta-diversity variations based on the *p* value. The explained variation in the axes and the significance of the predictor variables were assessed using the *capscale* and *anova* functions of the *vegan* R package.

Because 1 or 2 different fish species were observed in each lake, the effects of fish on phytoplankton communities were examined by testing differences in phytoplankton community composition among fish-based lake categories by applying a multivariate permutational analysis of variance using distance matrices (PERMANOVA). To examine whether the presence of fish affected the phytoplankton community, nonmetric multidimensional scaling analyses (NMDS) were applied to the Bray-Curtis dissimilarity matrix with 999 permutations of the double-square rooted biovolumes of taxonomic and functional groups. The categorical variable "introduced presented fish" was constructed to partition the rows in classes belonging to the same fish group. The functions *odispider* and *ordihulls* from the *vegan* R package were applied, in which the categorical variable "presented dominant fish" grouped the samples belonging to the same fish species. To further test whether the centroids had different positions, we performed a PERMANOVA using the *adonis* function with 999 permutations (Oksanen et al. 2013).

Alpha diversity, measured by the Shannon-Wiener index, and beta diversity, measured by the Bray-Curtis and Sørensen indices, were calculated for taxonomic composition and functional groups to investigate the environmental factors that determine diversity (Shannon 1948, Bray and Curtis 1957). To characterize alpha diversity of each lake, sample-based rarefaction curves were computed to generate the expected number of species by standardizing species richness by the sampling effort applied (Gotelli and Colwel 2001). Rarefaction analyses were performed using the *rarefy* and *rarecurve* in the package *vegan* in R. Generalized linear models (GLMs) were used with 13 variables as predictors to assess how environmental factors affect the alpha diversities of taxonomic compositions and functional groups (Pekár and Brabec 2016). The alpha diversities of each group were modeled with combinations of predictors with optional model inclusion rules. For model selection, the set of models was identified and averaged according to the criterion $\Delta AICc < 4$ using the *dredge* function in the *MuMIn* package. The contribution of each variable was estimated by summing the Akaike weights (AICc-w) of the models selected as the "best models," and the coefficients were estimated by adopting a model averaging approach (Kim and Kwak 2022). Pearson correlation analysis was used to evaluate the relationships between taxonomic and functional alpha diversity.

The relationships of beta diversity with morphometry, local environment, and geography were examined using linear regression (Pekár and Brabec 2016). Lake morphometry was assessed using 2 variables (lake area and lake depth) based on the Euclidean distance, and local environment heterogeneity was measured using 8 variables (pH, conductivity, TP, DIN, Chl-*a*, K_D, rotifera, and macrozooplankton) based on the Euclidean distance using the *dist* function of the *stats* R package. Geographic distances were calculated based on the lake elevation and longitude and latitude points using the *distm* function of the *geosphere* package. To test the significance of correlation coefficients between matrices of compositional similarity of taxonomic and functional groups and environmental distances (lake morphometry, local environment, and geography), we performed a Mantel test with 999 permutations (Legendre et al. 2005). The Mantel test performed on the basis of the entire dataset was used to test for correlations between similarity matrices of taxonomic and functional group compositions using the Bray-Curtis and Sørensen indices, respectively. We also performed partial Mantel tests to examine the pure effect of each distance in the compositions after controlling for the effect of other

distances (Legendre and Legendre 2012). All the statistical analyses were performed in R 3.1.0 and visualized in RStudio 3.0.0 (R Core Team 2018).

Results

Phytoplankton biovolume and environmental characteristics

The summary of lake morphometric, physicochemical, and biological factors observed in the studied lakes Table 1, Fig. 2) indicates that most lakes were oligotrophic ($n = 19$) and mesotrophic ($n = 5$) in terms of TP, with a range of 0.2–29 μg L^{-1}. Of the 24 lakes, 7 had minnows, 12 had trout, and 5 were fishless. Lakes with high TP concentrations had high Chl-*a* concentrations, high Rotifera biomass, and minnows (*Phoxinus* sp.), and lakes with low TP and high DIN concentrations had high macrozooplankton biomass. Lakes with trout were distinctive and associated with large lake area and depth and lower elevation. The environmental characteristics of the fishless lakes were intermediate along the trophic gradient and showed high pH and conductivity values.

