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Environmental and elevational drivers of diatom diversity in alpine temporary ponds

Davide Taurozzi [a,*], Massimiliano Scalici [a,b]

[a] Department of Sciences, University of Roma Tre, Viale G. Marconi 446, 00146, Rome, Italy
[b] National Biodiversity Future Center (NBFC), Università di Palermo, Piazza Marina 61, 90133, Palermo, Italy

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ABSTRACT

High-elevation temporary ponds (TPs) represent habitats of high ecological value, yet they are particularly vulnerable to ongoing climate change. Diatoms are excellent bioindicators, useful for detecting ecological shifts driven by natural fluctuations or anthropogenic impacts. This study investigates whether differences in the floristic composition, measured as diversity and uniqueness (i.e., the proportion of taxa occurring exclusively in one pond), of diatom communities at small spatial scales among alpine TPs (Central Apennines, Italy) are mainly driven by isolation, elevation, or environmental factors. We found that diatom diversity in alpine biomes primarily responds to local geographical gradients, which tend to obscure any detectable effects of environmental variables. Elevation plays a key role in shaping the uniqueness of diatom communities in TPs, as higher ponds host a greater proportion of exclusive taxa. Our results indicate that local environmental conditions associated with elevation override the effects of isolation (distance between ponds), leading to the development of functionally distinct diatom communities at higher altitudes. The diversity and uniqueness of diatom assemblages are influenced by a combination of geographic and, to a lesser extent, environmental factors, with elevation acting as a central driver, both enriching diversity and promoting floristically unique communities, especially in interaction with other variables. Furthermore, electrical conductivity appears to favour communities composed of similarly adapted species, likely reflecting specific ecological conditions or adaptive responses to environmental gradients. These findings highlight the importance of elevation and spatial gradients in shaping diatom community patterns in high-altitude ephemeral freshwater habitats.

1. Introduction

High above the world's forests and grasslands, where the air thins and temperatures plummet, lies a realm of extremes: the alpine biome (Myster, 2012; Woodward, 2008). Alpine ecosystems, i.e. high-elevation habitats above the climatic treeline, defined by the lack of trees due to cold temperatures, consist of a continuous range of shrubland and grassland habitats found above the climatic treeline across various latitudes (Pauli and Halloy, 2019; Nagy and Grabherr, 2009). The alpine biome, although its harsh climate and their complex history of climatic fluctuations (Körner and Hiltbrunner, 2021), is considered a biodiversity hotspot, including thousands of specialized plant and animal species (Vitasse et al., 2021). However, these ecosystems are particularly sensitive to climate change due to their specialized species and their restricted environmental tolerances. Indeed, with global temperatures rising, alpine habitats could face unprecedented modifications in temperature regimes, snow cover, and hydrological cycles, threatening their unique flora and fauna (Di Nuzzo et al., 2021; Haynes et al., 2021).

Alpine ecosystems supply freshwater to more than half of the human population and may stock up to 1 % of the global terrestrial carbon pool (Sharma et al., 2023; Schmeller et al., 2018). In this sense, the importance of temporary freshwater habitats, typical of this biome, is well documented. Temporary ponds (hereafter TPs, Richardson et al., 2022) represent one of the most particular environments that the Alpine biogeographical region host: they are critical freshwater habitats, supporting unique and specialized species adapted to their ephemeral nature (Fehlinger et al., 2025; Lamouille-Hébert et al., 2024). Despite their small size and often overlooked status, alpine TPs play a crucial role in maintaining regional biodiversity and supporting hydrological processes (Fehlinger et al., 2023). TPs networks can also enhance landscape connectivity, allowing populations to maintain genetic exchange and resilience by forming metapopulations, which is especially important in

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* Corresponding author.
E-mail address: davide.taurozzi@uniroma3.it (D. Taurozzi).

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the face of climate change (Hyseni et al., 2021; Howell et al., 2018).

Among the aquatic communities inhabiting TPs, diatoms represent a widely used biological indicator to detect such alterations (Van den Broeck et al., 2015). Diatoms are unicellular, photosynthetic algae widespread in all the water habitats. They show rapid response to changes in water quality, nutrient availability, and hydrological regimes allowing for sensitive detection of ecological shifts caused by natural fluctuations or anthropogenic impacts (Hamed, 2023; Kumar et al., 2015). Moreover, the species composition and diversity of diatom assemblages reflect specific habitat characteristics, enabling detailed insights into the ecological status and successional dynamics of TP ecosystems (Gottschalk and Kahlert, 2012). However, as reported by Blanco et al. (2020), there are two main scientific perspectives regarding factors shaping diatom communities: the first suggests that diatom community composition is primarily determined by local environmental conditions such as nutrients, pH, and conductivity (Shibabaw et al., 2021). Supporting this, studies indicate that at narrow spatial scales, dispersal limitations have little effect, as diatom species occur wherever suitable habitats exist (Soininen and Teittinen, 2019). The second perspective emphasizes broader-scale influences, noting that freshwater diatom distributions exhibit biogeographic patterns shaped by dispersal processes, climate, and evolutionary history. In other words, climate and historical processes dominate at regional scales, while local environmental factors govern community composition at smaller scales (Benito and Fritz, 2020; Vyverman et al., 2007). Many studies alternately support one theory or the other, highlighting that factors like altitude, seasonality, isolation, and physicochemical parameters vary in importance when shaping diatom communities depending on spatial scale and context (Bhatt et al., 2025; Gonzalez-Saldias et al., 2025; Liu et al., 2025).

Investigating elevational patterns in diatom diversity helps identify large-scale distribution trends and clarify how environmental factors shape these patterns, providing key insights for future conservation of high-mountain temporary ponds. Furthermore, in an era of rapid and unpredictable climate change, understanding how these vulnerable ephemeral ecosystems respond to shifts in temperature, water availability, and seasonal cycles can be crucial for anticipating global impacts on freshwater biodiversity and for developing effective conservation strategies.

