

Comparing continental and local distribution patterns of protists: A case study of silica-scaled chrysophytes

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Abstract: Free-living protists play important roles in biogeochemical cycling and food-web chains in both aquatic and terrestrial environments. However, their biogeography and spatial distribution remain poorly resolved. Here, we used silica-scaled chrysophytes to determine the most important climatic, historical, and environmental variables that explain biodiversity patterns across different geographical scales; the continental scale was represented by 473 European sites (gradient of 3,800 km), the local scale comprised 69 Aquitanien (France) sites (gradient of 186 km). Generalized Additive Models were used to evaluate the relationship between species richness and explanatory variables. Partition of community variance into fractions, explained separately by local environment, history, and climate helped us to track the main drives of community composition. While species richness was evenly influenced by all factors at the European scale and predominantly by environment (pH) at the local scale, the main factor shaping community composition was climate at both scales and history (geographical distance) at the European scale. Our results showed that silica-scaled chrysophytes respond strongly to climate-related variables at a broad geographical scale. Our work highlights the effect of climate on protist biogeographic structuring and suggests that climate-related variables may represent one of the main drivers of protist distribution, similarly as in macroorganisms.

Key words: biodiversity, climate, community composition, distribution pattern, protists, silica-scaled chrysophytes, species richness

INTRODUCTION

Free-living protists represent a diverse group of organisms that play important roles in biogeochemical cycling and food-web chains in both aquatic and terrestrial environments (FALKOWSKI et al. 2008). As the taxonomy of the majority of the protist groups is unreliable and the identification of units of diversity based on morphological traits is difficult, if not impossible, the prime of biogeographical studies followed the wider use of molecular tools. Moreover, detailed species inventories covering large geographical regions are extremely difficult and time-consuming to obtain and therefore highly limited (VYVERMAN et al. 2007).

It is now widely accepted that at least some protists could exhibit biogeographical patterns similar to those observed in macroorganisms (BOENIGK et al. 2018; HOLMAN et al. 2021). Two main hypotheses concerning protist distribution have been formulated. According to the “ubiquity theory”, the protists smaller than 1 mm are due to their large population densities, small body sizes, and non-existent dispersal limitation, able to occupy all suitable habitats (BAAS-BECKING 1934; FINLAY 2002).

Thus, their distribution would be mostly governed by environmental variables acting at a local scale. On the other hand, the “moderate endemicity hypothesis” states that some protists may be cosmopolitan (probably the majority) whereas others are biogeographically restricted (FOISSNER 2006), and their communities are driven by both local environmental and historical (evolution, dispersal limitation, glaciation) factors (SOININEN 2012; PAJUNEN et al. 2016). Using molecular tools to assess distribution of various eukaryotic microorganisms BASS et al. (2007), BOO et al. (2010), BATES et al. (2013), RYŠÁNEK et al. (2014), and others clearly showed that both restricted and globally distributed lineages may coexist even within the same protistan genus. Answering the question of what exact biogeographical patterns protists exhibit and what drives these patterns is the task of current and future studies of protist biogeography.

Silica-scaled chrysophytes (Chrysophyceae, Stramenopiles) represent free-living or colonial flagellates that produce ornamented siliceous components including bristles, spine-scales, cysts, and scales that are taxonomically diagnostic and have considerable preservation potential in the fossil record. The siliceous

components (especially scales bearing species-specific ornamentation) enable the concept of morphospecies to be applied reproducibly. Species inventories from all over the world have been published since 1960, when the electron microscope became a standard equipment for chrysophyte morphological identification. Even though an increasing number of isolated strains have been molecularly characterized over the past ten years (Jo et al. 2011; ŠKALOUD et al. 2014; JADRNÁ et al. 2021), molecular fingerprinting methods are still waiting to be massively implemented to unravel the full range of silica-scaled chrysophyte diversity. The first biogeographical studies were based on a review of all so far published records. While most of the species were globally dispersed, some followed distinct patterns of distribution (KRISTIANSEN 2001). The conventional view is that chrysophytes presumably respond to local environmental variables and are therefore considered valuable bioindicators (KRISTIANSEN 1986). Their distribution along pH, conductivity, temperature, and trophic gradients has been thoroughly studied (for review, see SIVER 1995). To elucidate the role of environmental variables on silica-scaled chrysophytes distribution, SIVER & LOTT (2012) studied the species distribution in fresh waterbodies along a 3,200-km-long transect on the eastern coast of North America. Local environmental variables clearly played a significant role in determining whether species will occupy a given site. However, species were not always found in waterbodies likely to support their growth, implicating also a history-driven pattern.

The partition of community variance into fractions explained separately by local environment, by history, and by their joint effect, can help us to track the main drivers of community composition (BORCARD et al. 1992). For free-living, unicellular protists, the results are variable. Communities were found to be structured by neither environment nor history (BEISNER et al. 2006; NABOUT et al. 2009; BOCK et al. 2022), predominantly by environment (VERLEYEN et al. 2009; GARNER et al. 2022), by historical factors (VYVERMAN et al. 2007; MEIER et al. 2015), or mostly by joint influence of both (SOININEN et al. 2009; PASSY et al. 2018). LÉBOUCHER et al. (2019) showed that the severity of the anthropogenic impact was also important in determining which driver dominated across the spatial scale. BOCK et al. (2020) emphasized the importance of cross-domain organismic interactions (bacterial OTUs) in shaping protists community patterns, and BOENIGK et al. (2018) showed that European mountain ranges acted as dispersal barriers at small and intermediate scale. Recently, PAJUNEN et al. (2016) emphasized that climate-related factors are important determinants of stream diatom distribution and may be stronger drivers than local environmental variables. Climate-related factors have also been used in former variation partitioning models (mostly included within history-related factors). However, in some studies, climatic variables (e.g., seasonality) were included in

environment-related factors (VYVERMAN et al. 2007). Although climate has been suggested to play an important role in the global distribution of silica-scaled chrysophytes (KRISTIANSEN 2001), the relative importance of this driver has not been tested.

In the present study, we aim to determine the most important climatic, historical, and environmental variables that explain the variation in silica-scaled chrysophyte species richness and composition on continental and local scales. The continental scale is represented by European sites, whereas the local scale comprises Aquitainien (France) sites. We hypothesized that local environmental factors would be more influential at the local scale, whereas at the continental scale both large-scale (climate and history-related factors) and local environment would explain a substantial fraction of silica-scaled chrysophytes community composition and richness.