Phytoplankton biovolume was low in Pyrenean lakes, with a median value of 0.5 mm^3 L^{-1} and a range of 0.1–21.2 mm^3 L^{-1}. Three samples, Lake Closell in 2014 (6.8 mm^3 L^{-1}), Lake Ventolau in 2016 (16.7 mm^3 L^{-1}), and Lake Gargolhes Inferior in 2016 (21.2 mm^3 L^{-1}), had the highest biovolumes. Among the taxonomic

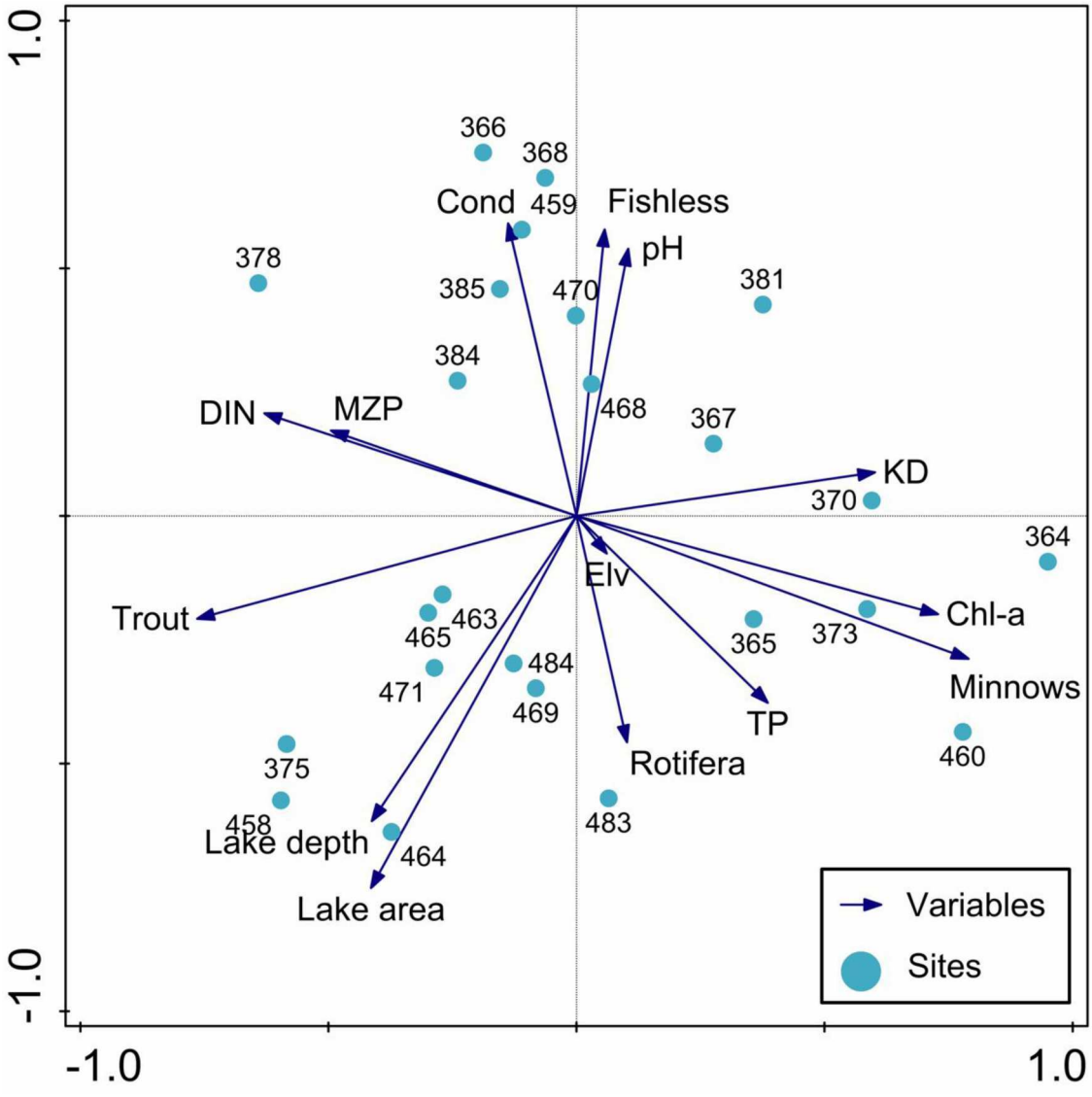


Figure 2. Principal component analysis of environmental variables included in the study. Abbreviations: Chl-*a* = chlorophyll *a*; Cond = conductivity; DIN = dissolved inorganic nitrogen; Elv = elevation; K_D = light attenuation coefficient; MZP = macrozooplankton; TP = total phosphorus. Lake codes described in Supplemental Table S1.

groups, 130 species belonging to 77 genera were identified within the study lakes (Supplemental Table S2). *Chlamydomonas* (5 lakes) and *Cryptomonas* (5 lakes) were the predominant genera and accounted for 16.7% and 14.4%, respectively, of the total biovolume. *Peridinium* sp. was the dominant species in 3 lakes (9.78%), and *Fragilaria nanana* was the dominant species in 3 lakes (8.3%). Of the 7 functional groups identified, unicellular flagellates of medium size (Group V) were the dominant group in 18 lakes and accounted for 53.2% of the total biovolume.