In their research, Blanco et al. (2020) investigated the role of geographical and environmental factors on diatom diversity inhabiting TPs in a mediterranean biome. Here, we applied a comparable research on diatom communities of TPs included into an alpine biome, aiming to investigate (i) whether the differences in the floristic composition of diatom communities between different high-elevation TPs are explained by geographical distance, altitude or environmental differences; (ii) if the spatial distribution of sites and their ecological characteristics (diversity and uniqueness) follows a specific pattern; (iii) which local environmental predictors and broader-scales patterns (like elevation and isolation) drive diatom community composition at smaller scales.

2. Materials and methods

2.1. Study area and sampling activities

The study was conducted in central Italy, on the Campo Imperatore plateau, which is part of the Gran Sasso and Monti della Laga National Park (Central Apennines, Italy), in the Alpine biogeographical region (European Environment Agency, 2020). The plateau stretches 18–27 km in length and 8 km in width, covering an area of about 75–80 km^2 and elevation range between 1300 and 2100 m above sea level (Cristofanelli et al., 2013). The landscape is shaped by glacial and alluvial processes, resulting in broad grassy meadows, small ponds, and scattered rocky outcrops. It is characterized by traditional summer grazing ground for sheep, cattle, and semi-wild horses.

Initially, TPs identification was carried out following the methodology from Taurozzi and Scalici (2024): we considered TPs as those showing a dry season during summer or those completely frozen and covered by snow during winter months. Out of the 22 ponds identified, only 12 contained water during the sampling campaign conducted during the wet season (July 2024). Consequently, all 12 available ponds were sampled (median elevation: 1690 m a.s.l., range: 1374–2007 m a.s.l.) (Fig. 1). All ponds were sampled once during the summer season (July 2024), without temporal replication. Therefore, temporal variation was not modelled, and the analyses focused exclusively on spatial differences in diatom community structure and environmental parameters among ponds. The sampling focused on epilithic diatoms collected from horizontal rock surfaces. Following the field protocol described by Balzano and Martone (2014), as referenced in Taurozzi et al. (2024), each rock was manually cleaned and thoroughly rinsed immediately before sampling to remove any deposited material or dead frustules. This procedure ensured that the biofilm collected represented only the living epilithic community present at the time of sampling. For each pond, three subsamples pooled into a single composite sample were collected, avoiding any implication of statistical replication at the pond level. Samples were oxidized in the laboratory following Balzano and Martone (2014), and 400 valves per slide (1200 per pond) were counted for community analyses. The morphological identification of diatom species was conducted under a microscope at 100 × magnification (Leica), using taxonomic guides (DREAL Languedoc Roussillon, 2021; Bahls et al., 2018; Taylor et al., 2007; Krammer et al., 2002; Krammer and Lange-bertalot, 1991b, 1991a, 1988; Krammer and Lange-bertalot, 1986).

To assess water physicochemical variables through the months, Temperature (T °C), pH, Oxygen Reduction Potential (ORP, mV), Electrical conductivity (EC, μS/cm), Dissolved oxygen (DO, ppm) were measured in each site during the two samplings. These parameters were recorded in the field using a multiparametric probe Hannah® HI98194 (Tab. S1).

2.2. Data analysis

All the statistical analyses were computed in R software (R Core Team, 2024). Alpha diversity was quantified for each site using the Shannon index (*diversity* function), which accounts for both species' richness and evenness. Site-level uniqueness (U) was calculated by weighting species' relative abundances by their inverse occurrence frequencies, providing a measure of how distinct each community is in terms of species composition: U values vary between 0 (all of the species of the sample are also found in all of the other ponds) and 100 (none of the taxa that were found occur in any other sample) (Ricotta, 2005).

The spatial distribution of sites was tested using the Nearest Neighbor index (R), which compares the observed mean distance between neighboring sites to the expected mean distance under complete spatial randomness. The null hypothesis was that sites were randomly distributed. Nearest Neighbour analysis was performed using *nndist* function (*spatstat* package), comparing the observed mean nearest-neighbor distance to that expected under spatial randomness (Baddeley et al., 2015). The R index (observed/expected) was used to infer clustering ($R < 1$), randomness ($R \approx 1$), or overdispersion ($R > 1$) in site distribution. Spatial autocorrelation in Shannon diversity and uniqueness was tested using Moran's I (*moran.test* function from *spdep* package), indicating whether similar diversity values cluster spatially (Bivand and Wong, 2018). A kernel-based isolation index was calculated for each site using a custom function that weighs distances from neighboring sites within a Gaussian kernel, with higher values indicating stronger spatial isolation. To assess the influence of spatial structure on diatom communities, we computed spatial eigenvectors (MEM, Moran's Eigenvector Maps) based on site coordinates (Longitude, Latitude). Positive MEMs were extracted and used as explanatory variables in redundancy analyses (RDA) together with key environmental factors (Elevation and Isolation) to test their combined effects on