MATERIALS AND METHODS

Datasets, sampling, and local study area. We used two morphological datasets to cover both continental and local scales. The first dataset was extracted from the “Silica-scaled chrysophytes of Europe” database (ŠKALOUD et al. 2013) comprising all so far published records from Europe. We analyzed 473 sites, containing 159 species altogether, where environmental variables (pH and conductivity) were provided. The second dataset was composed of 69 sites, containing 89 taxa, from three sampling campaigns in Aquitaine (France) during 2010–2018 (NEMCOVA et al. 2012) and from unpublished records. To account for differences in counting methods site-by-species abundance matrices were transformed to site-by-species presence-absence matrices prior to all analyses. In general, the material in Aquitaine was sampled by a plankton net with 20- μ m mesh, and local environmental factors including pH, conductivity, and surface temperature were measured using a combined pH/conductometer (WTW 340i; WTW GmbH). Samples were concentrated by sedimentation. Unfixed drops of samples were subsequently dried onto Formvar-coated transmission electron microscopy (TEM) grids. The dried material was washed by repeated transfer of the grid into drops of deionized water dispensed onto the hydrophobic surface of a Parafilm strip; three TEM examinations were performed per sample. The dried grids were examined using a JEOL 1011 transmission electron microscope. Photomicrographs were obtained using a Veleta CCD camera equipped with image analysis software (Olympus Soft Imaging Solution GmbH). Photomicrographs of scales were used for species identification.

The European localities spanned the latitudinal gradient of 3,300 km (the most distant sampling sites were 3,800 km apart). Aquitanian localities, spanning the latitudinal gradient of 186 km, were located in the western part of Aquitaine, adjacent to the Atlantic Ocean. Due to high annual precipitation and low permeability of bedrock clay layers numerous freshwater habitats were established within the region. For a detailed description of the region, see NEMCOVA et al. (2012).

Statistical analyses. Besides pH and conductivity, which were measured directly, conductivity was log-transformed ($\log_{10}(x)$) to reduce skewed distribution. Nineteen bioclimatic variables

were obtained from the WordClim database (HIJMANS et al. 2005) with 2.5 arc–min resolution to define baseline climate. Data for each site were extracted using the GPS coordinates of the sampling site. Lake densities 50 and 30 represented the total area of water bodies (m²) in the buffer zones of 50 and 30 km (for Aquitaine) from the sampling site. Connectivity was defined as the total area of water bodies in the area of annulus bounded by two concentric circles of a radius of 50 (30 for Aquitaine) and 150 km. Data on waterbody distribution were obtained from the Global Lakes and Wetlands Database (LEHNER & DÖLL 2004). Geographical distance (latitude and longitude) was transformed to the principal coordinates of neighbour matrices (PCNM; DRAY et al. 2006). Because of complex species concepts, *Synura petersenii* Korshikov and *Paraphysomonas vestita* (A.Stokes) De Saedeleer were omitted

from all species lists. Based on molecular data, a large number of new species, lumped within these species' complexes, has recently been described (ŠKALOUD et al. 2012, 2014, 2020; SCOBLE & CAVALIER–SMITH 2014). Although a detailed scale morphology has been provided with new descriptions, previously published surveys illustrated usually one scale to represent the taxon, even for those species found in numerous sites, and that is why reevaluation was not possible. The presence/absence matrix of species was transformed into principal component variables (PCs). Explanatory variables included in the variation partitioning analyses were selected by the forward selection of redundancy analysis (RDA; OKSANEN et al. 2017). Rarefaction curves were constructed to evaluate the degree of sample completeness in both data sets.

Generalized Additive Models (GAMs) were used to

Table 1. Results of the best fitted Generalized Additive Model describing variation in silica–scaled chrysophyte species richness: edf estimated degrees of freedom, Ref. df referenced degrees of freedom, % of expl. var. percentage of explained variation, Bio 1 annual mean temperature (°C), Bio 4 temperature seasonality (standard deviation ×100; °C), Bio 5 warmest month maximum temperature (°C), Bio 8 wettest quarter mean temperature (°C), Bio 9 driest quarter mean temperature (°C), Bio 12 annual precipitation (mm), Bio 15 precipitation seasonality (coefficient of variation; expressed as a percentage), Lake density 50 total area of water bodies in 50 km radius from the sampling site (m²), Lake density 30 total area of water bodies in 30 km radius from the sampling site (m²), Connectivity total area of water bodies in the area of annulus bounded by two concentric circles of 50 (30 for Aquitaine) and 150 km radius (m²). Statistical significances: *** p < 0.001; ** p < 0.01; * p < 0.05; p < 0.1.

Europe – continental scale					
Predictor	edf	Ref. df	Chi sq.	P value	% of expl. var.
pH	7.551	8.387	112.735	0.00000 ***	4.8
Conductivity	6.836	7.947	80.511	0.00000 ***	2.9
Annual mean temp. (Bio 1)	7.064	7.957	19.973	0.00858 **	1.5
Temperature seasonality (Bio 4)	3.354	4.162	8.474	0.08620	0.4
Warmest month max. temp. (Bio 5)	2.391	2.966	2.513	0.49258	0.1
Wettest quarter mean temp. (Bio 8)	1.000	1.001	25.821	0.00000 ***	0.9
Driest quarter mean temp. (Bio 9)	8.015	8.618	40.021	0.00000 ***	2.2
Annual precipitation (Bio 12)	7.954	8.646	47.233	0.00000 ***	2.1
Precipitation seasonality (Bio 15)	7.065	7.950	48.402	0.00000 ***	2.4
Latitude	8.610	8.861	131.002	0.00000 ***	5.3
Lake density 50	3.823	4.598	14.507	0.01001 *	0.6
Connectivity	2.563	3.242	3.246	0.36146	0.1
Aquitaine – local scale					
Predictor	edf	Ref. df	Chi sq.	P value	% of expl. var.
pH	6.566	7.644	38.191	0.00000 ***	17.2
Conductivity	1.000	1.000	0.151	0.69769	0.0
Driest quarter mean temp. (Bio 9)	1.000	1.000	4.600	0.03197 *	1.6
Precipitation seasonality (Bio 15)	1.886	2.383	12.886	0.00225 **	4.4
Latitude	1.325	1.521	5.656	0.06424	1.8
Lake density 30	1.000	1.001	1.229	0.26791	0.2
Connectivity	1.553	1.883	2.634	0.17997	2.0

evaluate the relationship between species richness and explanatory variables (predictors). The GAMs are likelihood-based regression models using smooth functions of covariates in addition to the linear covariate effect. The shape of the smooth curve describes how the predictor influences dependent variable (species richness) in a model where influence of several predictors is combined (HASTIE & TIBSHIRANI 1986; WOOD 2004; 2006). The significance of GAMs was analyzed by Chi-square tests. The relative proportion of the variance explained by each predictor in the final model was estimated. Poisson distribution was used for modelling species richness as counts are assumed to follow this function.