Phytoplankton compositional variations in relation to environmental variables

The 24 observations in Pyrenean lakes were clustered into 4 clusters for taxonomic composition and 3 clusters for functional composition (Fig. 3). For the taxonomic

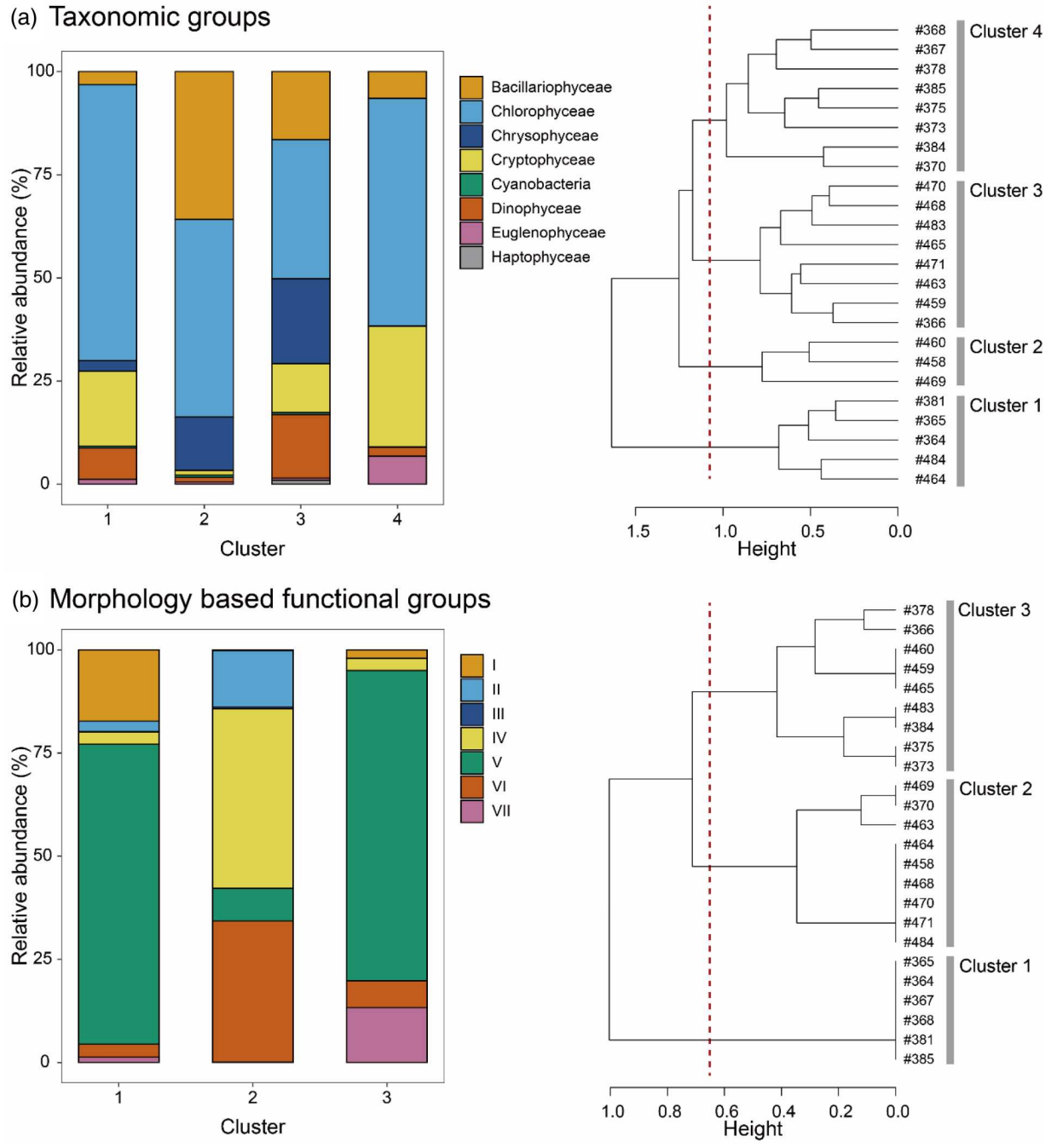


Figure 3. Phytoplankton community composition based on the relative abundance (% biovolume) and clustering results of (a) the taxonomic groups (TGs) and (b) morphology based functional groups (MBFGs). Vertical red dotted lines highlight the cluster level used in the figure.

composition, all clusters had Chlorophyta as the dominant group. Cluster 1 was primarily composed of Chlorophyceae (66.9%), with low relative abundances of other taxonomic groups. The main component of cluster 2 and 4 was Chlorophyceae (47.8% and 55.1%, respectively), but the subdominant Bacillariophyceae (35.9%, cluster 2) and Cryptophyceae (29.2%, cluster 4) had a high abundance. Cluster 3 had a relatively even distribution among taxonomic groups. For the functional composition, the main component of clusters 1 and 3 was group V (72.7% and 75.2%, respectively), which consisted of medium to large unicellular flagellates. The subdominant group differed for each cluster. Group I (small organisms with a high surface/volume ratio) was the second most abundant group in cluster 1 (17.2%), and group VII (large mucilaginous colonies) was the second most abundant group in cluster 3 (13.3%). Cluster 2 was differentiated by the high