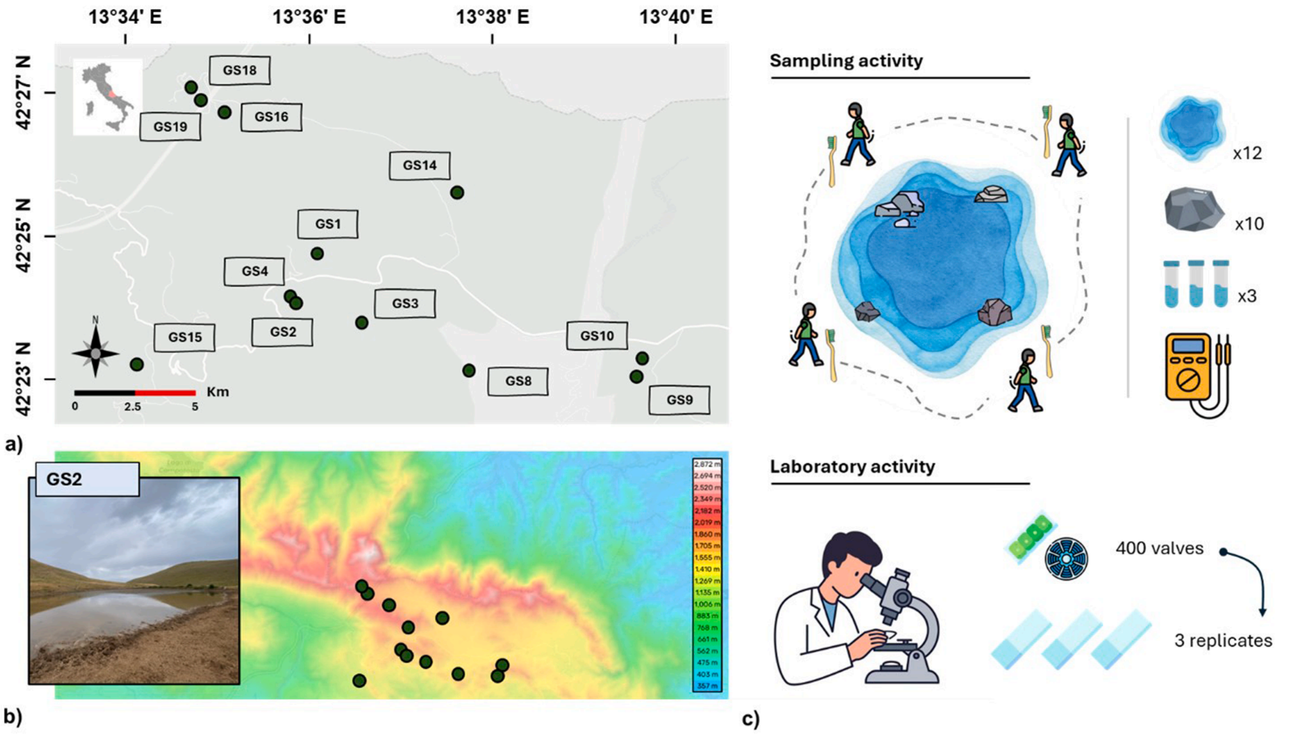

Fig. 1. a) Map of the sampling sites within the Campo Imperatore plain. Individual ponds are indicated by green dots. b) Below, the different colors of the map indicate elevation, expressed in meters above sea level (m a.s.l.). Satellite images are sourced from Carto® (https://carto.com/). c) On the right, sampling activities showing diatom sampling and laboratory activities showing diatom identification.

Shannon diversity and taxonomic uniqueness. Significance of the RDA models was evaluated using permutation tests with 999 iterations.

Then, we performed Generalized Linear Models (GLM) (*glm* function) to test the effects of elevation, environmental variables, and spatial isolation on Shannon diversity and uniqueness. Single-variable (additive) models were used to assess the independent effect of each predictor, while full (multivariable) models included all predictors simultaneously to evaluate their joint effects and account for potential covariation. Model fit and parsimony were assessed using Akaike's Information Criterion (AIC). This approach allows identification of both individual and combined contributions of environmental and spatial factors to diversity and uniqueness. Differences in significance or effect size between the two approaches do not indicate contradictions but reflect the influence of covariation among variables. To reduce multicollinearity among environmental predictors before fitting the models, we calculated the variance inflation factors (VIF) using the caret package in R. Variables showing high correlation (VIF > 5 or pairwise correlation > 0.5) were identified and removed from subsequent analyses. This procedure ensured that the selected explanatory variables in the GLMs for diversity and uniqueness were independent, improving model reliability and interpretability.

Sørensen dissimilarities (*vegdist* function, *vegan* package, method = "bray") on presence/absence-transformed data (*decostand* function, method = "pa") were calculated to assess taxonomic beta diversity between sites (Oksanen et al., 2025). Geographic distances between sites were calculated using the Haversine formula (distm function from the geosphere package), while environmental distances were derived using scaled Euclidean distances (dist function) across key physico-chemical variables (Temperature, pH, ORP, EC, and D.O.) (Hijman, 2024). Elevational distances were also computed separately. To assess distance–decay patterns, we performed partial Mantel tests (*mantel.partial, vegan* package) to evaluate the correlation between community dissimilarity and geographic distance while controlling for environmental distance (and vice versa) (Oksanen et al., 2025).

Taxonomic beta diversity analyses were performed using the *betapart* package (Baselga and Orme, 2012). Specifically, the functions *beta.pair* and *beta.multi* were applied to calculate pairwise and multiple-site Sørensen dissimilarity indices, respectively, partitioning total beta diversity into turnover and nestedness components. To evaluate the relationship between beta diversity and environmental gradients, we performed Mantel tests comparing Sørensen dissimilarity matrices with environmental distance matrices (elevation and isolation) using the vegan package (Oksanen et al., 2025). In this case, environmental distance, not geographic distance, was used as the explanatory variable. This dual approach allowed us to distinguish spatial effects independent of environmental variation (Partial Mantel test) from the overall association between beta diversity and environmental factors (Mantel test) (Oksanen et al., 2025). Pairwise Sørensen dissimilarity distances converted to a distance object and compared against geographic environmental distance matrices, specifically elevation and isolation distances.

Furthermore, to examine whether beta diversity dispersion differed among elevation groups, sites were categorized into three altitude classes based on elevation measurements: Low (1300–1600 m), Mid (1600–1800 m), and High (1800–2100 m). Ponds were grouped into three elevational classes to explore potential ecological gradients on environmental heterogeneity, as elevation in mountain ecosystems can affect environmental conditions over relatively short vertical distances (200–300 m) (Taurozzi and Scalici, 2025). Homogeneity of multivariate dispersion (PERMDISP) was then tested using the *betadisper* function from the *vegan* package, to evaluate whether the variance of beta diversity distances differs among the predefined elevational groups (Oksanen et al., 2025). An overall test of homogeneity of dispersions was performed with ANOVA, and pairwise group comparisons were conducted using Tukey's Honest Significant Difference (HSD) test.

Finally, to explore the relationship between species composition and environmental variables, we performed a distance-based redundancy analysis (db-RDA) using the *capscale* function from the *vegan* package. Variables with pairwise correlations above 0.5 were identified using the *findCorrelation* function from the *caret* package and removed to avoid multicollinearity (Kuhn, 2008). The db-RDA was conducted using a Bray-Curtis distance matrix (which is mathematically equivalent to the Sørensen–Dice index for binary matrices), derived from the presence/absence community data (*dist* function), with the selected environmental variables as predictors. The significance of the overall db-RDA model and individual environmental variables was tested via permutation tests with 999 iterations using the *anova.cca* function. The proportion of variance explained by the first two canonical axes was calculated from the eigenvalues of the constrained ordination.

