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Game of traits: diatom functionality in a changing landscape

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ABSTRACT

Temporary ponds (TPs) are ephemeral freshwater habitats underlying seasonal drying creating highly dynamic environments. Here, for the first time, we focused on the trait analysis of benthic diatom communities along an elevational and seasonal gradient, aiming at: a) analysing taxonomic and functional α diversity indices variations; b) discerning whether or not seasonality and elevation affected taxonomic and functional β diversity; c) investigating the main physical and chemical factors influencing diatom communities. Among the seasonal changes, diatom guild-based communities exhibited significant variations only for high-profile guild. Seasonality appeared not influencing diatom taxonomic and functional α diversity, while the effect of elevation was statistically significant for taxonomic Shannon (TSha), Simpson (TSim) and Evenness (TEve). Furthermore, our results highlighted that neither seasonality nor elevation significantly influenced total taxonomic and functional β diversity, with the turnover component accounting for most of the observed variation. However, taxonomic β diversity showed substantial seasonal and elevational fluctuations, unlike functional β diversity, which was not driven by neither elevation nor seasonality. Physical parameters (Temperature, pH) exerted a significant influence on taxonomic α diversity, while Oxygen Reduction Potential and Total Dissolved Solids were identified as the main drivers of diatom functional α diversity. Differently, changes in Temperature, Resistivity and Dissolved oxygen emerged as important predictors for shaping elevational taxonomic β diversity. Our results emphasize the importance of considering multiple facets of biodiversity when investigating diatom communities in temporary ponds, as different aspects may exhibit distinct patterns and be shaped by different ecological drivers, particularly in high-elevation systems.

1. Introduction

Temporary ponds (TPs) are ephemeral freshwater habitats characterized by a cyclic nature, with recurring wet and dry phases (Celewicz and Gołdyn, 2021). These habitats, defined as shallow (< 5 m), small water bodies (< 5 ha) with less than 30% of emergent vegetation, are distributed across diverse landscapes, from low-elevation coastal regions to high-elevation alpine areas (Richardson et al., 2022). The hydroperiod cycle (described as the proportion of time a pond is inundated, Crase et al., 2013) is generally regular: under normal conditions, TPs fill with water every late winter and become desiccated with the onset of summer (Celewicz and Gołdyn, 2021). However, high-elevation TPs (typically present in high-mountain landscapes, $>$ 1000 m a.s.l.) show a different hydroperiod, characterized by frozen waters during late autumn and winter, a wet phase during spring and early summer and a dry phase during late summer and early autumn (Taurozzi and Scalici, 2024b).

Both low- and high-elevation ponds are constantly under the siege of different anthropogenic direct and indirect threats, such as climate change, prolonged droughts, land-use changes, pollution, and habitat fragmentation, all of which can alter their hydrological regimes and compromise the ecological integrity of these sensitive aquatic systems (Bagella et al., 2016). Furthermore, monitoring programs frequently do not incorporate assessment techniques for temporary small waterbodies. In this perspective, the use of benthic diatoms as biological indicators is particularly valuable, as they are highly responsive to environmental changes and widely employed to assess the ecological health of aquatic ecosystems (Taurozzi et al., 2024).

Benthic diatom communities consist of ubiquitous, microscopic, photosynthetic algae that grow on submerged surfaces, such as rocks, sediments, and plants, in freshwater, marine, and brackish environments (Hamed, 2023). Currently, different methodologies including indicator species, diversity indices, and diatom indices have been developed according to the variations in the diatom species community

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(Liu et al., 2025). However, traits-based approaches can help increase our mechanistic understanding of how ecological communities assemble and function and how they change along different environmental gradients (Litchman et al., 2010). Ecological traits were firstly introduced by Passy (2007), categorizing diatom species on their responses to nutrient and disturbances gradients in rivers rather than their taxonomy (Ecological guilds; Liu et al., 2025; Jamoneau et al., 2018). This concept was further expanded by Rimet and Bouchez (2012), grouping diatom species based on their shared ecological strategies and functional traits, such as life-forms, mobility, cell-sizes and ecological preferences.

Intense modifications can occur in TPs regime hydrological and environmental variables along an elevational gradient, in relation with seasonality (Hayashi and van der Kamp, 2021). Benthic diatom communities of TPs are overlooked: only few research investigated the elevational and seasonal fluctuations of diatoms, with an almost complete knowledge gap regarding high-elevation ponds, in particular between 800 and 1600 m a.s.l. (Taurozzi et al., 2024) and above. Furthermore, the literature does not provide a universally accepted altitudinal range to define "high elevation" ponds; the elevational range considered here was taken from Krammer (2002) and Leuschner (2000), who suggested thresholds starting around 1000 m a.s.l. in temperate regions. The responses of benthic diatom communities appear to vary substantially depending on the type of freshwater habitat and the environmental gradients considered (Virta et al., 2020): temporary ponds, which represent extremely unstable habitats where diatom responses may substantially differ from those observed in more permanent water bodies, remain poorly investigated, making them key targets for advancing our understanding of diatom community dynamics under highly variable environmental conditions.

Finally, most of the very few existing studies have focused primarily on taxonomic (species-based) approaches, lacking functional trait-based analyses. Functional traits are morphological, physiological, or ecological characteristics of diatoms that reflect their ecological strategies, responses to environmental conditions, and roles in ecosystem functioning (Passy, 2007). Unlike purely taxonomic approaches (which focus on species identity), functional traits provide mechanistic insight into community assembly and ecosystem processes. By integrating both taxonomic and functional perspectives, this study provides a more mechanistic understanding of how diatom communities assemble and respond to environmental gradients in high-elevation temporary ponds, a context that remains largely unexplored. To translate these functional and taxonomic perspectives into measurable patterns of community structure, we examined both α and β diversity. α diversity captures local richness and functional attributes of communities, whereas β diversity reflects spatial and temporal differentiation (Arellano and Halffter, 2003), allowing the disentanglement of processes such as species turnover and nestedness. Turnover describes how species change between locations or time, involving the loss of certain species and the introduction of new ones: this process can be driven by ecological factors including spatial heterogeneity, species competition, and environmental filtering (Buckley and Jetz, 2008). Nestedness influences β diversity by explaining how species richness can change between sites: it indicates that some sites have a subset of species found in richer sites, which can lead to a more uniform distribution of species across habitats. Considering both alpha and beta diversity simultaneously provides a more complete understanding of diatom community dynamics, since local-scale patterns of diversity (α) are linked to regional or temporal differentiation (β).

In this study, we selected TPs along an elevation gradient to elucidate trends and potential causes of both taxonomic and functional diatom α and β diversity patterns. Assuming that hydrological regime cause variation in the biotic component, we expected differential structural and functional characteristics of the epilithic diatom community along an elevational gradient in different seasonality scenarios. To address this knowledge gap, our research, with a focus on diatoms as bioindicators, aimed to: (A1) Analyse guild-based diatom community variations across seasons and elevations; (A2) Investigate taxonomic and functional α diversity indices variations across elevation and season; (A3) Investigate the main physical and chemical factors influencing diatom communities. (A4) Whether or not seasonality and elevation affected taxonomic and functional β diversity patterns of benthic diatoms.

Following the taxonomic-based findings from existing literature (Virta et al., 2020; Cantonati et al., 2007), we hypothesized that: (H1) guild-based diatom community showed seasonal fluctuations; (H2) α diversity increased along the elevation gradient from low elevation to high elevation sites, with no effects of seasonality; (H3) Taxonomic and functional α and β diversity (and their components) showed different responses to the physical and chemical gradients; (H4) β diversity and its turnover component should be mostly influenced by elevation rather than seasonality.