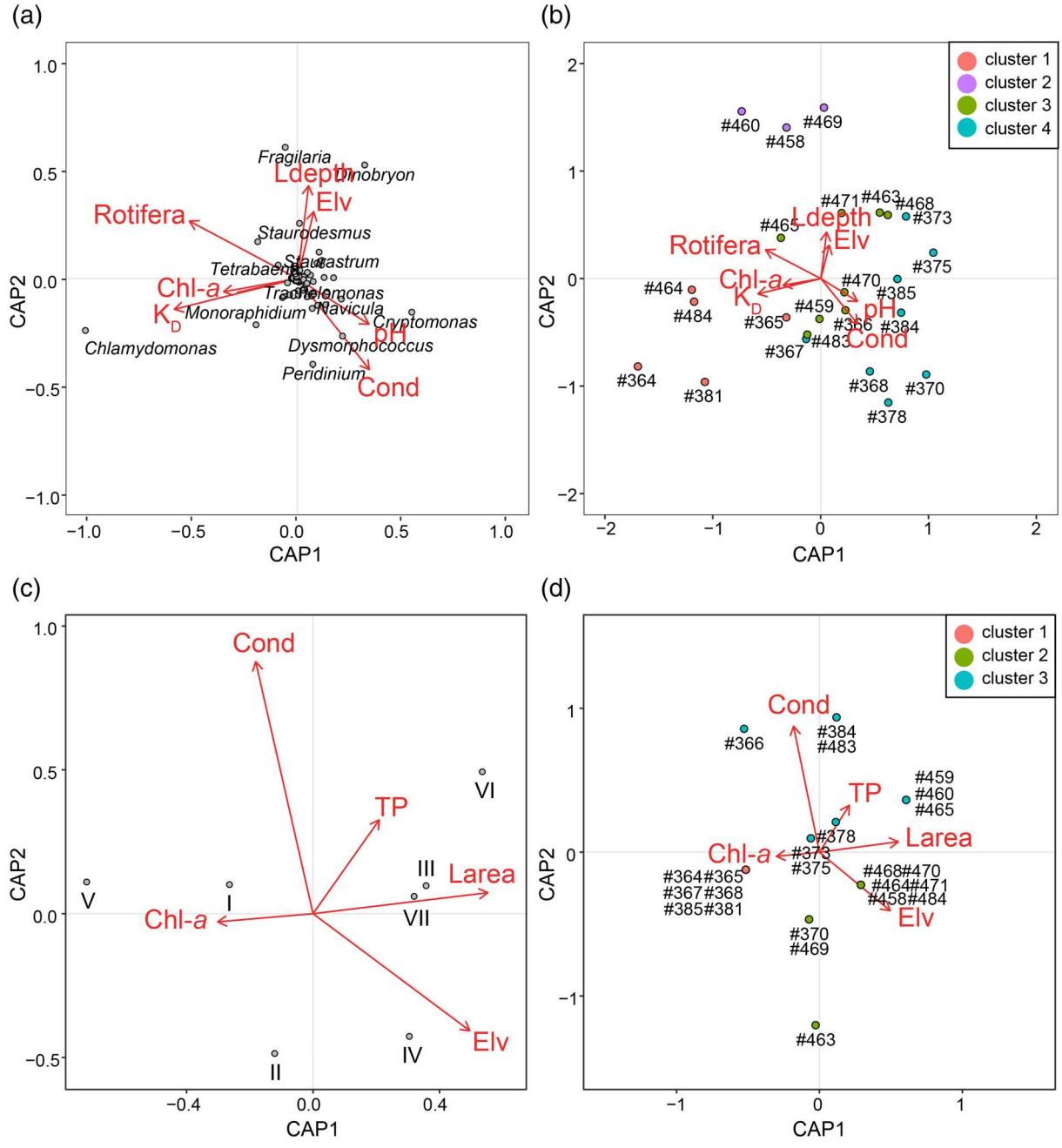


Figure 4. Distance-based RDA ordination biplots of (a) the phytoplankton taxonomic groups and (b) the lakes with the morphometric, local environmental, and geographic factors, and those of (c) the morphology based functional groups, and (d) the lakes with the morphometric, local environmental, and geographic factors. Abbreviations: Chl-*a* = chlorophyll *a*; Cond = conductivity; TP = total phosphorus. Only the top 15 abundant genera were displayed with their name; lake codes described in Supplemental Table S1.

abundances of group IV, medium-sized organisms lacking specialized traits (43.5%).