3. Results

We identified 123 diatom species belonging to 41 genera. The most occurring genera were Navicula (17 species), Gomphonema (14 species), Nitzschia (9 species), Pinnularia (7 species) and Achnanthidium (6 species). Maximal richness was observed in GS19 (32 species), GS3 (31 species) and GS4 (31 species). The most widespread species across the sampled sites were *Gomphonema parvulum* and *Navicula cryptocephala*, which were present in 11 out of 12 sites, followed by *Eolimna minima* (9 sites), *Encyonema minutum, Navicula cryptotenella, Nitzschia palea, Planothidium frequentissimum* each occurring in 8 sites. Conversely, 61 species were rare, occurring in only one site, indicating a large proportion of site-specific taxa. *Eolimna minima* ($n = 2051$), *Achnanthidium eutrophilum* ($n = 1791$), *Navicula cryptocephala* ($n = 1384$) and *Gomphonema parvulum* ($n = 1374$), were the most abundant species, capable of living from highly polluted (polysaprobic) and eutrophic environments with low dissolved oxygen, to moderately polluted and mesotrophic waters. Maximal uniqueness was observed in GS15, where 73 % of the individuals that were identified belong to taxa not found elsewhere.

The mean Nearest Neighbor distance observed was 0.01169 ($p = 0.36$), slightly higher (but not statistically significant) than the expected distance for complete spatial randomness (0.01087), resulting in an R index of 1.08. This value indicates that the sites can be considered randomly distributed, with no evidence of significant clustering or overdispersion.

However, while Shannon diversity did not show spatial autocorrelation (Moran's $I = -0.004$, $p = 0.256$), community uniqueness exhibited a significant positive spatial structure (Moran's $I = 0.181$, $p = 0.027$), suggesting spatial clustering of unique sites. Positive MEMs were then extracted and included in RDAs together with Elevation and Isolation to account for spatial structure. For Shannon diversity, the combined model (MEM1–MEM3 + Elevation + Isolation) did not significantly explain variation among sites ($F = 1.147$, $p = 0.433$), indicating that neither spatial structure nor these environmental variables had a strong effect on community diversity. For taxonomic uniqueness, the same model showed a marginally significant effect ($F = 3.931$, $p = 0.072$), suggesting that spatial structure and the two key environmental variables may contribute partially to differences in site uniqueness, although the effect was not strong.

The obtained results highlighted that the global GLM model better explained the variability in the data. Prior to fitting the models, we assessed multicollinearity among environmental variables using both correlation coefficients and variance inflation factors (VIF). Variables showing high pairwise correlations ($|r| > 0.5$) were removed to avoid redundancy (Table 1). Specifically, pH and ORP were excluded, while the reduced set of variables included Elevation, Isolation, Temperature, EC, and D.O., all with VIF values below 2, indicating low collinearity.

In the single-variable models, elevation showed a significant positive effect on Shannon diversity ($t = 2.42$, $p = 0.036$; AIC = 15.23) (Fig. 2b), indicating that higher elevation is associated with increased diversity. However, elevation did not significantly affect uniqueness ($t = 0.73$, $p = 0.480$; AIC = −8.08) (Fig. 2a). Isolation did not have a significant effect on either Shannon diversity ($t = 0.14$, $p = 0.890$; AIC = 20.74) or uniqueness ($t = -0.78$, $p = 0.454$; AIC = −8.16). In the global models including the reduced set of environmental variables (Elevation, Isolation, Temperature, EC, D.O.), elevation showed a marginally significant positive effect on Shannon diversity ($t = 2.21$, $p = 0.069$; AIC = 21.06) (Fig. 2c) and a non-significant positive effect on uniqueness ($t = 1.82$, $p = 0.118$; AIC = −9.52) (Fig. 2d). EC was marginally positively associated with uniqueness ($t = 2.41$, $p = 0.053$), while Isolation, Temperature, and D.O. did not show significant effects in either model.

DDS showed no significant trends. Partial Mantel tests revealed that neither geographic distance, elevational distance nor environmental distance significantly explained floristic dissimilarity among ponds after controlling for similarities (Table 2).

Taxonomic beta diversity among diatom communities across the elevational gradient was high, with a total Sørensen dissimilarity of 0.86. Pairwise taxonomic dissimilarities among the sampled sites, calculated using the Sørensen index, revealed moderate to high beta diversity, with values ranging from 0.42 to 0.91. The lowest dissimilarity was observed between sites GS18 and GS19 (β-sor = 0.42), indicating a relatively high similarity in species composition. In contrast, the highest dissimilarity was found between GS8 and GS16 (β-sor = 0.91), suggesting a pronounced turnover in community structure. Notably, sites GS14, GS15, and GS16 exhibited consistently high dissimilarity values (> 0.75) when compared with other sites, reflecting more distinct diatom assemblages (Fig. 3a). The partitioning of beta diversity revealed that turnover was the dominant component, accounting for 97.6 % of total dissimilarity, while nestedness contributed only 2.4 %. Pairwise comparisons between sites confirmed this pattern, with most dissimilarity values showing turnover rates above 90 %.

Mantel test analysis revealed a significant positive correlation between community dissimilarity and elevation (Mantel $r = 0.47$, $p = 0.005$), indicating that differences in diatom community composition increase with greater elevational separation (Fig. 2b).. Differently, Mantel test performed to examine the relationship between community dissimilarity and isolation distance among ponds did not reveal significant correlation (Mantel $r = 0.04$, $p = 0.38$). Results of ANOVA on the three elevational groups showed no significant differences in community dispersion among these altitude groups ($F = 0.48$, $p = 0.63$), indicating that within-group variability in diatom assemblages is relatively consistent across the elevational gradient.