2. Materials and methods

2.1. Study area and sampling activities

The study was conducted in the Italian Peninsula, considering six TPs along an elevational gradient through the two regions of Latium and Abruzzi (Table S1). The ponds were identified using GEE images and field surveys, while their temporary nature was analyzed with the use of the GEE historical imagery tool, following Taurozzi and Scalici (2024b) (Fig. 1a, 1b). The elevation of the six sites considered was chosen in the order of 400 ± 100 m a.s.l., from the Tyrrhenian coast to the Campo Imperatore plateau. The six ponds were named combining the abbreviation TP + the relative elevation (expressed as meters above sea level: TP0; TP400; TP800; TP1200; TP1600; TP2000) (Fig. 1c – 1i). The samplings were performed each month, one sampling per month for each pond, for one year (from March 2023 until February 2024), for a total of 41 samplings (Fig. 1j). Given the ephemeral hydroperiod, in some cases it was not possible to sample because of frozen or completely dryness conditions of the ponds (see Fig. 1j, red dots). In order to standardize the sampling methodology, samplings were conducted each time by the same operator at the same hour of the day (± 30 min). Summer was the only season where diatom data were available from all the ponds considered (i.e., at least one month sampled). High-elevation ponds were sampled only during summer and autumn.

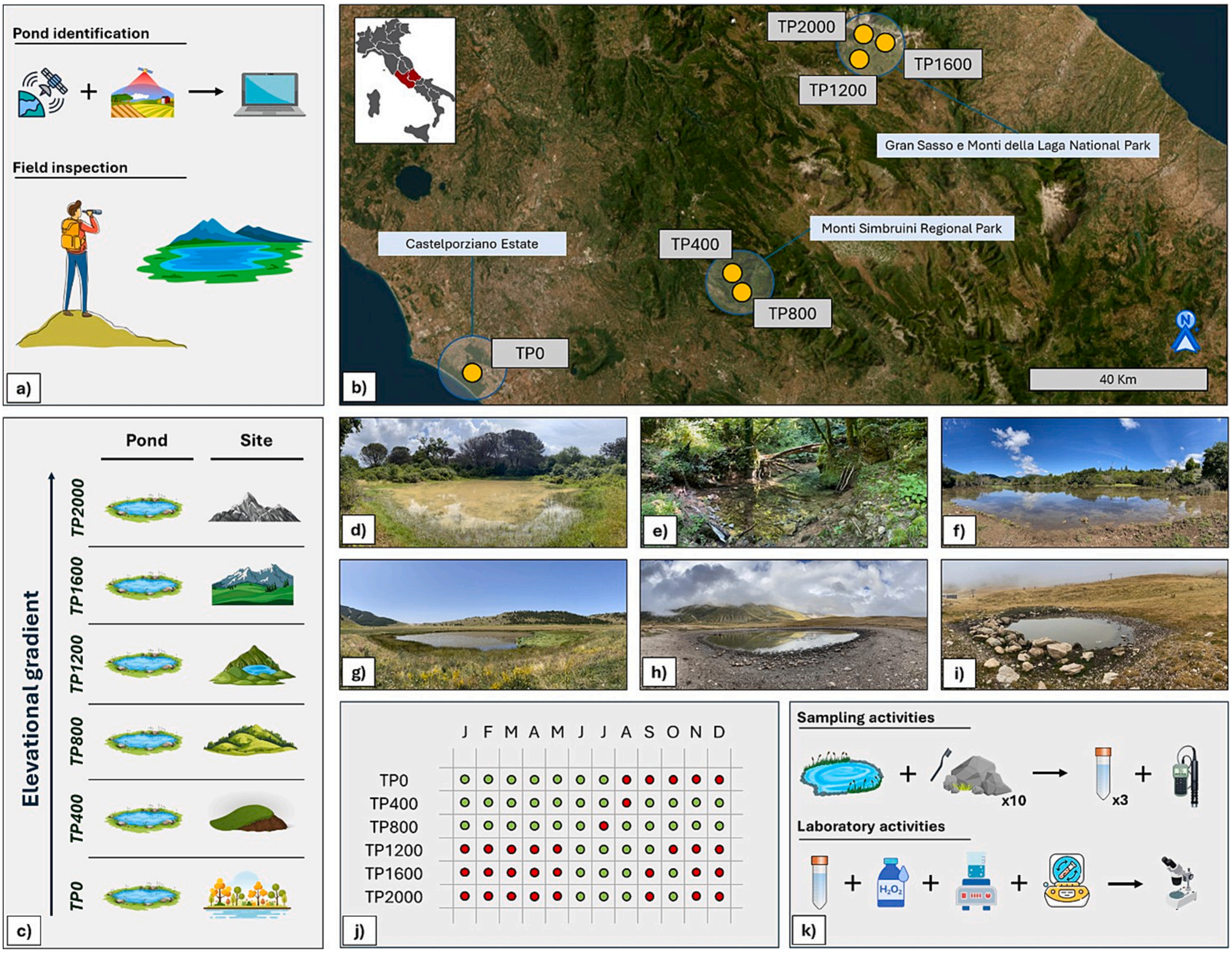
Diatom sampling activities were performed following Beltrami et al. (2007): For each sample, at least 10 stones (dimensions between 64 mm to 256 mm) were scraped using a commercial toothbrush (taking care to use a new toothbrush for each sampling site) to cover a total surface area of at least 1 m^2; then, the toothbrush was immersed in a 50 ml Falcon containing 70% diluted ethanol and distilled water (Fig. 1 k). Diatom oxidation operations followed in the laboratory using hydrogen peroxide method (Taurozzi and Scalici (2024a). For each site, three different replicates were performed as suggested by Maitland et al. (2020). Diatom identification (400 valves for each slide) was performed using a Leica microscope at 100× magnification, with the help of specific taxonomic guides (DREAL Languedoc Roussillon, 2021; Bahls et al., 2018; Taylor et al., 2007; Krammer, 2002; Krammer and Lange-bertalot, 1991b; Krammer and Lange-bertalot, 1991a; Krammer and Lange-bertalot, 1988; Krammer and Lange-bertalot, 1986).

At each sampling site, 8 physical and chemical parameters of ponds were directly measured using a multiparametric probe Hannah® HI98194: Temperature (T °C), pH, Oxygen Reduction Potential (ORP, mV), Electrical conductivity (EC, μS/cm), Total Dissolved Solids (TDS, ppm), Resistivity unit (RES, MΩ/cm) Salinity (psu), Dissolved oxygen (DO, ppm) (Fig. 1 k) (Table S4).

2.2. Statistical analysis

2.2.1. Seasonal composition of species- and guild-based benthic diatom communities

Prior to all analyses, data were tested for normality (Shapiro–Wilk



	J	F	M	A	M	J	J	A	S	O	N	D
TP0	🟢	🟢	🟢	🟢	🟢	🟢	🟢	🔴	🔴	🔴	🔴	🔴
TP400	🟢	🟢	🟢	🟢	🟢	🟢	🟢	🔴	🟢	🟢	🟢	🟢
TP800	🟢	🟢	🟢	🟢	🟢	🟢	🔴	🟢	🟢	🟢	🟢	🟢
TP1200	🔴	🔴	🔴	🔴	🔴	🟢	🟢	🟢	🟢	🔴	🔴	🔴
TP1600	🔴	🔴	🔴	🔴	🔴	🟢	🟢	🟢	🔴	🟢	🔴	🔴
TP2000	🔴	🔴	🔴	🔴	🔴	🟢	🟢	🟢	🔴	🟢	🔴	🔴

Fig. 1. a) Preliminary pond identification methodology and subsequent field inspection; b) geographical distribution of the study sites; c) schematic elevational distribution of the ponds and related habitat type; d) TP0; e) TP400; f) TP800; g) TP1200; h) TP1600; i) TP2000; j) Sampling activities calendar; green dots = sampling dates, red dots = unsampled dates; J – D = months of the year ordered from January to December; k) schematic representation of sampling (field) activities and laboratory activities (oxidation and identification processes).

test) and homogeneity of variances (Levene's test). Parametric tests were applied only when these assumptions were met; otherwise, non-parametric alternatives were used.

In the first part of our analysis, we focused on the principal ecological diatom guides proposed by Passy (2007): high profile, low profile, motile. The reported guilds represent the main functional traits generally used in diatom community ecology studies.

Normality and homogeneity of variances were tested prior to the analyses. When these assumptions were not met, non-parametric alternatives were applied. To test our first hypothesis (H1), ANOVA test was performed to identify seasonal fluctuations in the number of species for each guild. In instances of significance, subsequent pairwise Tukey's honestly significant difference (HSD) tests were performed to identify significant differences between ecological guilds. Similarly, ANOVA test and Tukey HSD were performed to identify significant seasonal differences between ecological guilds for each site. Kruskal-Wallis's tests and Dunn's post hoc tests were performed to identify significant differences in the distribution of guilds among ponds.