The Mantel test was conducted to study community turnover along geographical gradient. A standard Mantel test to compute the significance of correlation between corresponding position of community dissimilarity and spatial distance matrices was run using Jaccard distances between communities and 9,999 permutations (MANTEL 1967).

All analyses were performed in R (version 4.0.2; R Development Core Team), using the packages *vegan* (OKSANEN et al. 2017), *SoDA* (CHAMBERS 2013), *geosphere* (HIJMAN 2017), *mgcv* (WOOD 2011), and *locfit* (LOADER 2020).

RESULTS

European localities (473) spanned a pH gradient of 3.5–8.9 (median value 6.8) and a conductivity gradient 5–6,285 $\mu\text{S}\cdot\text{cm}^{-1}$ (median value 150 $\mu\text{S}\cdot\text{cm}^{-1}$); the most frequent taxa were *Synura echinulata* Korshikov, *Mallomonas caudata* Ivanov, *S. spinosa* Korshikov, *M. akrokomos* Ruttner, and *M. crassisquama* (Asmund) Fott accounted in 34, 30, 29, 28, and 27% of the investigated samples, respectively. Aquitanian localities (69) spanned a pH gradient of 4.5–8.9 (median value 6.6) and a conductivity gradient 78–794 $\mu\text{S}\cdot\text{cm}^{-1}$ (median value 178 $\mu\text{S}\cdot\text{cm}^{-1}$); the most frequent taxa were *Synura echinulata* (Fig. 1B), *S. spinosa* (Fig. 1C), *M. calceolus* D.E.Bradley (Fig. 1D), *M. papillosa* K.Harris et D.E.Bradley (Fig. 1E), and *M. akrokomos* (Fig. 1A), revealed in 51, 44, 36, 35, and 31% of investigated samples, respectively. On the other hand, several rare or worth mention species were recorded from Aquitanian localities. *Mallomonas costata* Dürschmidt (Fig. 1F) and *M. asmundiae* (Wujek et van der Veer) Nicholls (Fig. 1K) were rare in Aquitaine; however, frequent in Europe. *Mallomonas palaestrica* P.Hansen, J.E.Johansen et A. Skovgaard (Fig. 1I) was rare not only in Aquitaine, but also worldwide with just several confirmed localities. *Mallomonas phasma* K.Harris et D.E.Bradley (Fig. 1G), *M. cucullata* Barreto (Fig. 1H), and *M. koreana* H.S.Kim et J.H.Kim (Fig. 1N) were reported in Aquitaine for the second time since their original description from Southeast England (HARRIS & BRADLEY 1960), Visegrad-mountains, Hungary (BARRETO 2001), and Kyungpook province, South Korea (KIM & KIM 2008), respectively. Even though we sampled *M. alphaphora* Preisig (Fig. 1J) repeatedly in Aquitaine, two previous records came from Western Australia (PREISIG 1989) and southeastern Australia (FURLOTTE

et al. 2000). *Mallomonas jubata* Nemcova, Kreidlová, Pusztai et Neustupa (Fig. 1L) was originally described from Aquitaine and subsequently confirmed from two Czech localities (NEMCOVA et al. 2013). *Synura papillosa* Kapustin, Gusev et Siver (Fig. 1M) was described in 2018 from Vietnam (SIVER et al. 2018). Previously, all populations of this species were included together with *S. synuroidea* (Prowse) Pusztai, Čertnerová, Škaloudová et Škaloud and *S. proweei* Siver, Kapustin et Gusev under the epithet *Chrysodidymus synuroideus* Prowse. *Synura papillosa* is a relatively frequent species worldwide, however it was rare in Aquitaine.

Species richness

European and local (Aquitaine) species richness was estimated by rarefaction curves, linking the number of detected species to sampling effort. Both rarefaction curves reached the asymptote, indicating the stabilization of sample richness as the sample size increases. The sampling effort in both data sets seemed to be sufficient to characterize community diversity (Fig. 2).

Species richness in the European dataset varied from one to 37 species per sample. The best GAM model explained 23.2% of the total variation in species richness (SR). All three groups of factors (environmental, climatic, and historical), explain a comparable proportion of variation (7.7%, 9.5%, and 6%, respectively). Table 1 summarizes the results; only significant predictors are discussed below. The trends in relation of species richness and selected predictors are shown in Figure 3 (A–I). Except for Bio 8 (wettest quarter mean temperature; Fig. 3D), where SR decreased linearly with increasing temperature (edf = 1), all other significant relationships were treated as smooth nonlinear effect (edf > 1). The relatively high amount of variation in SR was explained by pH and conductivity (4.8% and 2.9%, respectively; Table 1; Fig. 3A and 3B). Species richness increased up to pH 5 and was more or less constant, with two slight peaks (at pH 5.2 and 6.7) up to pH close to 9 (the highest pH where silica-scale chrysophytes survive). The samples were regularly distributed over the whole pH range; see the regularly spaced x-values along the bottom of the plot in Figure 3A. Pattern in the relationship between species richness (SR) and conductivity was fairly consistent over the range from 50 to ca. 1,500 $\mu\text{S}\cdot\text{cm}^{-1}$ with indistinctive peak at 400 $\mu\text{S}\cdot\text{cm}^{-1}$. According to forward selection of climatic variables, only annual mean temperature (Bio 1), wettest quarter mean temp. (Bio 8), driest quarter mean temp. (Bio 9), annual precipitation (Bio 12), and precipitation seasonality (Bio 15) had a significant effect and explained 1.5, 0.9, 2.2, 2.1, and 2.4% of variation in SR, respectively (Table 1). Species richness fluctuated continuously with increasing annual mean temperature (Bio 1; Fig. 3C). There were not enough sampled sites within the area with lower annual mean temperature, except for Island (–6 to –8 °C; KRISTIANSEN 1995) and the foothills of the Alps (–2 °C; PICHRTOVÁ et al. 2013).