From the db-RDA for taxonomic and functional group composition, we identified significant factors affecting their variations (Fig. 4, Table 2). The analysis of the taxonomic groups revealed 7 factors that significantly ($p < 0.05$) affected the compositional variation with higher influences of local environmental variables: K_D ($F = 2.20$, $p < 0.01$), rotifers ($F = 1.92$, $p = 0.02$), and pH ($F = 1.84$, $p = 0.02$; Fig. 4a–b). The environmental variables explained 56.7% of the taxonomic group composition, and the first 2 axes accounted for 15.5% and 11% of the variation. The analysis of functional groups revealed 5 factors: Chl-*a* ($F = 5.44$, $p < 0.01$), conductivity ($F = 4.64$, $p < 0.01$), elevation ($F = 4.64$, $p < 0.01$), lake area ($F = 4.49$, $p < 0.01$), and TP ($F = 3.19$, $p = 0.03$), that significantly ($p < 0.05$) explained the observed compositional variation (Fig. 4c–d). The environmental variables explained 55.4% of the functional group composition, and the first 2 axes accounted for 31.8% and 18.4%, respectively, of the variation.

Permutational multivariate analysis of variance based on the NMDS indicated no significant difference in the centroid of the dominant fish species for segregating taxa ($F = 0.979$, $p = 0.450$) or for determining the functional group composition ($F = 0.744$, $p = 0.564$; Supplemental Fig. S2). This result demonstrated that the phytoplankton communities across the Pyrenean lakes studied were not significantly affected by direct effects of fish occurrence (i.e., trout or minnows).

Response of diversity indices to environmental variables

The rarefied alpha diversity ranged from 15.00 to 22.88 for the taxonomic composition and from 3.99 to 6.72 for the functional groups (Supplemental Fig. S1). The correlation between the taxonomic and functional group alpha diversities was high ($R = 0.63$, $p < 0.05$). The selected GLM models for the taxonomic and functional groups included K_D and TP as influential variables (Table 3, Supplemental Tables S4–S5). The alpha

Table 2. Result of environmental variable from the distance-based redundancy analyses for taxonomic and morphology based functional group composition.

	Taxonomic composition				Morphology-based functional group composition			
Variables	CAP1	CAP2	*F*	*p*	CAP1	CAP2	*F*	*p*
Lake area	Not selected				0.553	0.073	4.494	0.006
Lake depth	0.054	−0.447	1.755	0.021	Not selected			
Conductivity	0.333	0.439	1.653	0.044	−0.181	0.876	4.641	0.004
Total phosphorus	Not selected				0.209	0.326	3.191	0.036
Dissolved inorganic nitrogen	Not selected				Not selected			
Chlorophyll *a*	−0.325	0.013	1.718	0.047	−0.302	−0.028	5.435	0.001
Light attenuation coefficient (K_D)	−0.611	0.097	2.202	0.007	Not selected			
pH	0.320	0.204	1.841	0.020	Not selected			
Rotifera	−0.508	−0.286	1.918	0.022	Not selected			
Macrozooplankton	Not selected				Not selected			
Elevation	0.080	−0.317	1.759	0.032	0.495	−0.407	4.635	0.004
Longitude	Not selected				Not selected			
Latitude	Not selected				Not selected			

CAP1 and CAP2 indicates eigenvalues of the axis 1 and 2 of a canonical analysis on the principal coordinates.

Table 3. Coefficients and contributions of environmental variables from the averaged generalized linear models predicting alpha diversity of taxonomic groups (TGs) and morphology-based functional groups (MBFGs).

	TGs		MBFGs	
Variables	Coefficient	Contribution	Coefficient	Contribution
Lake area	0.478	0.036	0.462	0.096
Lake depth	−0.569	0.036	0.504	0.096
Conductivity	−0.473	0.033	−1.003	0.285
Total phosphorus	**5.465**	**1.000**	**1.588**	**0.959**
Dissolved inorganic nitrogen	−2.396	0.946	−0.180	0.037
Chlorophyll *a*	−1.502	0.062	0.982	0.141
Light attenuation coefficient (K_D)	**−6.258**	**1.000**	**−1.682**	**0.959**
pH	−1.170	0.072	−0.770	0.355
Rotifera	0.691	0.037	0.346	0.054
Macrozooplankton	1.433	0.179	0.353	0.064
Elevation	−0.487	0.032	1.595	0.842
Longitude	−1.254	0.174	−0.252	0.058
Latitude	−2.228	0.704	−0.180	0.102

Significant *r* values ($p < 0.05$) are indicated in bold.

diversities of taxonomic groups were well explained by the highest coefficients of K_D (−6.26) and TP (5.46), and those of functional groups were also highly affected by K_D (−1.68) and TP (1.59).