2.2.2. *Seasonal and elevational α diversity fluctuations in species-based and traits-based diatom communities*

In the second part of our analysis, we mainly focused on taxonomic and functional α diversity and physical and chemical variables. Taxonomic α diversity was calculated using the *diversity* function in vegan package (Oksanen et al., 2025) of R software (R Core Team, 2024). We calculated 5 α diversity indices: Richness (TRic); Shannon-Weiner (TSha); Simpson (TSim); Evenness (TEve); Margalef (TMar) (Description of the adopted indices was reported in Table S2). Similarly, functional α diversity was calculated using the *dbFD* function in R package FD (Laliberté and Legendre, 2010) on diatom matrix based on species composition and functional traits. 15 functional traits were selected (cell size, guild, and life forms), using 0–1 for presence and absence following Rimet and Bouchez (2012) (Table S3 and Table S5). Then, we calculated 5 α functional diversity indices: Functional Richness (FRic), Functional Evenness (FEve); Functional Divergence (FDiv); Functional Dispersion (FDis); Rao Quadratic Entropy (RaoQ) (Description of the adopted indices was reported in Table S2).

To test our second hypothesis (H2) and identify variability in the taxonomic and functional α diversity of diatom communities across seasons and elevations, we ran the non-parametric Kruskal–Wallis tests among the four seasons and the six elevations, followed by Dunn's post hoc tests. Non-parametric tests (Kruskal–Wallis and Dunn's post hoc) were selected because they are robust to unbalanced sampling designs, which are common in temporary pond datasets given the unpredictability of hydroperiods. To test our third hypothesis (H3) and evaluate the key physical and chemical factors determining spatial patterns of taxonomic and functional α diversity, we performed Random Forest Regression (RFR) (Genuer et al., 2010) for α diversity indices. RFR is a widely used non-parametric machine learning algorithm characterized by higher flexibility and robustness compared to traditional linear regression models (Genuer et al., 2010). RFR constructs multiple decision trees (in this case, 1000 trees) to identify the most important predictor variables for the target α diversity index. The model's performance was assessed using mean squared error (MSE) and R-squared (R2) values: MSE quantifies the average squared difference between observed and predicted values and R^2 quantifies the proportion of variance in the observed data explained by the model Pearson's correlation test was performed to test the RFR model performance as an additional indication of agreement between observed and predicted values. RFR was performed using the *randomForest* function in the R package randomForest (Breiman, 2001), followed by the importance function from the same package to rank the variable importance.

2.2.3. Seasonal and elevational β diversity fluctuations in species-based and traits-based diatom communities

In the third part of our analysis, we mainly focused on taxonomic and functional β diversity and physical and chemical variables. Taxonomic and functional β diversities were calculated based on the presence–absence matrix, utilizing the Sørensen dissimilarity index. Functional matrix was generated using the *pco* function from the vegan package. The decomposition of taxonomic β diversity into turnover and nestedness components was achieved using the *beta.pair* function from the R package betapart (Baselga et al., 2023). Concurrently, the computation of functional turnover and nestedness components followed the methodology proposed by Swenson (2011), using the *functional.beta.pair* function in the R package betapart. Subsequently, taxonomic and functional β diversities, along with their respective components, were calculated both for seasons and elevation gradient.

To test our fourth hypothesis (H4) and identify variability in the taxonomic and functional composition of diatom communities across seasons and altitudes, permutational analysis of multivariate dispersions (PERMDISP) was employed, utilizing the *betadisper* function in the R vegan package on dissimilarity matrices generated with the *gowdis* function from vegan package. Principal Coordinate Analysis (PCoA) and the Euclidean distance were used to characterize seasonal and elevational β diversity variations in species-based and guild-based communities, which were statistically assessed by permutational multivariate analysis of variance (PERMANOVA). The combination of PERMANOVA and PERMDISP was adopted, as both methods are suitable for unbalanced designs and allow us to disentangle differences in community composition from differences in within-group dispersion. Finally, to test our third hypothesis (H3) on β diversity, we performed distance-based redundancy analysis (db-RDA) (Legendre and Anderson, 1999) for β diversity matrices. Distance-based Redundancy Analysis (db-RDA) is a multivariate statistical technique that allows for non-Euclidean distances, commonly used in community ecology to examine the relationships between species composition or guild-based community and environmental variables. Following Wu et al. (2024a), we first applied the *findCorrelation* function in the R package caret to remove the physical and chemical variables with strong intercorrelation (i.e., Spearman's rank $|r| > 0.8$) and reduce multicollinearity. Then, we performed a global test (by ANOVA at a significance level of $p < 0.05$) for each value of taxonomic and functional β diversity by using *capscale* function in the vegan package. *Capscale* function and ANOVA test were then performed for each physical and chemical variable, looking for significant influences of each variable on β diversity.

Statistical tests were considered significant when *p*-value was <0.05. Statistical analyses were computed in PAST 4.17c software (Hammer et al., 2001) and R software (v. 4.4.2, R Core Team, 2024). Figures were drawn using R software and GraphPad Prism 8.0 software (GraphPad).

3. Results

3.1. Seasonal composition of species- and guild-based benthic diatom communities

A total of 232 benthic diatom species, belonging to 53 genera were identified across four seasons and six sampling sites (Table 1).

Overall, 116 motile, 67 high-profile, 51 low-profile species were observed. ANOVA test highlights no significant seasonal fluctuations for motile ($F = 0.6$, $p > 0.05$) and low-profile guilds ($F = 0.02$, $p > 0.05$). Differently, seasonal fluctuations were observed for the high-profile guild ($F = 4.14$, $p < 0.05$) with significant differences emerged between winter and summer ($Q = 4.66$, $p < 0.05$) and between summer and autumn ($Q = 3.85$, $p < 0.05$) (Fig. 2a). Kruskal-Wallis test highlighted significant differences in the distribution of guilds among ponds only for TP800 ($H = 7.53$, $p = 0.02$) (Fig. 2b).

ANOVA tests indicated that, in general, there were no significant differences in the abundance of motile, high-profile, and low-profile guilds between ponds in summer or autumn (TP0 excluded). Similarly, no significant seasonal fluctuations were observed within most ponds, except for the high-profile guild at TP1600 ($F = 3.2$, $p < 0.05$) and TP2000 ($F = 5.3$, $p < 0.05$), which showed significant seasonal variation according to Tukey's HSD (Fig. 2c).

3.2. Seasonal and elevational α diversity fluctuations in species-based diatom communities

Taxonomic α diversity indices of diatom communities showed no significant variations across the seasons (Fig. 3a, Table S6).

The α diversity indices exhibited a distinct increasing trend from low-elevation ponds to high-elevation sites, as observed in Fig. 3b (Table S7). TSha ($H = 17.7$, $p = 0.003$), TSim ($H = 17.8$, $p = 0.004$) and TEve ($H = 15.1$, $p = 0.009$) showed significant differences in α diversity values (Table 2).

The random forest regression (RFR) models reliably predicted the taxonomic α diversity indices, as indicated by MSE (13.4, 0.04, 0.002, 0.002, 0.26) and R^2 (0.79, 0.74, 0.73, 0.72, 0.79) for TRic, TSha, TSim, TEve and TMar, respectively.

Results from RFR highlighted pH and EC as the primary factor influencing taxonomic α diversity (TSha, TSim, Teve, TMar), with fine-scale spatial factors (e.g., RES, ORP) following closely (Fig. 3c). The relationship between observed and predicted values using Pearson's correlation test yielded a strong positive correlation which was highly significant for all the α diversity indices considered (TRic, $r = 0.94$, $p < 0.01$; TSha, $r = 0.93$, $p < 0.01$; TSim, $r = 0.94$, $p < 0.01$; TEve, $r = 0.95$, $p < 0.01$; TMar, $r = 0.95$, $p < 0.01$).

Table 1

| Dominant species found for each season (we reported only the percentage for the season exceeding 5% following Liu et al., 2025).

