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Has climate change over the last ten years caused a banalisation of diatom communities in Cypriot streams?

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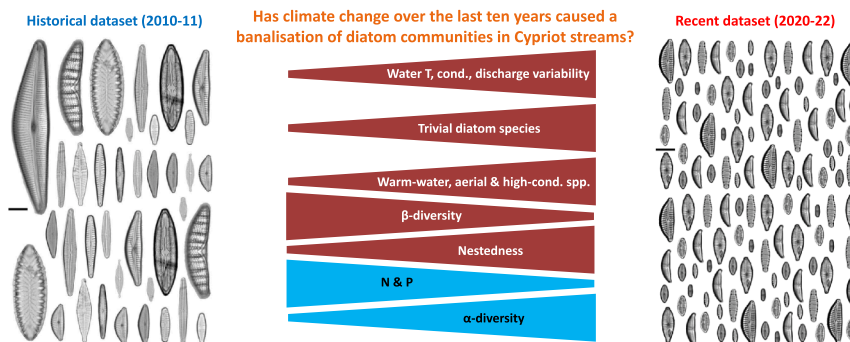
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HIGHLIGHTS

- The last ten years of climate change in Cyprus strongly influenced stream hydrology.
- Characteristic and sensitive species were replaced by trivial and opportunistic ones.
- Warm-water, aerial, and high-conductivity diatom species increased in abundance.
- β -Diversity decreased, nestedness increased, but α -diversity increased.
- Identification and protection of head-water reference sites to be used as refugia

GRAPHICAL ABSTRACT



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ABSTRACT

To unveil possible changes in diatom communities in Cypriot streams over the last ten years or so, we selected samples from the years 2020, 2021, and 2022 for the “recent” dataset ($N = 119$) and samples from the years 2010 and 2011 for the “historical” dataset ($N = 108$). Biotic homogenization has become a truly global phenomenon. Here we show that, over the last ten years, in response to increased water temperature, conductivity, and discharge variability due to climate-change, Cypriot stream diatom communities include a higher number of trivial (= widespread, tolerant, and opportunistic), aerial, and thermophilic species, have reduced β -diversity and

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increased nestedness. Moreover, IndVal analysis shows that indicator species from the historical dataset were characteristic, often relatively rare species, while the indicators of the recent dataset were a group of typical trivial, eutraphentic, and thermophilic species. As is almost always the case, the diatom communities we studied were subjected to multiple stressors, often affecting them in opposite ways. Besides the increase in trivial species, the reduction in β -diversity, and the rise in nestedness mentioned above, the diatom assemblages we studied also showed an increase in α -diversity that could be due to a moderate reduction in nutrients in several sites. High-ecological-integrity ecosystems, such as springs, waterfalls, and dripping rock-walls, in particular springs that were shown to be excellent hydrologic refugia in climates heavily affected by climate change, and the stream sites close to them should be carefully protected, as they can be refugia for sensitive and characteristic species that can recolonize the adjacent streams after adverse climatic events.

1. Introduction

Overwhelming climate change affects Earth, with a reported severe temperature rise of 0.25 to 0.45 °C per decade (Ullah et al., 2022). Extreme temperature rises were reported for the USA, Europe, and China in July of 2023 when the average global temperature was 1.54 °C above the preindustrial average for this period (Tollefson, 2023). The disproportionality of such extremes worldwide is of great concern, especially for certain vulnerable regions (Bolan et al., 2024).

Observation-based and modelling studies have identified the Eastern Mediterranean as a significant climate change hotspot that will continue to warm during the twenty-first century (Lelieveld et al., 2012; Coppola et al., 2021; Zittis et al., 2021). The use of an integrated watershed model, based on historical (1950–2015) and future (2021–2100) periods under Representative Concentration Pathways (RCP4.5 and RCP8.5) enabled assessing the impact of warming and drying trends on the hydrology of this region. The annual precipitation is predicted to exhibit weakly decreasing trends, even along with a mean warming rate of 0.03 °C/y for T_{\max} and 0.01 °C/y for T_{\min} . The projected streamflow seasonality points to a substantial decrease in discharge in all months (Krysanova et al., 2017).