The beta diversities of the taxonomic and functional groups exhibited significant positive relationships with local environmental heterogeneity (as shown by linear regression models; $R^2 = 0.071$, $p < 0.001$; $R^2 = 0.046$, $p < 0.001$, respectively; Fig. 5b and e; Supplemental Table S6). In response to lake geographic and morphometric heterogeneity, the taxonomic and functional group compositions differed. The relationship between geographical heterogeneity and beta diversity was not statistically significant for the taxonomical groups ($p = 0.102$) while it was significant for the functional groups ($R^2 = 0.017$, $p = 0.017$). The morphometric heterogeneity had no significant relationship with the beta diversity of functional groups ($p = 0.831$), but the relationship with the beta diversity of taxonomic groups was negatively significant ($R^2 = 0.028$, $p = 0.005$; Fig. 5a and d).

The Mantel and partial Mantel tests showed that the main factor structuring taxonomic and functional group similarity was local environment, which indicates that the variability of environmental conditions among studied lakes had the greatest influence on phytoplankton communities (Table 4). For the taxonomic group dissimilarity based on the Bray-Curtis distances, the effects of local environment increased when the effects of lake morphometric distances were removed. The Sørensen dissimilarities of functional groups had significant positive relationships with local environment distances after controlling for the influence of other distances. The greatest effects were observed for the relationships between the compositional similarity of genera and local environmental distances after controlling for the effects of geographic heterogeneity ($r = 0.288$, $p = 0.015$). Lake morphometric and geographical distances

Table 4. Results of Mantel test and partial Mantel test for the correlation (r) of taxonomic similarity (Bray-Curtis index) and morphology based functional group (MBFG) similarity (Sørensen index) with lake morphometry, local environment, and geography (Euclidean distance).

		Taxonomic similarity		MBFG similarity	
Effects of	Control for	r	p	r	p
Morphometry		−0.180	0.964	0.034	0.307
Morphometry	Local environment	−0.154	0.941	0.066	0.223
Morphometric	Geography	−0.186	0.977	0.042	0.309
Local environment		**0.267**	0.022	**0.238**	0.011
Local environment	Morphometry	**0.251**	0.032	**0.244**	0.011
Local environment	Geography	**0.288**	0.015	**0.219**	0.011
Geography		−0.093	0.865	**0.146**	0.039
Geography	Morphometry	−0.103	0.868	**0.148**	0.046
Geography	Local environment	−0.144	0.958	0.112	0.068

The two-tailed p-values were obtained by the bootstrapping procedure with 999 permutations. Significant r values ($p < 0.05$) are indicated in bold.