	Winter	Spring	Summer	Autumn
Achnanthidium eutrophilum (Lange-Bertalot 1996)	–	11%	6%	–
Achnanthidium minutissimum (Kützing, 1994)	–	13%	5%	9%
Cocconeis placentula (Ehrenberg, 1838)	15%	–	–	6%
Denticula tenuis (Kützing, 1844)	9%	–	–	12%
Diatoma mesodon (Kützing, 1844)	–	–	6%	–
Ephitemia adnata (Kützing, 1838)	–	–	6%	5%
Eunotia minor (Kützing, 1881)	–	5%	–	–
Gomphonema micropus (Kützing, 1844)	–	–	6%	–
Gomphonema minutum (Agardh, 1831)	–	–	–	6%
Gomphonema parvulum (Kützing, 1849)	–	–	9%	–
Navicula tripunctata (Müller, 1822)	–	–	–	8%
Navicula trivalis (Lange-Bertelatot,1980)	5%	–	–	–
Nitzschia frustulum (Kützing 1880)	–	–	8%	–
Nitzschia palea (Kützing, 1844)	11%	–	–	–

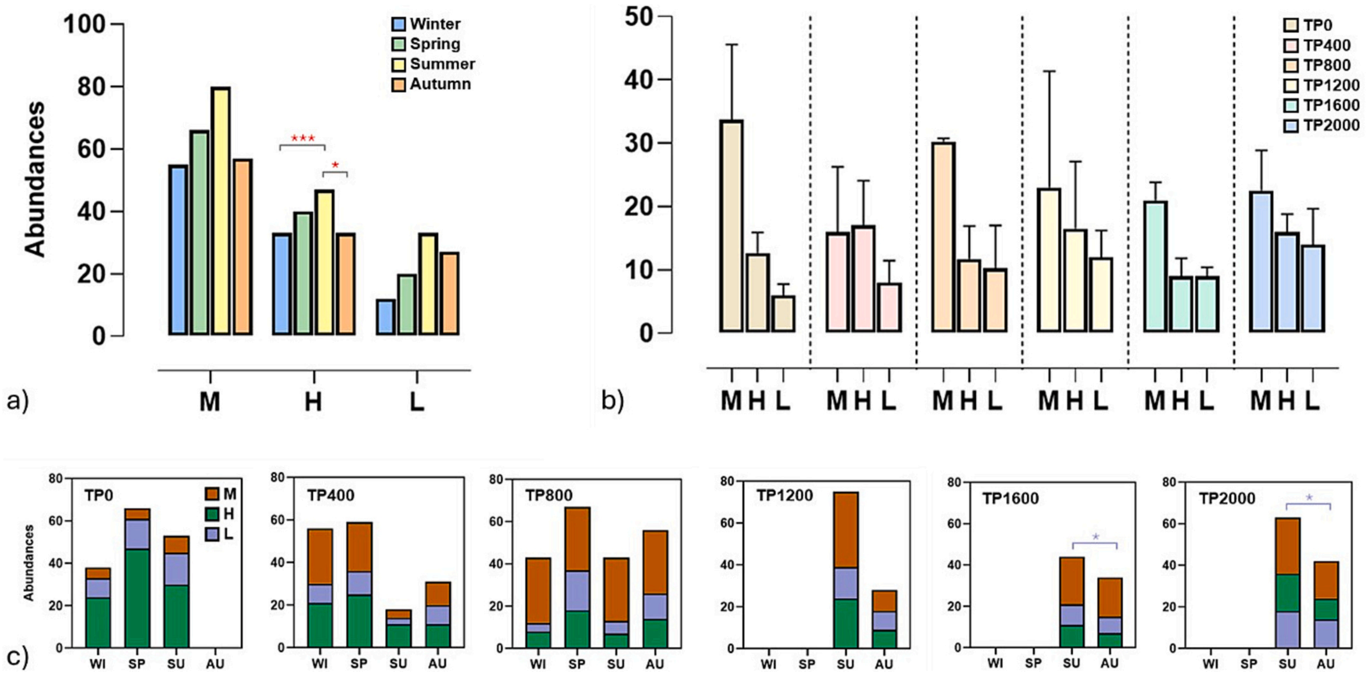


Fig. 2. a) Seasonal changes in the composition and relative abundance of the benthic diatom ecological guilds; b) Distribution of ecological guilds among ponds; c) Seasonal changes of guilds abundances among ponds. Asterisks indicate seasonal significant differences based on the ANOVA test and Tukey's pairwise (***$p < 0.001$; *$p < 0.05$). M = Motile guild; H = High-profile guild; L = Low-profile guild. WI = Winter; SP = Spring; SU = Summer; AU = Autumn.

3.3. Seasonal and elevational α diversity fluctuations in guild-based diatom communities

The results revealed that no significant differences were observed in functional α diversity among seasons (FRic, H = 1.851, $p = 0.6$; FEve, H = 1.312, $p = 0.7$; FDiv, H = 1.388, p = 0.7; FDis, H = 1.946, $p = 0.5$; RaOQ, H = 2.596, $p = 0.4$) (Fig. 4a) (Table S8 and Table S9).

Notably, functional α diversity indices exhibited a distinct increasing trend from low-elevation ponds to high-elevation sites, as depicted in Fig. 4b for FDiv (H = 13.15, $p = 0.02$), FDis (H = 14.4, $p = 0.01$) and RaoQ (H = 12.44, p = 0.02) (Table 3).

The random forest regression (RFR) models reliably predicted the functional α diversity, as indicated by MSE (12.16, 0.001, 0.001, 0.022, 0.34) and R^2 (0.77, 0.78, 0.77, 0.75,0.73) for FRic, FEve, FDiv, FDis and RaOQ, respectively (Fig. 4c).

Results from RFR highlighted ORP as the primary factor influencing functional α diversity (FDiv, FDis and RaOQ), with fine-scale spatial factors (e.g., pH, T) following closely (Fig. 4c). The relationship between observed and predicted values using Pearson's correlation test yielded a strong positive correlation which was highly significant for all the α diversity indices considered (FRic, r = 0.93, p < 0.01; FEve, $r = 0.92$, $p < 0.01$; FDiv, $r = 0.93$, p < 0.01; FDis, r = 0.96, p < 0.01; RaOQ, $r = 0.96$, p < 0.01).

3.4. Seasonal and elevational β diversity fluctuations in species-based diatom communities

Total elevational β diversity (0.697) was generally higher than seasonal total β diversity (0.542). Turnover and nestedness in the seasonal β diversity were 0.457 and 0.084. β diversity was mainly contributed by seasonal turnover (84.3% total) rather than nestedness (15.7% total) (Table S10). No significant differences between seasons emerged (F = 0.54, $p = 0.67$) (Fig. 5a and Table S11).

Similarly, turnover and nestedness in the elevational β diversity were 0.624 and 0.072. β diversity was mainly contributed by elevational turnover (89.6% total) rather than nestedness (10.4% total) (Table S12). No significant differences in dispersion among elevations emerged (F = 0.82, $p = 0.54$) (Table S13) (Fig. 5a).

PCoA showed that β diversity exhibited substantial seasonal (F = 2.05, $p = 0.003$) and elevational fluctuations (F = 3.94, $p = 0.001$). The first two axes (PCoA1 and PCoA2) together explain 30.66% of the variation in seasonal β diversity and 29.92% of the variation in elevational β diversity (Fig. 5b).

The db-RDA analysis revealed that the environmental variables explain 13.82% of the total seasonal variance and 17.96% of the total elevational variance. The first two axes accounted for 6.93% of the seasonal total variation (RDA 1 = 4.44%, RDA 2 = 2.49%) and 8.82% (RDA 1 = 5.39%, RDA 2 = 3.43%) of the elevational total variation, with no significant effects of physical and chemical parameters for seasonality (F = 0.9, $p = 0.862$) and significant effects for elevation (F = 1.24, $p = 0.006$) (Fig. 5c). Permutational analysis highlighted that T (F = 1.59, $p = 0.07$), RES (F = 1.62, p = 0.006) and DO (F = 1.37, $p = 0.047$) can be considered important predictors for shaping elevational β diversity.