The db-RDA based on Sørensen (binary Bray–Curtis) dissimilarities showed that environmental variables accounted for a substantial portion of the variation in community composition (Fig. 2c). The first two canonical axes (CAP1 and CAP2) captured 39.2 % and 26.3 % of the

Table 1

Pearson correlation matrix of the environmental variables measured across all sampling sites. Values represent the correlation coefficients between pairs of variables. Strong correlations ($|r| > 0.5$) were considered when selecting variables for inclusion in multivariate models to avoid collinearity.

Variable	Elevation	Temperature	pH	ORP	EC	D.O.	Isolation
Elevation	1.000	0.309	0.274	0.048	−0.380	−0.453	0.145
Temperature	0.309	1.000	0.332	−0.295	0.072	0.149	−0.050
pH	0.274	0.332	1.000	−0.660	−0.522	0.190	−0.420
ORP	0.048	−0.295	−0.660	1.000	0.482	−0.603	0.143
EC	−0.380	0.072	−0.522	0.482	1.000	0.071	−0.364
D.O.	−0.453	0.149	0.190	−0.603	0.071	1.000	−0.223
Isolation	0.145	−0.050	−0.420	0.143	−0.364	−0.223	1.000

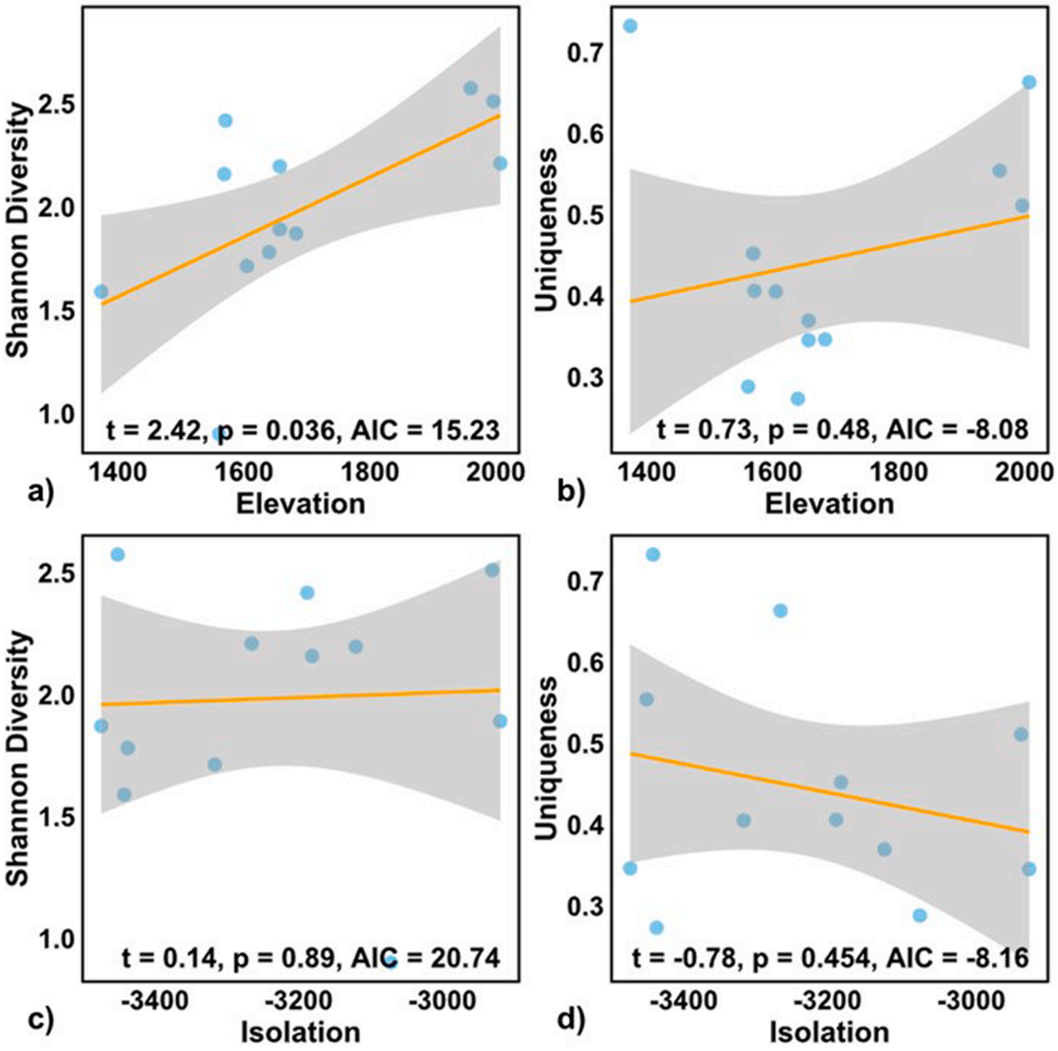

Fig. 2. Linear relationship between elevation and the biodiversity metrics: a) Shannon diversity and b) Uniqueness in single-variable GLMs. Each dot represents a sampling site, and the orange line shows the fitted values with 95 % confidence intervals. Coefficient plots representing standardized coefficients from global generalized linear models (GLMs) showing the effects of environmental variables, including elevation, isolation, temperature, EC, and D.O., on c) Shannon diversity and d) taxonomic Uniqueness across all sampled sites. Dots represent estimated effect sizes with 95 % confidence intervals. Orange points indicate statistically significant predictors ($p < 0.05$), while blue points are non-significant. The dashed red line indicates the null effect (estimate = 0).

Table 2
Partial Mantel test results from the comparison between floristic distance matrix and geographical, elevational and environmental distance matrices.

Compared matrix	Distance matrix tested for	r	p
Geographical	Environmental	−0.02	0.55
Geographical	Elevational	0.02	0.41
Elevational	Geographical	0.01	0.49
Elevational	Environmental	−0.05	0.62
Environmental	Elevational	0.18	0.17
Environmental	Geographical	0.18	0.17

constrained variance, corresponding to 22.5 % and 15.1 % of the total variance, respectively. A permutation test (999 permutations) confirmed that the overall model was statistically significant ($F = 1.61$, $p = 0.017$), indicating that environmental gradients structured species assemblages across ponds. Among the individual predictors, only elevation significantly explained variation in community composition ($F = 2.22$, $p = 0.010$). In contrast, temperature ($F = 1.29$, $p = 0.177$), electrical conductivity ($F = 1.26$, $p = 0.237$), dissolved oxygen ($F = 1.33$, $p = 0.154$), and isolation ($F = 0.96$, $p = 0.528$) did not show significant effects when tested individually. Overall, elevation emerged as the dominant environmental driver shaping community turnover across ponds.