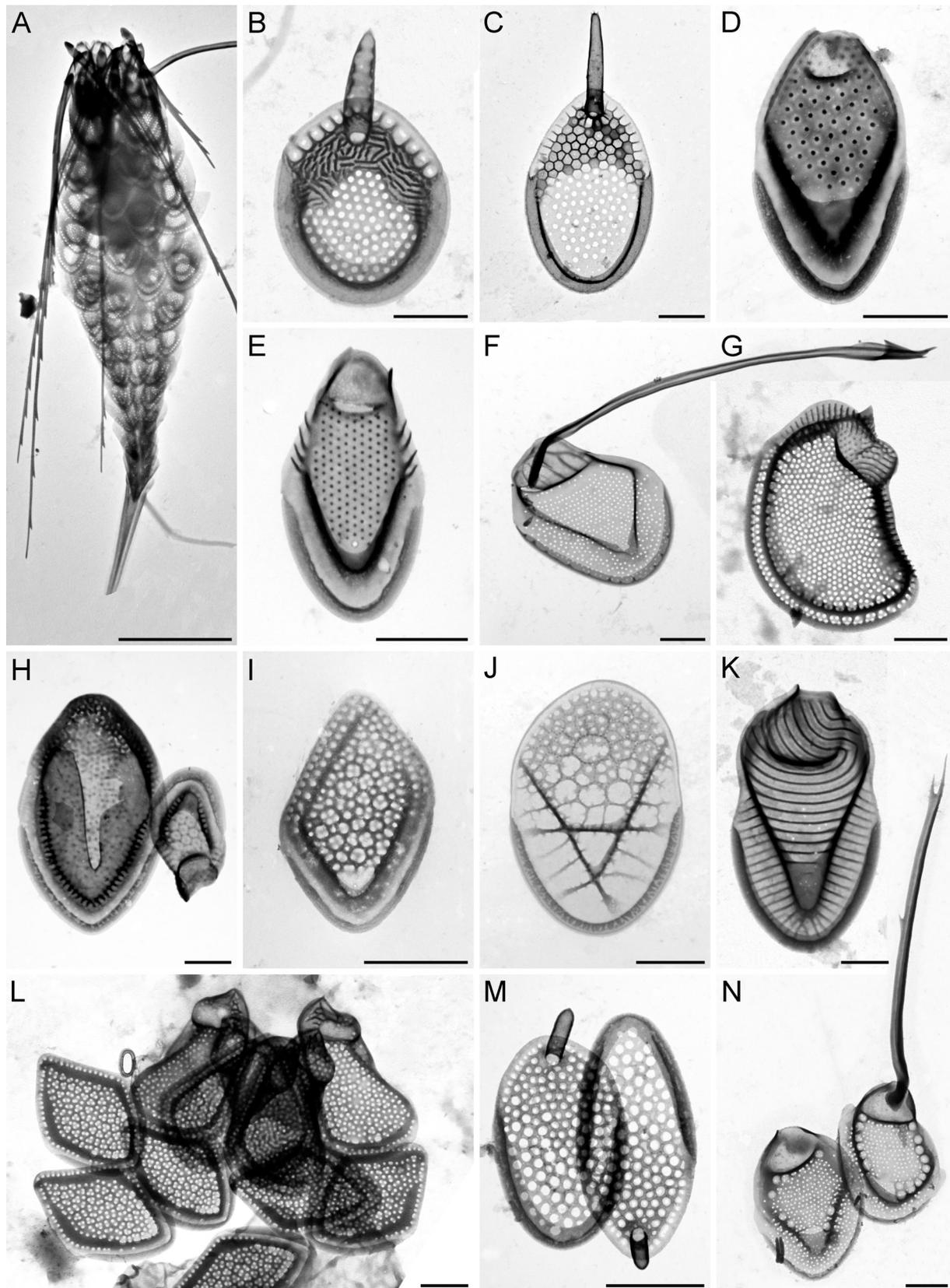


Fig. 1. (A–E) The most frequently sampled taxa of Aquitanian localities: (A) *Mallomonas akrokomos*; (B) *Synura echinulata*; (C) *S. spinosa*; (D) *M. calceolus*; (E) *M. papillosa*. (F–N) The rare species of Aquitanian localities: (F) *M. costata*; (G) *M. phasma*; (H) *M. cucullata* (larger scale) and *M. tubulosa* (smaller scale); (I) *M. palaestrica*; (J) *M. alphaphora*; (K) *M. asmundiae*; (L) *M. jubata*; (M) *S. papillosa*; (N) *M. koreana*. Scale bar 5 μ m (A) and 1 μ m (B–N).

There was a slight increase in SR at 5 °C and a plateau up to 10 °C, as well as a slight increase at 13 °C. While SR showed a linear decrease with the wettest quarter mean temperature (Bio 8; Fig. 3D), the relationship with the driest quarter mean temperature (Bio 9, Fig. 3E) was nonlinear, with a slight increase of SR from −10 °C to 9 °C. Most of the investigated sites received 500–850 mm of precipitation per year (Fig. 3F). One slight maximum of SR was at 800 mm and the second one at 1,200 mm of average annual precipitation. Species richness tended to vary slightly along precipitation seasonality (Bio 15; Fig. 3G) and increased gently with increasing variation in monthly precipitation totals (around 40%). Latitude explained 5.3% of variation in SR (Fig. 3H). Three distinct peaks in SR were detected along the latitude gradient; first at 47.5 N corresponded to the North Tyrol Alpine region (PICHRTOVÁ et al. 2013) and Central Hungary (BARRETO 2005), the second peak at around 53 N represented Ireland (ŘEZÁČOVÁ & ŠKALOUD 2005) and the lake district in Northern Germany (HICKEL & MAASS 1989), and the last peak at 62.5 N reflected the species-rich sites of the Lake Ladoga region in Russia (VOLOSHKO & GAVRILOVA 2001) and the central Finland (IKÄVALKO 1994). The last variable used in the generalized additive model with a slightly significant effect on SR was lake density (Fig. 3I). Most sites were surrounded by 0–4,000 m² of surface freshwater in a 50–km radius (corresponding to 0–0.5% of the total surface). Species richness was uniform along this gradient.

The number of species in the Aquitaine dataset varied from two to 29 species per sample. The best GAM model explained 27.2% of the total variation in

SR. The trends in relation of species richness and significant predictors are shown in Figure 4. The significant predictors pH, driest quarter mean temperature (Bio 9), and precipitation seasonality (Bio 15) explained 17.2, 1.6, and 4.4% of variation in SR (Table 1), respectively. This makes environment (pH) the most important factor, succeeded by climate and leaving historical factors insignificant. Species richness increased up to pH 5.5 and decreased again at pH 7; there was not enough sampled sites at pH higher than 8 (Fig. 4A). Species richness increased linearly (edf = 1) with increasing driest quarter mean temperature (Bio 9; Fig. 4B) and increased non-linearly (edf = 1.886) with increasing variability in precipitation (Bio 15; Fig. 4C). In both climatic models, the Aquitaine localities were divided into two groups. While driest quarter mean temperature (Bio 9) separated sites based on the northern–southern gradient (Fig. 5B), precipitation seasonality (Bio 15) separated sites on oceanic–continental gradient (Fig. 5C). On the other hand, low- and high-pH sites were scattered all over the area, with no obvious gradient (Fig. 5A).