3.5. Seasonal and elevational β diversity fluctuations in guild-based diatom communities

Total elevational β diversity (0.288) was generally higher than seasonal total β diversity (0.183). Functional turnover and nestedness in the seasonal β diversity were 0.068 and 0.11, respectively. Functional β diversity was mainly contributed by seasonal nestedness (62.8% total) rather than turnover (37.2% total) (Table S14), except for summer, with no significant differences between seasons (F = 1.98, $p = 0.14$) (Fig. 6a and Table S15).

Differently, turnover and nestedness in the elevational β diversity were 0.17 and 0.11, respectively. Functional β diversity was mainly contributed by elevational turnover (61.8% total) rather than nestedness (38.2% total) (Table S16), with no significant differences in dispersion among elevations (F = 0.74, $p = 0.59$) (Fig. 6a).

PCoA showed that β diversity exhibited no substantial seasonal (F = 0.8, $p = 0.4$) and elevational fluctuations (F = 0.6, $p = 0.07$). The first two axes (PCoA1 and PCoA2) together explained 71.61% of the variation in seasonal β diversity and 72.05% of the variation in elevational β diversity (Fig. 6b).

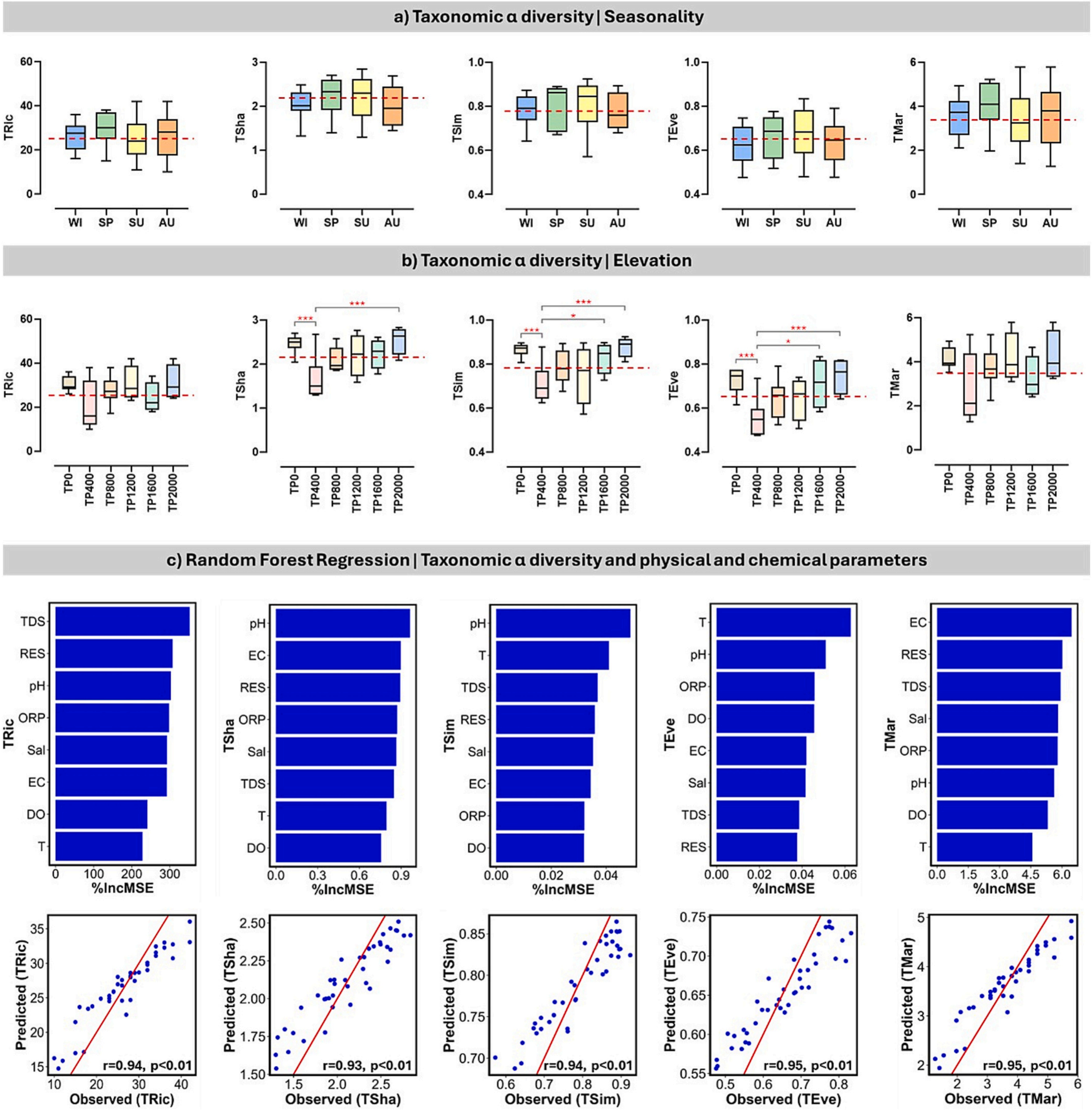


Fig. 3. Taxonomic α diversity values for the five indices: a) across seasons; b) across elevations. c) Above: Random forest regressions showing the 8 physical and chemical predictors for taxonomic α diversity indices; Below: Pearson's correlation tests. %IncMSE = increased in mean squared error (%). TRic = Taxonomic richness; TSha = Taxonomic Shannon; TSim = Taxonomic Simpson; TEve = Taxonomic evenness; TMar = Taxonomic Margalef. WI = Winter; SP = Spring; SU = Summer; AU = Autumn. DO = Dissolved oxygen; EC = Electrical conductivity; ORP = Oxygen Reduction Potential; RES = Resistivity unit; Sal. = Salinity; T = Temperature; TDS = Total Dissolved Solids. Asterisks indicate significant differences based on the Kruskal-Wallis test and Dunn's post hoc (***$p < 0.001$; *$p < 0.05$).

The db-RDA analysis revealed that the first two axes accounted for 10.74% of the seasonal total variation (RDA 1 = 7.43%, RDA 2 = 3.31%) and 10.49% of the elevational total variation (RDA 1 = 7.19%, RDA 2 = 3.3%), with no significant effects of physical and chemical parameters on functional β diversity (Season, F = 0.68, $p = 0.72$; Elevation, F = 0.66, $p = 0.70$) (Fig. 6c). Permutational analysis highlighted that no physical and chemical parameters can be considered important predictors for functional total β diversity.

4. Discussions

Our study aimed to assess, for the first time, the effect of two significant geographical factors, elevation and seasonality, on diatom communities in TPs, a field where existing research is limited (Taurozzi and Scalici, 2025). The novelty of our work lies in adopting an integrated approach that simultaneously considers taxonomic and functional α and β diversity in relation to both broad-scale geographical gradients and local physical and chemical conditions across contrasting

Table 2
| Dunn's post hoc pairwise z-values and *p*-values for variables with significant Kruskal-Wallis results.

Index	Comparison	z-value	p-value
TSha	TP0 – TP400	3.5	0.0004
	TP400 – TP2000	3.3	0.0001
TSim	TP0 – TP400	3.4	0.0006
	TP400 – TP1600	2.1	0.028
	TP400 – TP2000	3.3	0.001
TEve	TP0 – TP400	3.1	0.001
	TP400 – TP1600	2.4	0.01
	TP400 – TP2000	2.9	0.003

environmental contexts.

4.1. Seasonal composition of guild-based benthic diatom communities

Guild-based community analysis higlighted no significant variations across seasons both for motile and low-profile guilds, partially supporting our H1. Motile guild species show the ability to move actively, which helps them navigate through their environment and avoid sedimentation (Rimet and Bouchez, 2011). The observed similar occurrence of this guild among different seasons is consistent with the unstable conditions of TPs, which are subject to large daily and seasonal variations (Van den Broeck et al., 2015). Similary, low profile guild species are generally small and attached to the substrate by their entire valve area which helps them withstand high currents and physical disturbances. Their ability to resist to unfavorable conditions, generally present in all the season in TPs, make them suitable for inhabiting ephemeral waterboides, making their presence in all seasons predictable.