Cyprus is one of the five most water-stressed Mediterranean countries at the EU level and is the one facing the most significant water scarcity conditions on the seasonal scale according to the Aqueduct Water Risk Atlas. Water resources in Cyprus are limited, unequally distributed, and frequently inadequate to meet demands. The predominance of evaporation (~85 %) over precipitation results in the loss of surface water resources. Specifically, for Cyprus, the business-as-usual scenario predicts a 20–40 % decrease in precipitation by the end of the century (Zittis et al., 2022). With climate-induced changes in precipitation patterns and seasonality, warmer temperatures, increased evapotranspiration, reduction in snow cover in upstream regions, and elevated water demand, the water scarcity issue is projected to be exacerbated further (Zittis et al., 2022).

Changes in the hydrological cycle during the previous century have already led to reduced rainfall, especially during the wet season, and alongside the ongoing trend of warming in the Eastern Mediterranean, this creates a severe threat to the region (Zittis, 2018; Zittis et al., 2022). For impacted countries like Cyprus, decreasing trends for annual and seasonal stream flow and more intense drought trends were revealed. The dry season is expected to be prolonged by 1–2 months by the end of the century. Thus, since Cyprus has already been importing fresh water from neighbouring countries, the increase in severe droughts could worsen the situation (Myronidis et al., 2018). The projected changes in the severity of such events are more pronounced when the synergistic impact of temperature is also considered (Driouech et al., 2020; Spinoni et al., 2020). Furthermore, the results of climate change are expected to lead to longer dry periods, after which more cases of torrentiality of precipitation will follow. Thus, extreme weather events (heatwaves, droughts, dust storms, and torrential rainfall events, which may lead to flash floods) are expected to continue affecting Mediterranean stream ecosystems (Llasat, 2021). Droughts, along with temperature increases over the land, could be, in general, predictable and periodic in Mediterranean regions, but dramatically unpredictable interannually (Lake,

2003). Moreover, because of the hydrologically diverse and highly dynamic nature of streams in Mediterranean climates, the effect of such condition changes will spread in the region with high spatial variability.

The different, and often combined, direct and indirect impacts, including rapid climate change and anthropic pressure, can result in the simplification, banalization, and biotic homogenization of biological communities (Baiser et al., 2012). Some even acknowledge the homogenization of species that is coming as a part of the Anthropocene and all the human activities that it entails, describing the current ecological era as Homogenocene (see, e.g., Rosenzweig, 2001). A typical cause of biotic homogenization is, e.g., urbanization, with one of the hypothesized trajectories of urban ecosystems and communities being homogenized, possibly leading to very similar assemblages in cities across the globe (Lokatis and Jeschke, 2022).

Despite all efforts to prevent a biodiversity crisis in freshwater ecosystems, biodiversity decline has intensified over the last decade (Reid et al., 2019). Furthermore, the loss, degradation, and simplification of some habitats, alterations in water quality, and climate change caused not only the decline of freshwater biodiversity (Darwall et al., 2018) but also affected the species distribution, survival chances, extinction, endemism, and phenology (van Rees et al., 2021; Ahmed et al., 2022). Climate change and more regional- and local-scale impacts stimulate the decline of habitat-forming (or foundation) species in communities, altering the composition structure and decreasing its stability (Bulleri et al., 2012; Hawkins et al., 2009; Lemieux and Cusson, 2014).

In freshwater ecosystems, the leading investigated causes of biotic homogenization are non-native species introduction, damming, and land-use changes, with other natural and anthropogenic causes, such as climate change, changes in productivity, and flood and drought events, also increasing similarity among aquatic biota (Petsch, 2016). Zuo et al. (2023) investigated cyanobacterial communities in 59 waterbodies in China. They showed that taxonomic diversity increases along a trophic gradient, but phylogenetic diversity decreases, niche width and overlap decrease, and assemblages become more uniform with eutrophication. Wengrat et al. (2018) applied paleolimnological approaches to eutrophic reservoirs to show a marked decrease in β -diversity, suggesting that eutrophication leads to homogenization of the diatom assemblages.

Biotic homogenization of communities and reduction of species richness are two distinct phenomena, and a decrease in β -diversity is not systematically associated with a decrease in α -diversity. Anthropogenic disturbances are associated with taxonomic homogenization (loss of β -diversity); one general pattern often reported is the elimination of sensitive species (McKinney and Lockwood, 1999; Olden et al., 2004; Socolar et al., 2016) and subsequent replacement by generalist species (Gutiérrez-Cánovas et al., 2013). However, considering nutrient enrichment in particular, if high levels cause widespread regional biodiversity declines in diatoms, insects, and fish, they also tend to increase local diversity in nutrient-poor watersheds (Budnick et al., 2019).