4. Discussions

Understanding the factors that determine the diversity and uniqueness of aquatic communities in small high-elevation ecosystems is one of the main challenges of modern ecology. Recent studies, mainly conducted in Mediterranean biomes, have highlighted how community composition is often influenced by a combination of local environmental factors, geographic isolation and large-scale spatial processes (Blanco et al., 2020).

4.1. *Diatom community drivers*

In this study, elevational distance was the only factor significantly explaining differences in diatom community composition, while geographic and overall environmental distances did not show significant effects. Under the conditions and limited sample size of our study, we did not detect a clear spatial structure in community turnover; in other

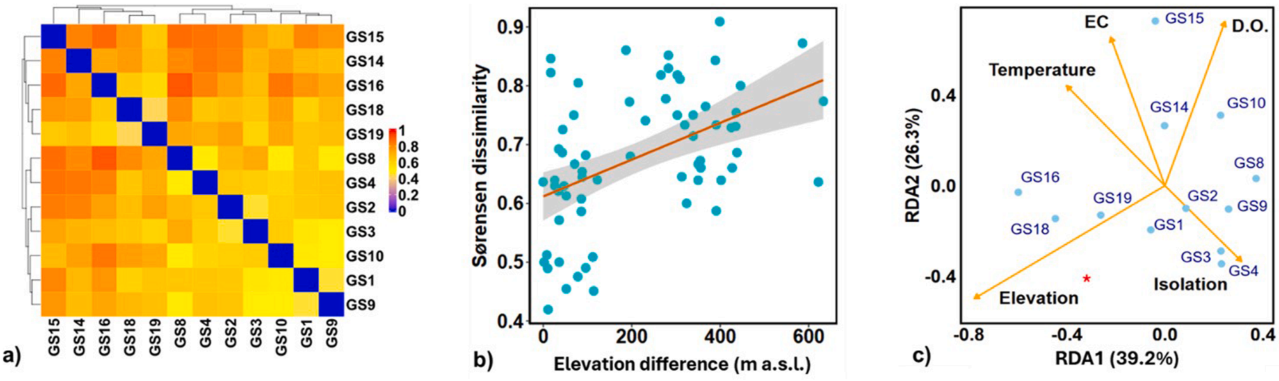

Fig. 3. a) Heatmap of pairwise Sørensen dissimilarity values (β-Sørensen) among sampling sites, illustrating taxonomic beta diversity with a color gradient from blue (low dissimilarity) through yellow to red (high dissimilarity). Row and column labels correspond to site codes; b) Scatterplot showing the relationship between elevation difference (m a.s.l.) and Sørensen dissimilarity, with a fitted linear regression line indicating increasing beta diversity with greater altitudinal separation; c) Redundancy Analysis (RDA) biplot illustrating the ordination of sampling sites (blue points) along the first two RDA axes, which explain 39.2 % and 26.3 % of the variance, respectively. Site labels are shown in dark blue. Orange arrows represent environmental vectors, indicating their direction and strength of influence on species composition. Asterisk represents significant variables.

words, community similarity did not show a pronounced decline with increasing geographic distance ("distance decay"). In contrast, Blanco et al. (2020) reported that the number of co-occurring taxa, measured as Sorensen similarity, decreased with increasing distance among Mediterranean high-elevation ponds. However, this absence of a statistically significant pattern should not be interpreted as evidence that spatial processes are unimportant in these systems. Given the relatively small number of ponds ($n = 12$), the lack of nutrient measurements, and the single sampling campaign, low statistical power may have limited our ability to detect subtle distance-related effects. Alternative explanations for the non-significant relationships include unmeasured variables that are likely important for diatom dynamics in temporary ponds, such as hydroperiod and nutrient availability. The lack of temporal replication also implies that communities integrate environmental conditions over weeks or months, whereas the physico-chemical measurements represent instantaneous snapshots; this temporal mismatch could attenuate detectable spatial signals. Within these constraints, two non-exclusive ecological interpretations remain possible: (a) local environmental filtering may be strong, with each pond's specific physicochemical conditions shaping community composition independently of spatial proximity or elevation (Schulze-Makuch et al., 2015); however, this hypothesis is only partially discounted by our results; and (b) stochastic processes may play a prominent role, generating turnover patterns that are weakly related to distance (Sun et al., 2018). The extent to which each mechanism contributes cannot be fully resolved with the present dataset, and future studies including temporal replication and nutrient and hydroperiod measurements will be necessary to clarify the relative importance of spatial versus local processes.

In practice, aquatic communities often result from the interplay between environmental filtering and stochastic processes (Moritz et al., 2013; Stegen et al., 2012). In highly selective or extreme environments, such as alpine biomes, environmental filtering tends to dominate, making community composition largely predictable from environmental parameters (Bello et al., 2013). In accordance with Szabo et al. (2018), where environmental factors played a relatively minor role compared to spatial ones, our results suggest that local environmental conditions do not have a strong influence on diatom diversity. In contrast, elevation appears to be a more relevant factor, although this effect could be partly confounded with spatial structure, as higher-elevation ponds tend to be more dispersed and may experience different disturbance regimes. This inference should be interpreted with caution given the limited sample size and the absence of nutrient data, as well as the single-season sampling.. Similarly, Teittinen et al. (2016) reported that diatom diversity along stream elevational gradients was shaped by interacting regional factors, such as dispersal and geographical variables, together with local environmental conditions. In our study, however, measured local environmental factors (e.g., pH, conductivity, temperature) appear to play a minor role in structuring diatom diversity, likely due to the limited set of variables considered and the spatial distribution of sites. While our results are consistent with general trends in the literature, such as those highlighted by Soininen (2007), we emphasize that the apparent influence of environmental factors can be context-dependent, and in our alpine temporary ponds, spatial and elevational patterns are more prominent than the measured local environmental parameters. Similarly, Van de Vijver et al. (2010) reported strong effects of local environmental parameters on diatom composition in subantarctic environments, but in our system, these factors seem less influential compared to elevation and spatial structuring.. In our case, however, the lack of temporal replication and the instantaneous nature of the physico-chemical measurements relative to the longer integration time of diatom communities limit our ability to fully disentangle the relative roles of environmental versus spatial processes. Therefore, although the supporting literature on this topic is still scarce, our findings support the idea that spatial predictors over local environmental factors could shape diatom communities in these systems, but the strength of this conclusion remains constrained by the data available and should be interpreted as a pattern detected under the specific conditions of this study