Community composition

In the European dataset, the largest amount of variation was explained simultaneously by climate and history (both 8% net effect, $p = 0.001$, combined effect between them 15%), whereas environment explained only a small proportion of variation (1% net effect, $p = 0.001$, combined effect 2%; Fig. 6A). Almost all bioclimatic variables were selected by the forward selection procedure, with the maximum warmest month temperature (Bio 5) and

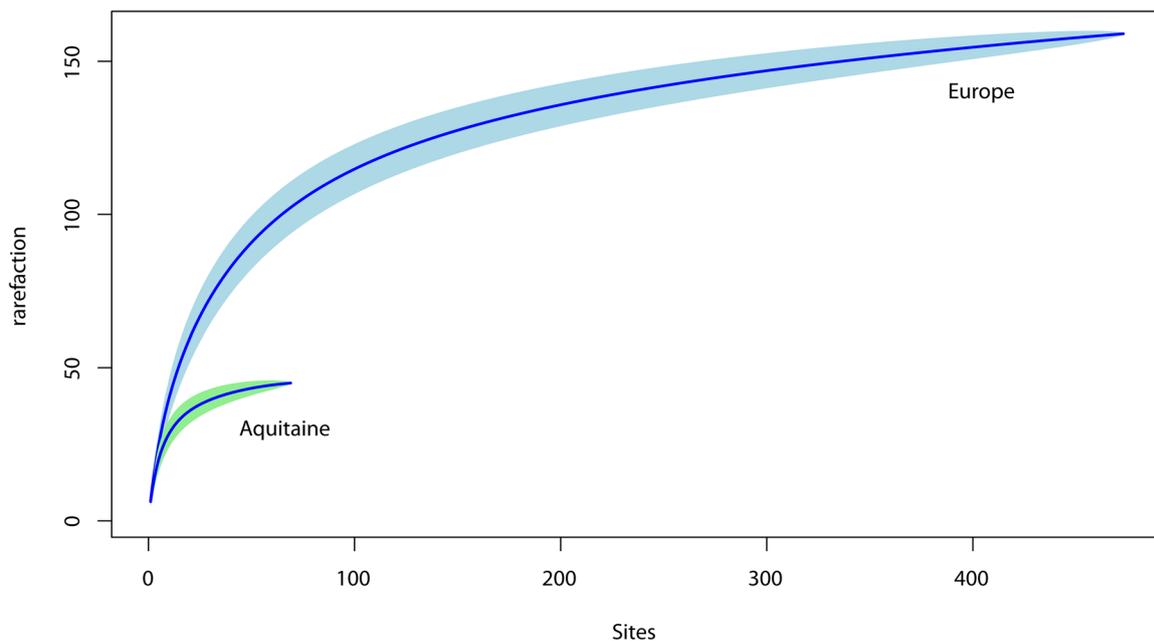


Fig. 2. Rarefaction curves and standard deviation curves for continental (Europe) and local (Aquitaine) samples showing the diversity detected compared with the predicted total diversity; the x axis represents number of investigated sites while y axis represents species richness; curvature towards the horizontal indicates sufficient sampling effort to get reasonable estimate of species richness.

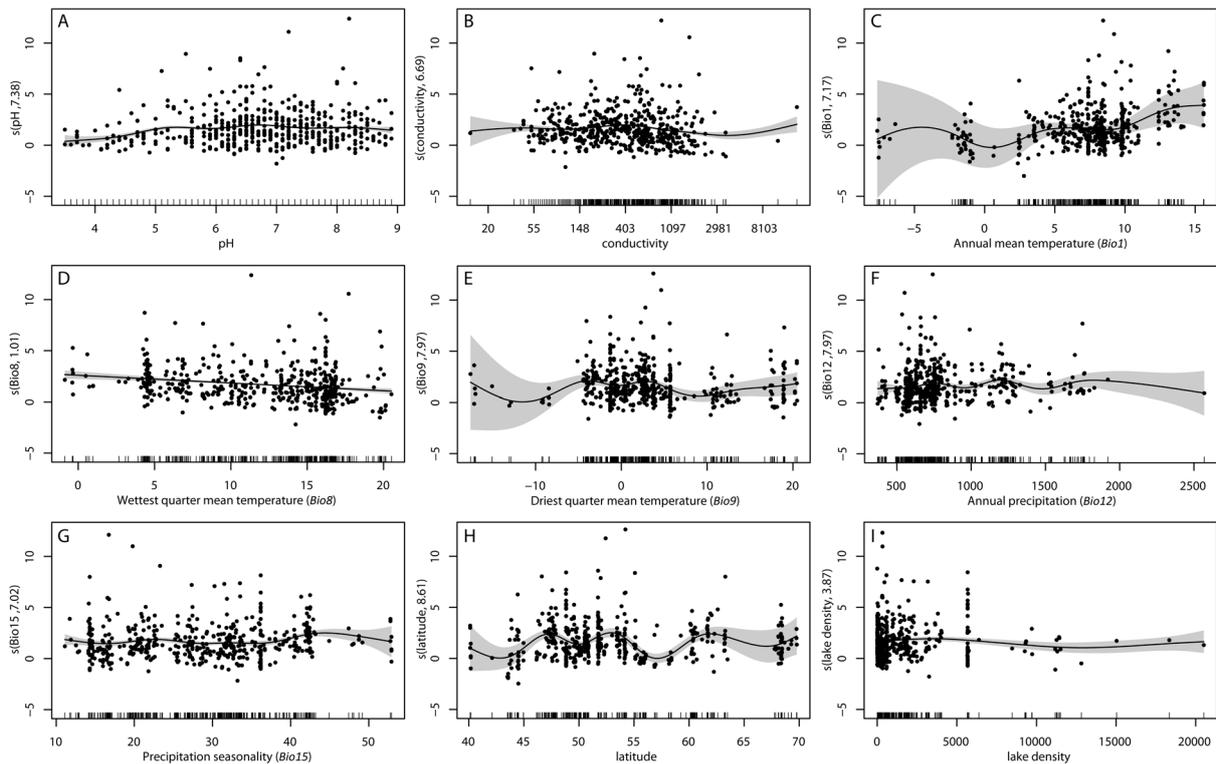


Fig. 3. Results of Generalized Additive Model (GAM) for species richness as a function of significant predictors at continental (European) scale: (A) pH; (B) log–conductivity; (C) annual mean temperature Bio 1; (D) wettest quarter mean temperature Bio 8; (E) driest quarter mean temperature Bio 9; (F) annual precipitation Bio 12; (G) precipitation seasonality Bio 15; (H) latitude; (I) lake density. The approximate 95% confidence envelopes are indicated (grey shading). Rug plot on the x axis shows density of data points; y axis shows smooth term of dependent variable.