Mediterranean freshwater biodiversity distinctly reacts to climate change, owing to drastic alterations in the stationarity of thermal and hydrological regimes (Markovic et al., 2014; da Silva et al., 2023). In conjunction with local threats such as pollution, overexploitation, artificial human regulation, and changes in flow, global warming has long-term consequences for species composition, leading to species losses and

changes in the distribution and abundance of some taxa (Reid et al., 2019).

Diatoms are highly sensitive to flow-reduction and desiccation impacts (e.g., Cantonati et al., 2020a). They may therefore represent an ideal model group on which to investigate the response of communities to water-flow reductions associated to global climate change (Tornés et al., 2022). Artigas et al. (2012) showed that Mediterranean streams' biofilms had a more significant amount of early colonizing diatom species (*Ulnaria ulna*, *Karayevia clevei*), as well as higher rates of polysaccharide production in the extracellular matrix. Diatoms are overwhelmingly affected by hydrological variables in Mediterranean streams (e.g., Cantonati et al., 2020a). Diatom teratological forms can occur because of water intermittency intensifying chemical pollution (Tornés et al., 2018). Increases in nutrient concentrations, siltation and reduced water availability can cause dramatic changes in diatom assemblages and lead to the extinction of vulnerable species (Novais et al., 2020). The development of generalist (tolerant) species that can occupy available niches, regional extinctions of rare and specialist species, and, as a result, taxonomic simplification of the communities (β -diversity) will be a consequence of such changes (Petsch, 2016; Zorzal-Almeida et al., 2021). Diatom communities are hypothesized to persist in banalization until a greater diversity of ecological niches is generated (Morin et al., 2015).

The objectives of this paper are to verify if climate-change-driven alterations of the hydrology of Cypriot streams might have caused a banalization of the diatom communities reflected in the pronounced spread of widely distributed, opportunistic ("trivial") species, biotic homogenization, and reduction in species richness and community

diversity. We also intended to ascertain if diatom species known to occur abundantly in freshwater bodies with relatively elevated temperatures increased in abundance. Finally, we aim suggesting for strategies to mitigate or halt the reduction or local extinction of characteristic and rare diatom species and communities.

2. Methods

2.1. Study area and sample collection

In the territories under the control of the Republic of Cyprus, the hydrological network has a total length of about 2630 km, corresponding to 70 catchments covering an area of about 6500 km² (Fig. 1). Only 22 % of the river water bodies have perennial flow while 56 % have intermittent flow and 22 % exhibit ephemeral/episodic flow. Perennial rivers are mainly found in the western and central regions of the Troodos Massif at elevations over 300 m. A few perennial rivers can also be found at lower altitudes, usually sustained by springs. Many catchments have a typical succession of flow regimes from perennial to intermittent to ephemeral/episodic. The perennial headwaters are absent in catchments with less rainfall, and in arid catchments situated in the lowlands, the intermittent reaches may also be absent (RBMP, 2020).

To unveil possible changes in diatom communities in Cypriot streams over the last ten years or so, we selected samples from the years 2020, 2021, and 2022 for the "recent" dataset (36 + 45 + 38 = 119 samples) and samples from the years 2010 and 2011 for the "historical" dataset (70 + 38 = 108 samples). We started with a crosswalk from all the samples from sites from 2020, 2021, and 2022 to those included in