Differently, high-profile diatoms, often found in nutrient-rich environments, are sensitive to physical disturbances which can disrupt their growth and stability (Tapolczai et al., 2016). Given their affinity for nutrient-rich waters, our findings are consistent with their ecology: our results higlighted different abundances of high-profile guilds between summer and winter and between summer and autumn, confirming previous research (Snell et al., 2019). We could hypothesize that elevation amplified differences between seasons, given that nutrient enrichment during the summer season is more pronounced in high-elevation ponds (Gardner et al., 2008).

4.2. Seasonal and elevational α diversity in species- and trait-based diatom communities

Taxonomic α diversity did not reflect benthic guild-based outcomes: seasonality appeared not influencing diatom communities confirming our H2, differently from Liu et al. (2025), where spring showed significant lower values of diatom richness. Previous studies have observed bimodal patterns in diatom species richness, with peaks occurring during specific seasons, such as February–March and possibly another peak later in the year (Breton et al., 2021). However, the lack of statistical significance observed here suggests two main possible explanations: a) diatom communities in TPs reach taxonomic stability in a relatively short time, without the alternation of pioneer species and secondary and tertiary colonizers; or, in alternative, b) diatom communities are largely resistant to large-scale environmental changes (seasonal variations). The first hypotesis was supported by Taurozzi and Scalici (2024a), were no statistical differences emerged between TPs, permanent ponds and wetlands. Differently, although diatom communities exhibit resilience, their resistance to large-scale environmental changes might be limited, as they are influenced by factors such as nutrient supply and water temperature (Liu et al., 2022; Wang et al., 2023b).

Functional α diversity (considering all the 15 traits) showed similar patterns between different seasons. Our results partially agree with Liu et al. (2025), further confirming the limited influence of the succession of seasons on functional composition of diatom communities; on the other hand, taxonomic α diversity, here reported as being similar among seasons, was statistically different in Liu et al. (2025), where significant differences between spring and the other seasons were reported.

An interesting finding of our study was that taxonomic and functional α diversity differed significantly among elevations, confirming H2. Specifically, the most diverse diatom communities were observed in high-elevation ponds, in agreement with Blanco et al. (2020). This pattern is consistent with other studies reporting that elevation influences diatom diversity through changes in environmental conditions such as water temperature, ionic content, and dissolved oxygen (Şahin & Barinova, 2022; Feret et al., 2017). These environmental gradients can affect species distribution and abundance. For example, high-elevation conditions, which are more extreme and variable, may favor only a subset of well-adapted species. This can lead to decreases in evenness, as reflected by the Simpson index, and corresponding shifts in the Shannon index, which integrates both richness and evenness (Wu et al., 2024b). Differences in functional traits, such as motility and nutrient uptake strategies, may also contribute to these patterns, as species respond variably to environmental constraints (Padula et al., 2021). Overall, our results highlight that elevation acts as a key driver of both taxonomic and functional diversity. In our study, TSha, TSim, and TEve showed highly significant differences between low- and high-elevation ponds, suggesting that harsher conditions at higher elevations can filter species, altering community composition and functional diversity. On the contrary, fluctuations in functional diversity indices (FDiv, FDis, RaOQ) were observed in all the sites considered, regardless of elevation. FDiv was significantly higher in comparisons such as TP0–TP400 and TP400–TP1200, indicating that the dominant species in these ponds were functionally more divergent, suggesting the presence of specialized strategies among the most abundant diatoms. Analogous patterns have been observed in studies of diatom communities in stress-prone or highly variable systems. For instance in Central European soda pans, trait-based analyses showed that under harsh conditions functional diversity is reduced via filtering (Stenger-Kovács et al., 2019) In periphytic diatoms, microhabitat heterogeneity was shown to increase functional dispersion (FDis) and divergence (FDiv) (Nemes-Kókai et al., 2024). These patterns suggest that diatoms, due to their small size and rapid growth rate, are particularly sensitive to local environmental factors (Tapolczai et al., 2016), and that functional diversity in these ponds may respond more to local habitat variability than to general seasonal trends.

4.3. Diversity of benthic diatoms in relation to abiotic factors

Our results showed that taxonomic and functional α and β diversity, along with their components, responded differently to physical and chemical variables, supporting H3. Our findings are consistent with previous research showing that environmental factors such as T, pH, and conductivity (EC) shape diatom communities. In Mediterranean high-elevation lakes, differences in water chemistry were linked to distinct diatom assemblages (Padula et al., 2021), while other studies in coastal lagoons and rivers have highlighted both significant (Fernández-Moreno et al., 2024; Flower et al., 2012; Ali et al., 2015) and minor effects of EC on diatom diversity (Stefanidou et al., 2020). In the ponds analyzed here, variations in T, pH, and EC likely acted as filters, favoring species with traits adapted to specific conditions, which is reflected in both taxonomic and functional diversity indices. Functional traits, including motility and nutrient uptake strategies, further mediate these responses, allowing communities to cope with environmental heterogeneity.

It must be noticed that the physical and chemical parameters investigated explained very few variations of both taxonomic and functional β diversity components. This findings implied the main limit of our research, i.e. the possible influence of abiotic (nutrients, light availability, flow regime, trampling, pesticides and other contaminants) and biotic factors (competition, grazing and predation) not considered here. Indeed, the lack of significant relationships between physical and