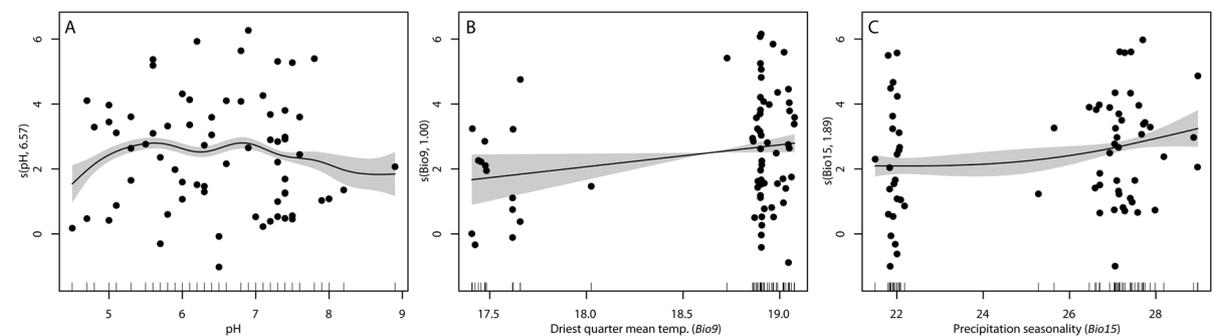


Fig. 4. Results of Generalized Additive Model (GAM) for species richness as a function of significant predictors at local (Aquitaine) scale: (A) pH; (B) driest quarter mean temperature Bio 9; (C) precipitation seasonality Bio 15. The approximate 95% confidence envelopes are indicated (grey shading). Rug plot on the x axis shows density of data points; y axis shows smooth term of dependent variable.

the mean driest month temperature (Bio 9) being the most informative. The high effect of history was driven mostly by geography, whereas the effects of lake density and connectivity were minor (data not shown).

The Aquitaine community composition was also mainly driven by climatic variables (net effect 5%, $p = 0.012$, combined effect 10%), whereas the effects of history and environment were not significant (Fig. 6B). In total, seven out of 19 bioclimatic variables were forward selected; mean coldest quarter temperature

(Bio 11) and mean driest month temperature (Bio 9) were the most important ones.

The Mantel test was used as an alternative method to evaluate the importance of spatial processes in community composition. At European scale, community dissimilarity was significantly correlated with geographical distance ($r = 0.068$; $p = 0.001$); however, the correlation coefficient was relatively low. At the local scale (Aquitaine), this relationship was not significant ($p = 0.2892$).

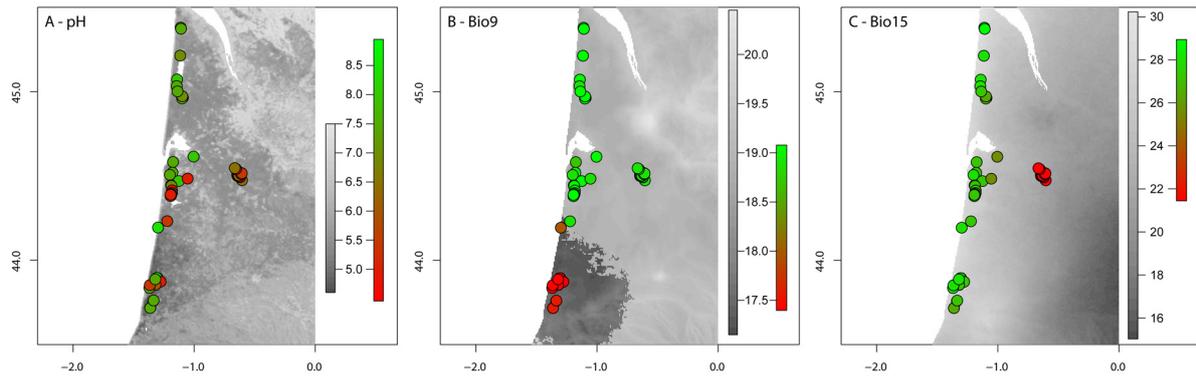


Fig. 5. Map of sites sampled in Aquitaine. Symbols colored according to: (A) site's pH, map of estimated soil pH values served as a base-map; (B) driest quarter mean temperature ($^{\circ}\text{C}$; Bio 9); (C) precipitation seasonality (coefficient of variation, expressed as a percentage; Bio 15). The legend shows the correspondence between shade of symbol and respective variable value. X axis represents longitude; y axis represents latitude.

DISCUSSION

The relative importance of the local environmental, climatic, and historical factors on species occurrence may differ according to the scale of the study (MARTINY et al. 2006), and these patterns may also vary among taxonomic groups of protists (PAJUNEN et al. 2016; OLEFELD et al. 2020). We analyzed species richness and community composition of the silica-scaled chrysophyte morphospecies at continental European and local Aquitanian scales. Here, we transformed all data to presence-absence matrices prior to analyses, which resulted in the loss of species abundance information. Most recent studies (e.g., BOCK et al. 2020; OLEFELD et al. 2020; BOCK et al. 2022; GARNER et al. 2022) use molecular data and read abundances as a proxy for OTU abundance, so some systematic differences between these two types of studies are to be expected. In addition, we used a 20 μm plankton net for sampling instead of whole water samples, so some extremely small taxa (e.g., *Paraphysomonas* spp.) may have been lost. The advantage of the morphospecies-based study is that we are working with well-defined, taxonomically described species instead of OTUs. We hypothesized that local environmental factors would be more influential at the local scale, whereas at the continental scale, both large-scale (climate and history-related factors) and local environment would explain a substantial fraction of silica-scaled chrysophyte community composition and richness.