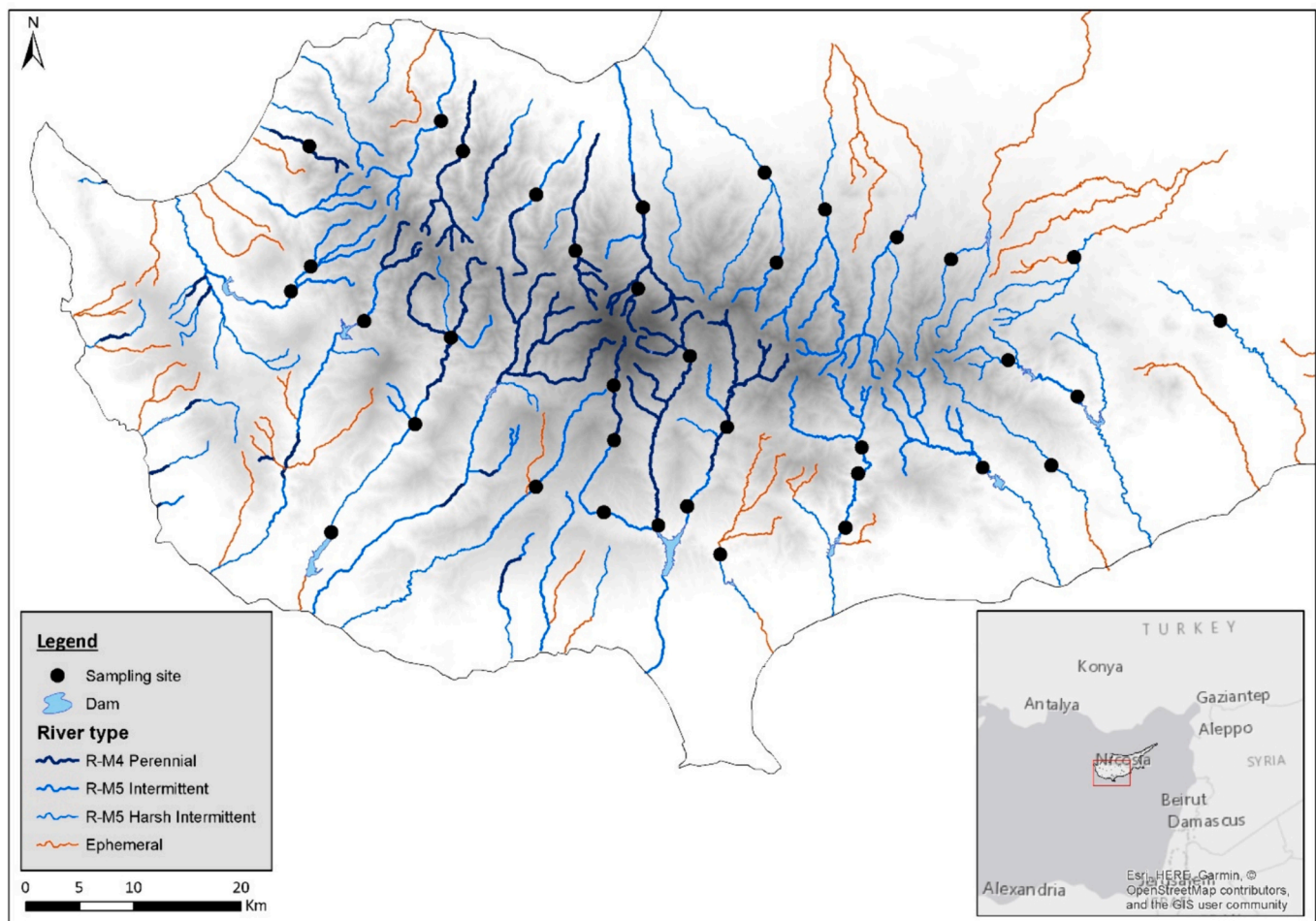


Fig. 1. Location of Cyprus in the Eastern Mediterranean (inset) and of the sampling sites investigated in this study.

Cantonati et al. (2020a), which are relative to 2005, 2006, 2010, 2011, and 2012. We considered only the 2020, 2021, and 2022 samples included also in Cantonati et al. (2020a). We discarded all samples related to 2005, 2006, and 2012 (a few samples).

Thirty-seven sites on 26 rivers were sampled on at least one occasion in two main periods: spring and summer, during 2010–2011 and 2020–2022. Some sites were sampled several times (up to 11), but the maximum number of samples collected per site, each year was two (spring and summer). All rivers belonged to one of two main types, as defined by the European Commission's intercalibration exercise (Birk et al., 2013):

- a) perennial; comparable in terms of flow regime and overall environmental features to intercalibration type R-M4 (Erba et al., 2009; EC, 2018); or,
- b) intermittent, belonging to intercalibration type R-M5 (EC, 2018).

The investigated river sites' mean catchment area and altitude were 60 km² and 405 m a.s.l., respectively. The sites' elevation ranged between 83 and 1030 m a.s.l. The predominant catchment geology was ophiolitic formations; some sites were located on carbonate rocks of the *Circum Troodos* sedimentary succession, although the headwaters of all catchments were within the ophiolitic Troodos rocks. Very few catchments were located entirely on rocks conferring high bicarbonate/carbonate content to the waters.

Streams were selected to cover the entire quality range in the region, from undisturbed and nearly natural sites (reference sites) to human-impacted sites. The reference sites were described based on land use, physical and chemical parameters, and hydromorphological alteration criteria specified in Feio et al. (2014). Of 37 sampled sites, 9 (= 58 samples) were designated as "reference sites" based on these criteria.