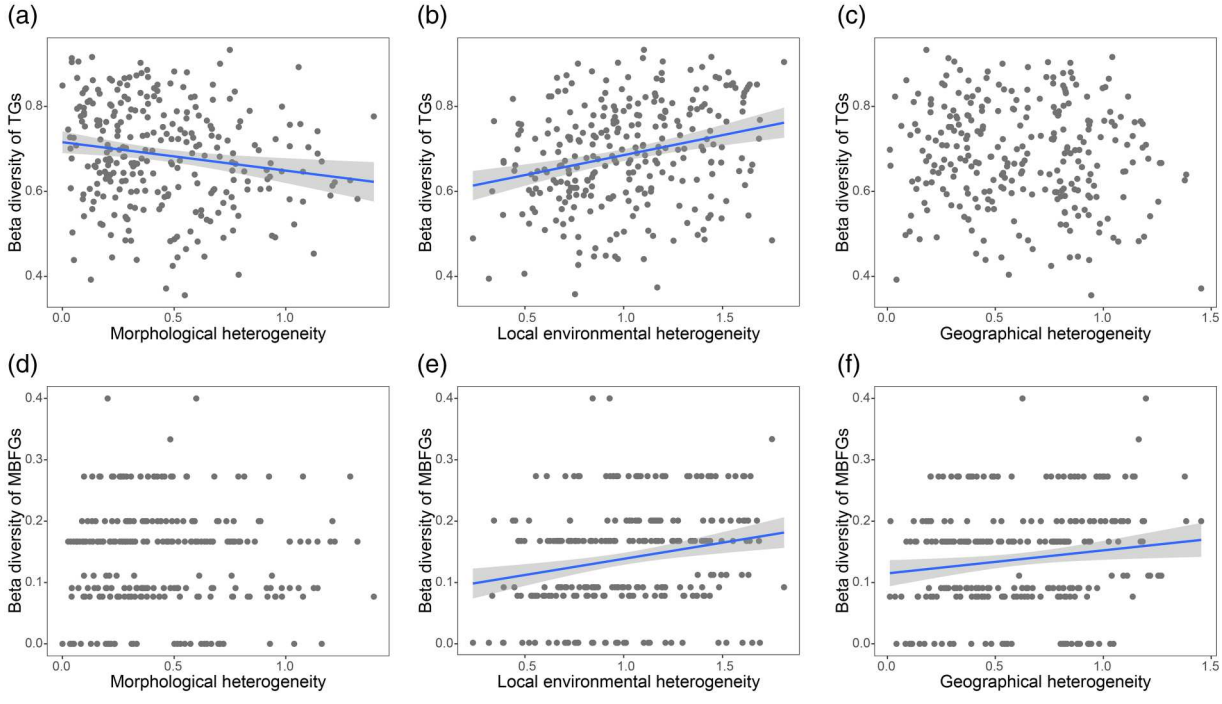


Figure 5. Relationships of phytoplankton taxonomic groups (TGs) beta diversity (Bray-Curtis index) with (a) lake morphometric, (b) local environmental, and (c) geographic distance, and the relationships of morphology based functional groups (MBFGs) beta diversity (Sørensen index) with (d) morphometric, (e) local environmental, and (f) geographic heterogeneity. Regression lines present significant ($p < 0.05$) linear relationships (see Supplemental Table S5 for details of the statistical models).

did not significantly affect the beta diversity of taxonomic groups, even when its pure influence was considered. As for functional groups, the effects of geographic heterogeneity were significant ($r = 0.146$, $p = 0.039$), but its pure effect excluding local environmental heterogeneity was insignificant ($r = 0.112$, $p = 0.068$). The greatest effects were also identified for the relationships between the compositional similarity and local environmental heterogeneity after controlling the effects of morphometric heterogeneity ($r = 0.244$, $p = 0.011$).

Discussion

Current views acknowledge that the factors affecting species diversity and community composition include local environmental and regional dispersal dynamics in metacommunities (Leibold et al. 2004). Based on this scheme, we found that only local environmental heterogeneity significantly contributed to the phytoplankton community structure in high mountain lakes, and the nutrient- and light-associated variables were the major drivers of local and regional diversity and compositional variations.

We expected that local processes, driven by environmental factors specific to each high mountain lake, would predominantly shape phytoplankton community structure. Our results support this expectation, revealing a significant and positive relationship between beta diversity and local environmental heterogeneity, a result consistent with earlier studies on phytoplankton assemblages in various lake systems, which asserted that environmental heterogeneity is the only primary factor influencing phytoplankton diversity patterns (Vanormelingen et al. 2008, Huszar et al. 2015, Benito et al. 2018, Rusanov et al. 2022). However, given the limited geographical extent of our study within the Pyrenees, differences in phytoplankton community composition may not be readily apparent because of the relatively short dispersal distance of microorganisms, and our taxonomic resolution may not capture finer-scale variations. Over large regions, endemism can be found (Popovskaya et al. 2006), and biogeography and vicariance could make sense, as found in the ocean (Graff et al. 2016, Filatov et al. 2021). By expanding the spatial scope and taxonomic resolution of research efforts, we can gain a deeper understanding of the drivers of phytoplankton community dynamics across different geographic scales under the analytical framework.

Lake morphometric heterogeneity showed a significant negative relationship with beta diversity only for the taxonomic group; by contrast, the Mantel test did not support these results. This discrepancy between the 2 results may be attributed to a lack of lake morphometrical heterogeneity because the selected Pyrenean lakes are highly similar in terms of depth, and area and are located at ~2200 m (except Lake Estanho de Vilac, which has an elevation of 1600 m). Similarly, variables associated with lake morphometry were not observed as important drivers explaining alpha diversities (Table 3), which may explain the discrepancy in the significance of lake morphometry for both diversities. Even when the pure effect was considered, only local environmental heterogeneity was significantly correlated with community structure, which indicates that local features strongly contributed to the phytoplankton communities in the lake district.

Our results from db-RDA analyses indicated that community differentiation of taxonomic groups and functional groups were differently attributed to environmental and biological factors. While TP and Chl-*a* concentrations were observed to be strongly correlated from PCA (Fig. 2), they contributed differently to the composition of taxonomic and functional groups from db-RDA (Fig. 4, Table 2), indicating that the phytoplankton community composition can independently represent habitat characteristics and be shaped by differences in the sensitivity of taxonomic and functional groups to environmental drivers (Kim et al. 2019, 2020). These findings shed light on the intricate relationship between environmental drivers and phytoplankton composition of taxonomic and functional groups, highlighting that both groups can capture local environmental characteristics.