Our Generalized additive models of European data showed that chrysophyte species richness was related to all three groups of factors (environmental, climatic, and historical), explaining a comparable proportion of variation (7.7%, 9.5%, and 6%, respectively). As we predicted both climate and history-related factors played important role in synergism with environment. On the contrary, the number of chrysophyte species (SR) in Aquitanian localities was mostly influenced by the local environment (namely by pH, 17.2% of

variation explained) as was hypothesized; climate-related factors explained 6% of variation and historical factors were not significant. In our study, we included environmental variables (pH and conductivity) that have previously been documented to be the most important drivers of chrysophyte species richness and community composition (SIVER & HAMER 1989; SIVER 1995; SIVER & LOTT 2012; NEMCOVA et al. 2016). Although it is generally accepted that the most diverse chrysophyte communities thrive predominantly in neutral to slightly acidic waters (SANDGREN 1988; SIVER 1995) the average number of species in our European GAM model was relatively uniform over the wide range of pH values (5–8.5), indicating numerous species-rich waterbodies with higher pH (Fig. 3A).

The same relationship between species richness and pH was demonstrated at the local scale (Aquitaine). However, two SR maxima in slightly acidic and neutral pH were more pronounced (Fig. 4A). The sharp decrease in species richness at pH approaching 9 could be due to the lack of carbon concentrating mechanisms in phototrophic chrysophytes that catalyze the transformation of bicarbonate to CO_2 (SAXBY-ROUEN et al. 1997; RAVEN et al. 2005; BHATTI & COLMAN 2008). On the other hand, for mixotrophic species this argument is disputable and for heterotrophs (e.g., *Paraphysomonas*) it is not relevant at all. BOCK et al. (2022), however, could not confirm that environmental factors (in particular pH) affect phototrophic and heterotrophic chrysophytes differently. Most evidence worldwide indicates that the chrysophytes are more tolerant of localities low in conductivity (SANDGREN 1988; SIVER & HAMER 1989; SIVER 1995; NEMCOVA et al. 2002). Our GAM model of European data showed that the peak of SR shifted towards higher conductivity (400 $\mu\text{S}\cdot\text{cm}^{-1}$; Fig. 3B) which is a slightly higher value compared to above-mentioned studies. This shift could be caused by brackish sites of the Baltic Sea, where diverse chrysophyte communities have been revealed.

Species of the genus *Paraphysomonas* contributed significantly to the number of species, as this genus comprises both freshwater and brackish species (IKÄVALKO 1994; IKÄVALKO & THOMSEN 1996; NEMCOVA et al. 2016). As most of the species have relatively broad ecological tolerances with respect to investigated environmental variables (pH and conductivity), it is not surprising that there were not severe fluctuations of the curve within the range of suitable conditions.

We have demonstrated that climate played the crucial role in determining European chrysophyte species richness. Climate-related variables explained 9.5% of variability. In general, temperature influences metabolic processes (BROWN et al. 2004), and therefore, primary production is higher in waterbodies within warmer regions. As a group, chrysophytes often have been reported to prefer lower temperatures (SANDGREN 1988; SIVER 1995). In temperate oligotrophic lakes, silica-scaled chrysophytes may dominate throughout the year. On the other hand, in mesotrophic to eutrophic lakes, especially in warmer European regions, chrysophytes usually occur in spring to avoid competition of green algae and cyanobacteria (KRISTIANSEN 1988; SANDGREN 1988; GUTOWSKI 1989; SIVER 1995).

In Europe, sites with high annual precipitation corresponded either to areas exposed to the Atlantic Ocean or to mountain ranges. BOENIGK et al. (2018) compared high mountain lakes to biogeographic islands with a low protist diversity and a high degree of endemism. Moreover, study of post-glacial protist distribution pattern verified decreasing richness and diversity across altitudinal gradient (VOGT et al. 2021). We do

not have sufficient information on the occurrence of silica-scaled chrysophytes in European high-mountain lakes. NEMCOVA & ROTT (2018) sampled high-elevation Alpine sites and reported an average of 2.9 species per lake. On the other hand, PICHROVÁ et al. (2013) investigated lakes and reservoirs in the valleys of the same region and obtained an average of 10.7 species per site. These species-rich localities contributed to the peak of SR in 1,250 mm of our GAM annual precipitation model (Fig. 3F). Altered precipitation regimes may cause variation in proximate drivers, such as flow rate, residence time, dilution, advection, salinity, nutrient delivery, population of grazers, stratification, mixed layer depth, or irradiance; all of which influence plankton communities (THOMSON et al. 2015). We also searched for a latitudinal gradient of species richness in silica-scaled chrysophytes from subtropic to polar regions (ca. 3,300 km). In the majority of taxa investigated so far, species richness tended to decrease from the tropics to the poles in both terrestrial and aquatic habitats (for review, see HUSTON 1994). The strength of the gradient was positively correlated to the size of the organism. In protists, including diatoms, weak or no correlation was revealed (HILLEBRAND & AZOVSKY 2001). PASSY (2010) recorded U-shaped latitudinal distribution of diatom richness in U.S. running waters, congruent with latitudinal distribution of wetlands, which affected flux of micronutrients into streams. On the other hand, in Finish streams, the diatom richness peaked at high elevations (PASSY et al. 2018). OLEFELD et al. (2018) studied the patterns of protist species richness at the European scale. Regions of high taxon richness differed