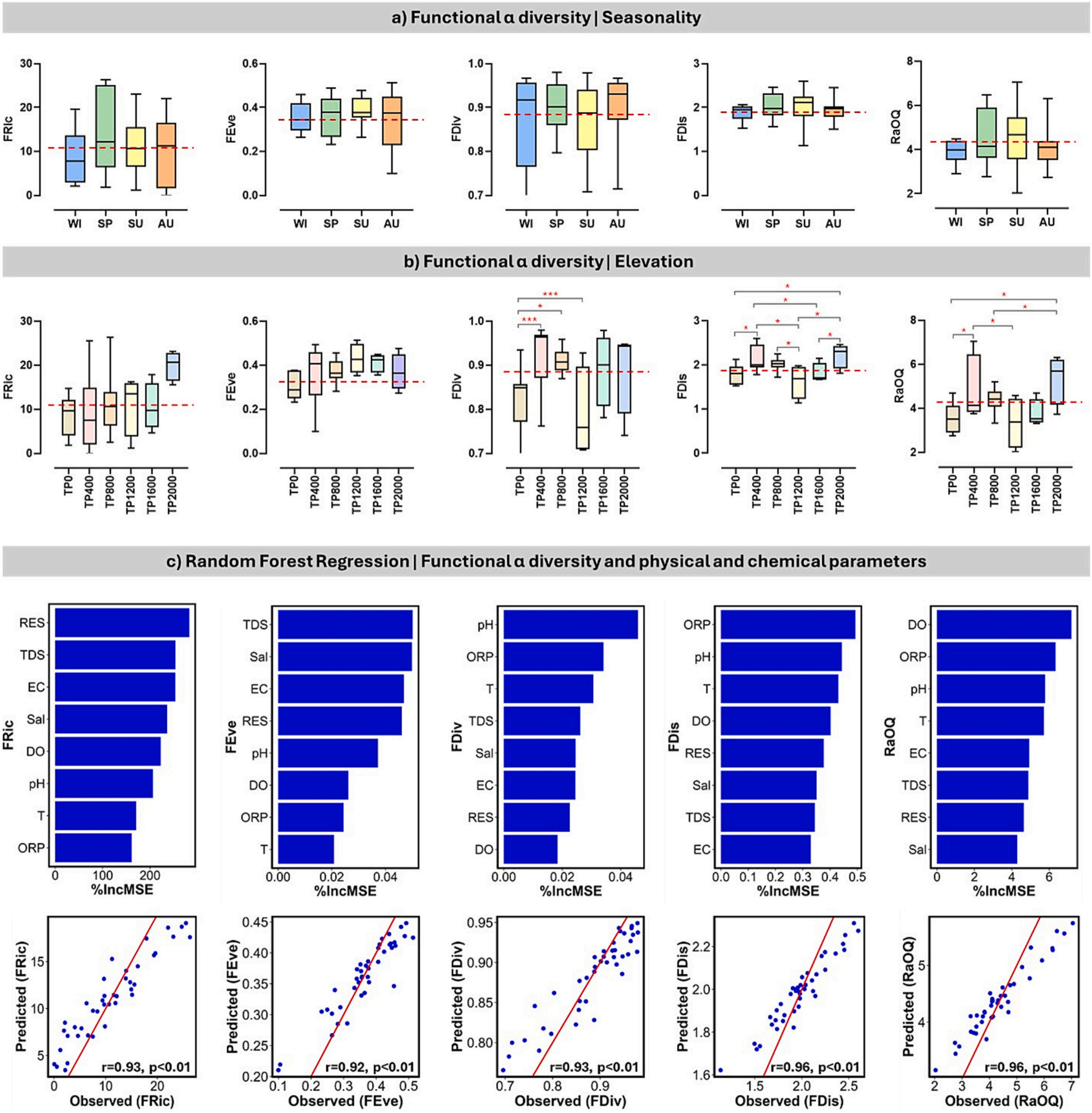


Fig. 4. Functional α diversity for the five indices: a) across seasons; b) across elevations c) Above: results of Random forest regressions showing the 8 physical and chemical predictors for functional α diversity indices; Below: Pearson's correlation. %IncMSE = increased in mean squared error (%). FRic = Functional richness; FEve = Functional evenness; FDiv = Functional divergence; FDis = Functional dispersion; RaOQ = Rao Quadratic Entropy. WI = Winter; SP = Spring; SU = Summer; AU = Autumn. DO = Dissolved oxygen; EC = Electrical conductivity; ORP = Oxygen Reduction Potential; RES = Resistivity unit; Sal. = Salinity; T = Temperature; TDS = Total Dissolved Solids. Asterisks indicate significant differences based on the Kruskal-Wallis test and Dunn's post hoc (***$p < 0.001$; *$p < 0.05$).

chemical parameters and functional β diversity suggests that other factors might play a predominant role in shaping diatom community structure. However, our outcomes are not consistent with previous studies: following Blanco et al. (2020), the lack of general trends in diatom communities pattern suggests that diatom diversity could be more affected by local environmental factors rather than by climatic variables that are associated with elevation. Here, although the db-RDA model explained low variability, physical and chemical factors emerged as significant drivers influencing diatom taxonomic diversity along the elevational gradient. Differently, physical and chemical parameters appeared not driving diatom functional β diversity along the elevational gradient, as they do in different seasons for taxonomic and functional diversity: these findings underscore the resilience of functional β diversity in diatom communities, with functional traits exhibiting stability despite environmental variation caused by both seasonal and elevational fluctuations.

In addition to the physical and chemical factors analyzed here, further spatial processes such as geographical distance among sites,

Table 3

| Dunn's post hoc pairwise z-values and *p*-values for variables with significant Kruskal-Wallis results.

Index	Comparison	z-value	p-value
FDiv	TP0 – TP400	3.1	0.002
	TP0 – TP800	2.0	0.04
	TP400- TP1200	2.7	0.007
FDis	TP0 – TP400	2.4	0.01
	TP0 – TP2000	2.3	0.02
	TP400 – TP1600	2.1	0.03
	TP800 – TP1200	1.9	0.04
	TP1200 – TP2000	2.4	0.01
	TP1600 – TP2000	2.1	0.03
RaOQ	TP0 – TP400	2.4	0.01
	TP0 – TP2000	2.3	0.02
	TP400 – TP1200	2.1	0.03
	TP1200 – TP2000	2.1	0.03

pond connectivity, isolation, and dispersal limitation can strongly influence diatom communities in TPs (Blanco et al., 2020). For completeness, we refer the reader to Taurozzi et al. (2025), which specifically addressed these aspects using the same set of samples and study sites. This allows our two studies to be read in a complementary way, highlighting both local and regional drivers of diatom diversity in TPs.

4.4. Seasonal and elevational β diversity fluctuations in species- and trait-based diatom communities

Unexpectedly, we found that the components of taxonomic and functional β diversity did not vary as a function of seasonality and elevation. Differently, as expected (H4), our results found that both taxonomic and functional total β diversity where mainly driven by the elevational gradient rather than seasonality, with the turnover component explaining most of the observed β diversity, except for seasonal functional diversity. As demonstrated here, nestedness contributes to β diversity by explaining variations in species richness between sites, but its contribution is typically smaller compared to turnover (Baselga, 2010). In diatoms, significant species composition shifts along environmental gradients, such as those seen in elevational gradients, can result in high turnover (Wu et al., 2024). Our findings are consistent with previous studies on benthic algae (Jamoneau et al., 2018) and diatoms (Wu et al., 2023) where taxonomic β diversity was predominantly attributed to turnover, while nestedness, was moslty influent in functional β diversity, Possible reasons behind this patterns include that: a) higher elevations may impose stronger constraints on functional traits (e.g., temperature tolerance, nutrient use), leading to a nested functional structure where only a subset of traits can persist in harsher conditions (Wang et al., 2023a); b) some species may be replaced taxonomically, but their ecological roles are maintained, leading to lower taxonomic nestedness but stronger functional nestedness; c) functional traits adapted to lower elevations may not persist at higher elevations, creating a nested structure where high-elevation communities are functionally filtered subsets of lowland ones.

However, these results, both and functional total, showed statistically significant shifts among seasons and elevations for taxonomic β diversity, and no statistically significant shifts among seasons and elevations for functional β diversity, challenging H4 but partially in line with previous findings. In recent studies, diatom taxonomic β diversity has been found to be relatively stable across seasons, despite changes in community composition, due to factors like functional redundancy and effective dispersal mechanisms (Virta et al., 2020). On the contrary, regarding elevation, while specific studies on diatoms and elevational β diversity are limited, research on environmental gradients suggests that β diversity can be high in areas with significant environmental changes, such as estuaries or mountainous regions (Virta et al., 2020; Eliasz-Kowalska et al., 2022). With different species assemblages linked to each season and location, our findings suggest that seasonal and elevational variations significantly influence the taxonomic diversity of diatom communities, while functional diversity is overall similar across seasons and elevations.

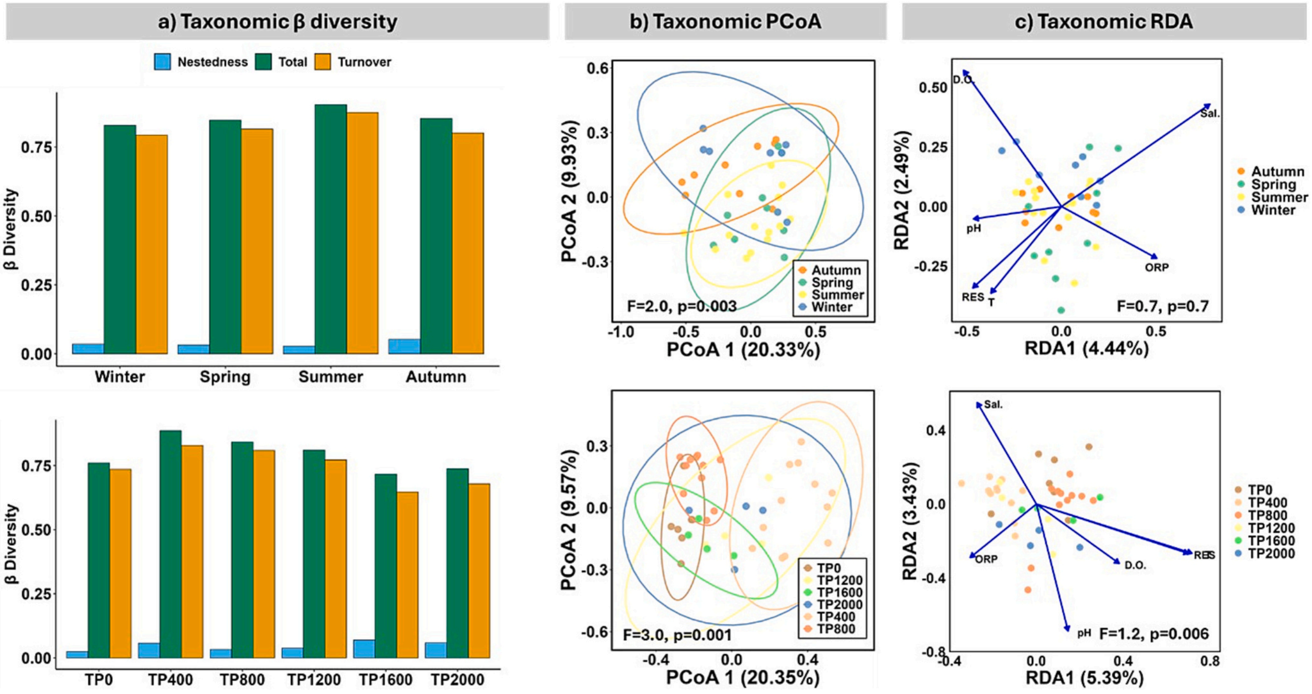


Fig. 5. a) Statistic description of taxonomic β diversity components (total, turnover, and nestedness) for seasons and elevational gradient; b) PCoA of seasonal and elevational β diversity of the taxonomic diatom communities; c) Plots of Redundancy Analysis for Seasonal and elevational taxonomic β diversity. DO = Dissolved oxygen; EC = Electrical conductivity; ORP = Oxygen Reduction Potential; RES = Resistivity unit; Sal. = Salinity; T = Temperature.