Beta diversity was mainly correlated with environmental heterogeneity in the same direction. These findings are consistent with earlier studies on oligotrophic to mesotrophic lakes, which reported that TP was the major determinant shaping phytoplankton compositions as trophic state variable (Anneville et al. 2005, Pacheco et al. 2010, Molina-Navarro et al. 2014). The studied lakes exhibited oligotrophic and mesotrophic states (19 oligotrophic lakes and 5 mesotrophic lakes in terms of TP), which is a typical characteristic of high mountain lakes (Catalan et al. 2006, Buchaca and Catalan 2024). The dominant functional group was group V, which included most unicellular flagellated species (e.g., chlorophytes such as *Chlamydomonas* sp. and dinoflagellates such as *Peridinium* sp. were common in this study). These organisms exhibit motility and cyst production, strategies for surviving periods of adverse environmental conditions such as nutrient depletion, avoiding the death of an entire population (Reynolds et al. 2002). The mixotrophic character of some species, such as the dinoflagellate *Gymnodinium* sp. and the cryptophyte *Cryptomonas* sp., which can behave as autotrophs or heterotrophs, is also an

adaptation to survive low nutrient conditions (Graham and Wilcox 2000, Kruk et al. 2011).

Our analyses confirmed that niche conditions were more influential than geographical or lake morphometric distances in shaping communities grouped by species traits (functional groups) and revealed lake trophic-associated predictors (e.g., light attenuation, TP) from the GLM and db-RDA analyses. Light conditions were the prominent threshold variable for classifying habitat templates for functional groups (Kruk and Segura 2012). According to the K_D values of the Pyrenees lakes, they had moderate light and low trophic conditions for phytoplankton species, which supports the dominance of unicellular flagellated species (group V). The specific variations explained by group III (large filaments with aerotopes) and group VII (large mucilaginous colonies) were strongly associated with high nutrient (TP) and high light attenuation coefficient (K_D) levels, which indicated the success of these groups under relatively poor water quality conditions or during transitional ecosystem stages (Reynolds et al. 2002). The high abundance of group II, which contains small flagellated Chrysophyceae with siliceous exoskeletal structures, was significantly related to conductivity, consistent with the findings of a few studies reporting that pH and conductivity explain the variance in this group (Siver and Hamer 1989).

The amount of variability explained by local factors and the degree of relatedness were similar between phytoplankton communities sorted by functional groups (55.4%) and those sorted by taxonomic groups (56.7%). Several studies have shown that a reduction in complexity allows this grouping to be more efficient at describing the responses of phytoplankton to environmental conditions than taxonomic and other functional groupings (Petar et al. 2014, Wang et al. 2020). This approach was successfully used for evaluating the relative importance of environmental and spatial processes in a large subtropical river basin (Huszar et al. 2015). In the context of the Pyrenees, sorting phytoplankton communities into functional groups may indeed be beneficial for assessing water quality and ecological status. Certain functional groups may serve as indicators of ecosystem health or be associated with specific ecological conditions, making them valuable tools for monitoring and management purposes (Kruk et al. 2010, Kruk and Segura 2012). Our results support the applicability of functional group classification for determining the influences of local factors in high mountain lakes and explaining the relationships between site-specific phytoplankton community characteristics and environmental conditions.

Our findings suggest that phytoplankton are not limited by dispersal but are limited by local environmental characteristics in each lake, assuming that the species-sorting model represents the metacommunity perspective. As passive dispersers, freshwater phytoplankton species compositions typically track environmental heterogeneity (Finlay 2002, Cottenie 2005). In Pyrenean lakes, rotifer communities are shaped by environmental conditions and carbon fluxes and show limited by dispersal constraints (Bartumeus et al. 2009). Although the high degree of isolation of high mountain lakes may impose dispersal limitations, which results in an association with geographical distance, the ubiquitous characteristics of phytoplankton confirmed the species-sorting model in the high mountain lake system.

While our analysis did not explicitly account for trophic interactions between phytoplankton, zooplankton, and fish, it was evident that such relationships significantly influenced the alpha and beta diversities of taxonomic and functional groups (Fig. 5, Table 3). However, NMDS analyses revealed insignificant differences in phytoplankton community compositions between lakes categorized by the present fish species. Additionally, the presence of zooplanktivorous fish can induce shifts in phytoplankton community structure because of zooplankton predation exerting control over phytoplankton populations (Hembre 2019, Yin et al. 2022). Therefore, acknowledging the potential impacts of biological factors on phytoplankton communities is crucial.

Given the spatial scale limitations of our study and the exclusion of other biotic communities, an unexplained fraction of phytoplankton structures potentially influenced by dispersal or top-down control processes remains (Vanormelingen et al. 2008). Future research efforts should aim to expand the number of studied lakes and incorporate additional biotic information to better understand the multifaceted factors shaping plankton communities in high mountain lake ecosystems.

Conclusions

This study supported the view that niche-related local factors are the main drivers that explain the phytoplankton composition in high mountain lakes within the Pyrenean Lake district. The traditional view that dispersal limitation is not notably influential when investigating phytoplankton abundance and composition is supported by our findings. Our results highlight the contributions of the main predictors, TP and light attenuation, to the shaping of phytoplankton assemblages in high mountain lakes and the main role of

the environment, rather than space, in determining phytoplankton community structure in lakes.

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