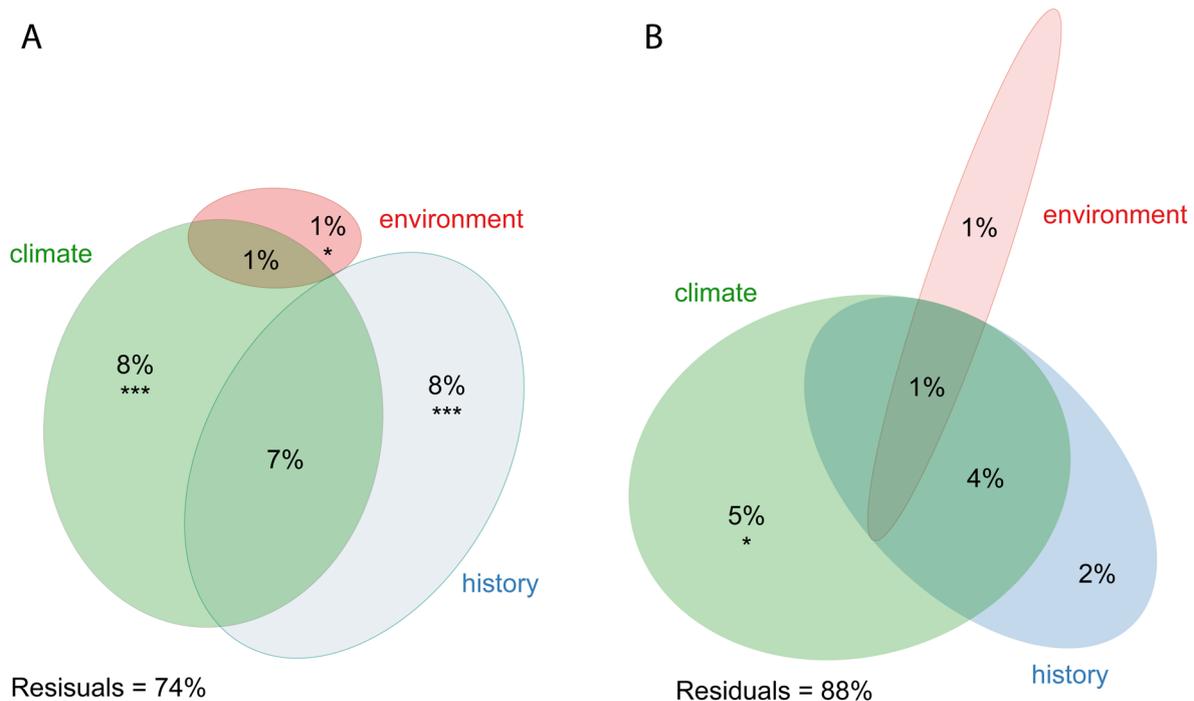


Fig. 6. Venn diagrams showing the relative effects of climate, environment, and history on the variance in community composition: (A) continental scale; (B) local scale. Significant net effects are indicated by asterisks (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$ *)

among taxonomic groups. Chrysophyceae were exceptionally diverse in Scandinavia. In our GAM model, the response of SR to latitude was neither a monotonic decline nor a hump-shaped pattern. Species richness fluctuated continuously with an increase in latitude (Fig. 3H), reflecting the distribution of species-rich regions (silica-scaled chrysophytes biodiversity hotspots).

The main factor shaping community composition was climate at both scales and history (namely geographical distance) at the European scale. Surprisingly, environmental factors were of minor importance in both datasets (Fig. 6). The explanation could be that we did not include other physico-chemical and geomorphological variables that influence silica-scaled chrysophyte distribution, e.g., dissolved reactive silica content, total nitrogen and phosphorus, calcium content or lake depth (PICHRTOVÁ et al. 2013) in our analysis. Similarly, contrary to our prediction for local scale (Aquitaine region), where we favored local environment, climate was found to represent the strongest factor to shape community composition. These results should be handled with certain care. Some local environmental variables could have been masked by climatic factors (especially by the temperature-related ones). Strong influence of climate in Aquitaine region could be possibly justified by vicinity of the Atlantic Ocean; precipitation seasonality (Bio 15) was found to show pronounced climatic gradient towards the Atlantic Ocean (Fig. 5C). Moreover, there was also difference in the amount of precipitation during dry season between northern and southern investigated regions (Fig. 5B). To generalize importance of climate on the local scale, more similar-sized regions (including deep-inland regions) should be investigated. The WordClim database is derived from long-term temperature and precipitation data, and the effect of the local temperature may be partly submerged in climatic data. In some studies, long-term temperature-related variables were accounted for environmental factors, contributing to the importance of environment (VYVERMAN et al. 2007; SIVER & LOTT 2013). On the other hand, local effects, such as pH and conductivity, are climate-independent.

Nevertheless, we clearly demonstrate, that climate represents an important driver of silica-scaled chrysophytes' distribution. Similarly, PAJUNEN et al. (2017) found that at a broad geographical scale, climate-related factors were important determinants of diatom distribution, overriding local environmental variables, and PLANTE et al. (2021) found that individual environmental factors played a negligible role in community composition of saltmarsh benthic diatoms. Relative importance of the local environment, history, and climate was hypothesized to reflect the study scale. Previously, it had been assumed that at continental scale, distance and climatic effects may shade local environmental factors, whereas at intermediate or regional scales (100–3,000 km), microbial distribution is shaped by both large-scale and local factors (MARTINY

et al. 2006; ASTROGA et al. 2012). Accordingly, our results suggest that climate-related factors seem to be important drivers of species richness and community composition in silica-scaled chrysophytes at continental and presumably also at local scales. On the other hand, species richness (however, not community composition) at the Aquitanian local scale was primarily regulated by local environmental factors (pH), while impact of history (geographical distance) was not significant. Waterbody's pH represented a strong local filter independent of both geographic location and climate. As species richness decreased considerably in both extremes of pH (Fig. 4A), and low (pH < 5) and high (pH > 8) pH sites were scattered all over the studied area (Fig. 5A), it is not surprising that pH was an important driver of SR. Similar conclusions have been drawn by VIRTA & SOININEN (2017), who found that diatom SR in the Northern Baltic Sea is driven mostly by local environment, whereas community composition was mostly affected by climatic factors and history. Interestingly, it seems that pH does not shape the community composition of both diatoms and chrysophytes, but significantly affects the species' carrying capacity at a given site.

The proportion of unexplained variance was comparable to similar studies on protists (e.g., VIRTA & SOININEN 2017; BOCK et al. 2020). Our variation partitioning showed that 74% and 88% of variation in European and local Aquitanian data remained unexplained, indicating that other than analyzed factors may also play an important role in structuring the silica-scaled chrysophyte communities. Recently, BOCK et al. (2020) demonstrated that bacterial composition explained almost 9% of variation in protist community composition data. VINCENT & BOWLER (2020) studied the co-occurrence network of planktonic diatoms with other organisms in global oceans (Tara Oceans data). Diatoms displayed a high proportion of negative correlations, particularly toward their potential predators and parasites, signaling a notable effect of biotic interactions in community assembly. While it is extremely difficult to decipher biotic relations, long-term climatic data can be easily drawn from numerous databases. Studies considering the effect of climate on protist distribution are rare (PAJUNEN et al. 2016; VIRTA & SOININEN 2017; ŠKALOUD et al. 2018; VANČUROVÁ et al. 2018). However, together with this study, they suggest that climate-related variables may represent one of the main drivers, similarly as in macroorganisms, and may become indispensable data type in species distribution modeling.

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Supplementary material

The following supplementary material is available for this article:

S1. The data set containing 473 investigated European sites accompanied by list of variables (lat – Latitude; lon – Longitude; pH, Conductivity) and species (presence = 1; absence = 0).

S2. The data set containing 69 investigated sites of Aquitaine accompanied by list of variables (lat – Latitude; lon – Longitude; pH, Conductivity) and species (presence = 1; absence = 0).

This material is available as part of the online article (<http://fottea.czechphycology.cz/contents>)

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