4.2. Diatom spatial patterns

Our results showed a random spatial distribution of sampling sites, with no evidence of clustering or significant dispersion among their physical locations. However, communities' uniqueness showed a significant positive spatial structure: sites with particularly unique communities tend to cluster in space, creating floristic clusters. In contrast, Shannon diversity did not show spatial autocorrelation, suggesting that species richness and uniqueness were homogeneously distributed among sites. These results agree with Blanco et al. (2020), where no spatial autocorrelation was detected for diatom diversity along the distance gradient. These findings indicated that, even in the absence of a spatial pattern in the arrangement of sites, there were processes which could favor the geographic concentration of floristic unique communities, probably linked to specific local environmental factors or to particular ecological dynamics (Khan et al., 2013; Jurasinski and Kreyling, 2007; Gentry, 1988).

Indeed, the value of "uniqueness" of communities (i.e., how different or special they are compared to others) was not randomly distributed in space but showed a tendency to cluster in certain areas. There is evidence in literature that communities with unique characteristics are more often found close to each other, forming spatial clusters, rather than being randomly distributed in space (Lozada and Bertin, 2022; Altermatt and Holyoak, 2012). The occurrence of spatially clustered communities with unique characteristics represents an ecologically relevant phenomenon that can be interpreted through the lens of various environmental and ecological processes. Positive spatial autocorrelation indicates that similar values tend to occur in geographically proximate areas. This pattern suggests that shared environmental or ecological drivers, such as climatic conditions or environmental disturbances, may shape local communities, promoting the formation of clusters of floristically distinctive assemblages (Mathur, 2015). According to the literature, there are two ecological processes that could contribute to the spatial structuring of communities (Legendre, 1993): (i) large-scale processes, such as habitat connectivity and environmental gradients, which tend to generate positive spatial autocorrelation (Booker, 2023; Biswas et al., 2021); (ii) local-scale processes, such as biotic interactions (e.g., competition), which can instead lead to greater local inhomogeneity (negative autocorrelation) (Biswas et al., 2017). In our research, where unique communities form clusters, it is likely that factors such as habitat connectivity, environmental variability and the presence of natural barriers favor the concentration of these communities in certain areas.

From an ecological perspective, the presence of clusters increases the dissimilarity between communities of different areas (beta diversity), enriching the overall landscape variability (Wayman et al., 2021; Womack et al., 2021; Legendre et al., 2005). However, it may affect overall ecological resilience and vulnerability: if unique communities are concentrated, localized disturbance events (such as pollution or climate change) may simultaneously threaten many of these communities, reducing ecosystem resilience (Sankaran et al., 2019). Understanding where these clusters occur is critical for planning nature reserves and conservation strategies, as protecting key areas can safeguard a significant portion of diatom diversity.

In the single-variable models, elevation showed a significant positive effect on Shannon diversity, indicating that higher-altitude sites tend to host more diverse diatom communities (Blanco et al., 2020). In contrast, elevation did not significantly influence community uniqueness, nor did isolation have a significant effect on either diversity or uniqueness. However, when accounting for covariation among environmental predictors in the global model, elevation emerged as a significant positive driver of uniqueness, while its effect on Shannon diversity remained marginally significant. Among local environmental parameters, electrical conductivity (EC) was a significant predictor of uniqueness, whereas ORP (oxidation–reduction potential) showed a weak negative trend, and temperature, pH, and dissolved oxygen had no detectable effects. These results suggest that elevation acts as an integrative driver, shaping community composition both directly and indirectly through its association with other environmental gradients. This pattern aligns with Blanco et al. (2020), who found greater diatom diversity in high-elevation ponds, and is consistent with observations from Pescador et al. (2021) and Sreekar et al. (2018) that local environmental effects may be weak relative to broader integrative drivers. It is also important to consider that diatom communities integrate environmental conditions over extended periods, whereas our physico-chemical measurements represent instantaneous snapshots; this temporal mismatch may reduce the detectability of environmental effects, meaning that some variables that appear non-significant could still influence communities more strongly than our dataset allows to detect.

According to Blanco et al. (2020), diatom communities in Mediterranean biomes are mainly influenced by elevation: findings from our study are consistent with the above-mentioned research but, contrary to the latter, environmental variables did not mask this effect.. Contrasting findings were reported from Heikkinen et al. (2022), where subarctic ponds diatom communities were mainly shaped by a variety of local-scale environmental variables, some of which are in turn correlated with elevation. In this context, it is also important to acknowledge that key drivers such as nutrient concentrations and hydroperiod length, both known to affect diatom structure and function, were not measured in this study. Their omission, together with the limited sample size, could lead to underestimating the actual importance of local environmental conditions or to attributing effects to elevation that may instead be mediated by these unmeasured variables. Both the marginal effect of elevation on diversity and the weak influence of EC observed in our study have also been reported in other high-elevation systems, although findings across habitats and biogeographical regions remain partially contrasting: for instance, Teittinen et al. (2016) found no clear richness–elevation relationship in streams, with conductivity emerging as a more relevant driver; conversely, Taxböck et al. (2020) documented a monotonic increase in diatom richness with elevation in Swiss springs, and He et al. (2020) reported a similar positive trend in mountain streams. Likewise, Pestryakova et al. (2018) identified EC as the most important predictor of diatom diversity in high-elevation lakes. Despite these heterogeneous patterns, the broader evidence indicates that elevation often exerts a stronger and more consistent influence than individual physicochemical variables, acting as an integrative gradient that encompasses multiple environmental and spatial processes not captured by single measurements.