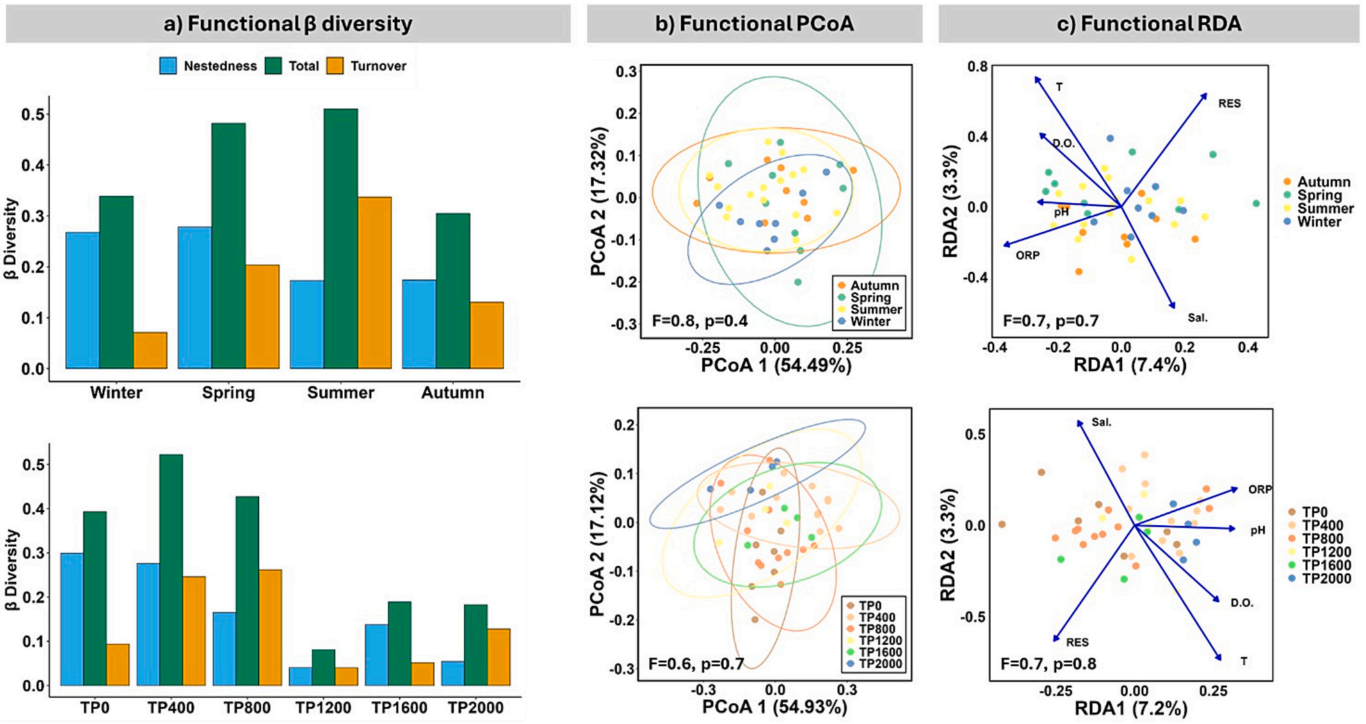


Fig. 6. a) Statistic description of functional β diversity components (total, turnover, and nestedness) for seasons and elevational gradient; b) PCoA of seasonal and elevational β diversity of the guild-based diatom communities; c) Plots of Redundancy Analysis for seasonal and elevational functional β diversity. DO = Dissolved oxygen; EC = Electrical conductivity; ORP = Oxygen Reduction Potential; RES = Resistivity unit; Sal. = Salinity; T = Temperature.

4.5. *Limitations of the study*

Despite the novel insights provided by our research, several limitations should be acknowledged. First, the lack of comprehensive nutrient data across all ponds and seasons restricts our ability to fully assess the role of trophic status in shaping diatom community composition. Parameters such as total phosphorus (TP), inorganic nitrogen forms (ammonium, nitrite, nitrate), orthophosphate, and proxies of primary productivity (e.g., chlorophyll-a and water transparency) were not consistently measured. These variables can be useful to understand algal growth potential and ecosystem productivity, and their absence limits interpretations on the nutrient–diatom diversity relationship. However, such analyses were not feasible due to budgetary constraints and limited access to the necessary instrumentation.

Additionally, the spatial and temporal resolution of our dataset was uneven, particularly in the high-elevation TPs (1200–1600 m a.s.l.), where only 4 out of 12 samples were collected, with 3 of them limited to the summer season. This limited dataset reduces our ability to draw robust conclusions about seasonal variation in those sites. It is important to highlight that, due to the unpredictable hydroperiod of temporary ponds, sampling was conducted whenever water was present and accessible, an inherent challenge when working in such dynamic and ephemeral environments. Moreover, the elevational gradient was represented by only six discrete levels, which inevitably reduces the generalizability of our conclusions.

Considering data analysis, although Hill numbers offer a more consistent and interpretable framework for biodiversity assessment, we used Shannon and Simpson indices to maintain comparability with the scarce previous studies on diatom communities in temporary ponds. Future research would benefit from the adoption of Hill numbers to provide a unified basis for biodiversity comparisons.

Finally, given the scarcity of studies on diatom communities in TPs, our interpretations were necessarily based on comparisons with other permanent freshwater systems, such as streams and lakes. However, these ecosystems differ markedly in terms of hydroperiod, connectivity, and ecological dynamics. Therefore, increasing the number of studies specifically focused on TPs, especially from different biogeographical regions, is crucial to enable more appropriate and ecologically meaningful comparisons.

5. Conclusions

In a world increasingly affected by anthropogenic pressures, climate change, and water scarcity, temporary ponds are becoming ever more exposed to intense, sometimes irreversible, stress. Our study represents a starting point for investigating the factors shaping diatom communities in these fragile ecosystems, offering valuable insights for future conservation efforts. We observed that elevation, rather than seasonality, was the main driver of diatom community structure. This suggests that local environmental gradients linked to altitude, such as changes in water chemistry or hydrological regimes, exert stronger control than short-term seasonal fluctuations. Functional diversity, in contrast, appeared relatively stable, indicating that diatoms may maintain similar functional strategies even under variable conditions, possibly reflecting resilience mechanisms typical of fast-growing organisms with diverse trait repertoires. The identification of specific chemical parameters, such as ORP and TDS, as significant predictors of functional α diversity further underlines the importance of fine-scale abiotic filters in shaping community assembly. This supports the view that temporary ponds are not homogeneous habitats but rather mosaics of environmental conditions where both local and regional drivers interact in complex ways.

From a broader perspective, our findings emphasize the value of using diatom communities as bioindicators for monitoring ecosystem health in temporary ponds. Conservation strategies should consider elevation-related variability as well as local water chemistry to better predict biodiversity responses under scenarios of climate change and water scarcity.

CRediT authorship contribution statement

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

Consent to participate

Not applicable.

Ethics approval

Not applicable.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.114696.

Data availability

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

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