Comparable findings also emerged from β -diversity partitioning, highlighting how communities differ mainly due to species replacement, rather than nested loss or gain. This pattern is in line with ecological theories predicting that species turnover dominates in environmentally heterogeneous landscapes, such as elevational gradients (Kasel et al., 2017; Dufour et al., 2006). The strong pairwise dissimilarity values, especially between distant sites like GS8 and GS16, suggest that spatial filters act to shape distinct community compositions. That GS14, GS15, and GS16 consistently showed high dissimilarity relative to other sites further suggests that spatial conditions at these ponds may be particularly selective, hosting unique diatom assemblages. The positive Mantel correlation between beta diversity and elevation supports the role of elevation as a key structuring factor, probably due to differences in temperature, hydroperiod, or nutrient availability (Dodds et al., 2019). However, partial Mantel tests controlling for geographic distance revealed that the correlation between community dissimilarity and elevation was not significant (partial Mantel $r = 0.01$, $p = 0.49$), indicating that the apparent effect of elevation observed in the standard Mantel test may be partly confounded by spatial separation among high-elevation ponds. On the other hand, the lack of a significant relationship with geographic isolation in both standard and partial Mantel tests suggests that dispersal limitation alone was not a major determinant of diatom beta diversity in this system. Interestingly, no significant differences in community dispersion were found among elevation groups, suggesting that while community composition shifts strongly between elevation classes, the within-group variability remains relatively consistent. This could reflect a consistent level of environmental heterogeneity within each elevation group, or similar levels of ecological drift or stochasticity affecting communities regardless of elevation (Gilbert and Levine, 2017; Purves and Pacala, 2005). However, it should be noted that the lowest group (1300–1600 m a.s.l.) includes 4 ponds, the middle group (1600–1800 m a.s.l.) 5 ponds, and the highest group (1800–2100 m a.s.l.) 3 ponds. These numbers are relatively balanced, reinforcing the idea that the elevational classes, at least in our study, provide a reasonable framework to explore how elevational range may (or may not) influence diatom community diversity. The db-RDA results indicate that elevation is among the variables most strongly associated with community variation but given the moderate strength of correlations and the small number of ponds, this conclusion should be interpreted with caution.

In conclusion, unlike Blanco et al. (2020), where isolation was identified as a key factor influencing the ecological uniqueness of Mediterranean high-elevation ponds, our study provides, to the best of our knowledge, the first evidence that elevation may play a major role in shaping the uniqueness of diatom communities in TPs within the alpine biome, although this effect appears partly confounded by spatial separation among high-elevation ponds.. Our results suggest that, in alpine TPs, elevational gradients appear to influence community composition independently of isolation but given the small number of ponds and the moderate strength of correlations, this conclusion should be interpreted with caution, leading to the development of functionally unique diatom communities at higher elevations. These findings highlight how the mechanisms structuring diatom communities can differ substantially depending on the biogeographical context.

The diversity and uniqueness of diatom communities are influenced by a combination of geographic factors, with elevation appearing as one of the strongest correlations of diversity and uniqueness within the limited set of variables measured, especially when considered together with other environmental variables. Electrical conductivity, in particular, seems to favor the presence of communities with similar adapted species, probably reflecting specific ecological conditions or adaptive responses to environmental gradients. Overall, the results highlight the importance of adopting an integrated approach when analyzing biodiversity determinants, as interactions between geographic and environmental factors can better explain the complexity and distribution of communities in high-elevation aquatic ecosystems. Furthermore, this emphasizes the importance of considering regional context and specific environmental gradients when investigating drivers of community diversity and uniqueness.

4.3. Limitations of the study

This study represents an initial attempt to explore the environmental and geographic drivers of diatom diversity and uniqueness in high-elevation temporary ponds, a type of habitat that remains largely understudied. However, some limitations should be acknowledged. First, our results are based on a single sampling campaign and a limited number of ponds, which does not allow for the assessment of temporal variability or interannual dynamics. Future studies including repeated sampling across different seasons and years would provide a more comprehensive understanding of community stability and environmental responses. Moreover, only a limited set of physicochemical variables was measured in situ; the inclusion of nutrient concentrations and additional hydrological parameters would likely refine the interpretation of environmental filtering processes. Despite these constraints, the patterns detected here highlight clear relationships between elevation, environmental conditions, and diatom community structure, offering a valuable baseline for future ecological and bioindicator research in alpine temporary ponds.

5. Conclusions

Although alpine biomes have received less attention than other ecosystems, they represent some of the most important and vulnerable environments in the context of climate change. The extreme conditions typical of high-elevation habitats foster distinctive biodiversity, and their sensitivity makes them among the first regions to exhibit the effects of global environmental change. In this regard, diatoms play a crucial role as bioindicators, providing valuable insight into the ecological responses of alpine ecosystems due to their rapid reactions to environmental fluctuations.

Our results show that the variability in diatom community diversity and uniqueness is best explained by geographic factors. Elevation and electrical conductivity emerged as significant predictors, whereas isolation did not significantly influence either community diversity or uniqueness. Although no clear spatial structure was observed among sites, floristic clustering (uniqueness) was evident, suggesting that specific local environmental factors—particularly elevation and conductivity—play a central role in shaping distinctive diatom assemblages rather than simple geographic distance. Furthermore, habitat connectivity, environmental heterogeneity, and natural barriers may contribute to the spatial concentration of floristically unique communities.

Understanding how alpine ecosystems respond to ongoing climate change is essential for predicting future biodiversity patterns and informing effective conservation strategies. Broader and long-term ecological research on alpine temporary ponds is therefore crucial to safeguarding their biodiversity and ecosystem functions in an increasingly changing world.

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

CRediT authorship contribution statement

Davide Taurozzi: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Massimiliano Scalici:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecohyd.2025.100726.

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