2.2. Diatom analysis

2.2.1. Diatom sampling and preparation of permanent slides

A total of 227 (108 in 2010–11 and 119 in 2020–21–22) diatom samples were collected and treated following the European standard CEN 13946 2003 and CEN 14407 2004 (European Committee for Standardization, 2003, 2004). At least five cobbles were sampled from the river's main flow, and an area of approximately 10 cm² was scraped from each.

After collection, all samples were kept in a cool, dry place, preserved with formaldehyde (final concentration ca. 3 %), and delivered to the MUSE - Museo delle Scienze laboratory (Trento, Italy) for analysis. Samples were digested using 30 % hydrogen peroxide, and the cleaned material was mounted in Naphrax (refractive index of 1.74) according to European Standard EN 13946: 2003 (CEN, 2003) and labeled accordingly. Each slide was labeled with the station name, station code, date of sampling and date of mounting.

2.2.2. Identification of taxa

Identification and enumeration of diatoms followed European Standard EN 14407 (CEN, 2004). All samples were identified to the species or lower taxonomic level (i.e., variety) as required for indices' calculation in the OMNIDIA software version 6.0.8 (Lecoinge et al., 1993, 1999), with a minimum of 400 valves identified and counted per slide. As required by the international tenders for which the materials included in the present contribution were initially analyzed, at least one digital micrograph of every species identified in each count was taken to document the work done. Broken valves were included in the analysis if at least three-quarters of the valve was present. Girdle views were included if several valve characteristics (e.g., length, shape, types of striae, number of striae) could be unambiguously matched to valve views of the same species. Identification literature was reported in detail by Cantonati et al. (2020a). Nomenclature and some taxonomic concepts were updated using Cantonati et al. (2017), AlgaeBase (Guiry and

Guiry, 2023), Diatoms of North America (Spaulding et al., 2021), the Freshwater Diatom Flora of Britain and Ireland (Jüttner et al., 2023). Moreover, several new species were identified (e.g., Cantonati et al., 2016, 2018, 2024).

To harmonize the identifications performed on the materials 2010–11 and 2020–22, a workshop involving three authors of the present paper (MC, RS, KM) was organized at the University of Bologna – BiGeA Department (May 22nd–June 1st, 2023). All species listed in Supplementary material Table 2 were discussed to ensure that the taxonomic concepts used for the recent material could be applied to the historical one, primarily using the digital images mentioned above, databases, and taxonomy reports of the individual project years. For special needs, slides borrowed from the MUSE collections were also available and reviewed.

2.3. Environmental analysis

In order to characterise the sites and their biological communities, information about different environmental variables were provided for each river site.

As typological descriptors, river-type (i.e., RM4 perennial or RM5 intermittent), drainage area (km²) and elevation were provided for each sampling site.

As hydrological variables, sampling season and instant discharge values (m³/s) were available for all the sampling sites and both sampling periods (2010–11 and 2020–22).

Physical and chemical parameters were also available for all the sampling sites and both sampling periods. In Supplementary material Table 1 are listed all the parameters with a consistent set of values in both the sampling periods: pH, conductivity (µS/cm), oxygen saturation deficit (%), water temperature (°C), turbidity (NTU), sulphate (mg/L), chloride (mg/L), sodium (mg/L), biological oxygen demand (BOD₅ O₂) (mg/L), total nitrogen (mg/L), nitrate-N (mg/L), chemical oxygen demand (COD) (mg/L), and total phosphorus (mg/L). The Water Development Department collected the water quality data as part of the Department's routine monitoring.

2.4. Data processing and statistical analyses

For all diatom species collected in this study, a threat status (a measure of rarity) was assigned, according to current (Hofmann et al., 2018) and previous (Lange-Bertalot, 1996) Red List data for Central Europe (the only currently available diatom Red Lists). A check was made for the species present in both lists to confirm whether conservation status was improving or declining. Hofmann et al. (2018) provide further ecological attributes (trophic and mineralization preferences, aerial species) used in this study (Supplementary material Table 2), along with life-form/growth-form, guild, and size indications as provided by Rimet and Bouchez (2012). Also, the ecological characteristics (aerophyte, halophile, etc.) of the species as available in Levkov (in prep., *Diatom Atlas of Macedonia*). This book is still in the manuscript stage, and data were kindly made available by Prof. Zlatko Levkov. The designation of diatom species as "aerial" greatly benefited from consultation of the list of terrestrial diatoms published by Foets et al. (2021), who also provide volumetric soil moisture content (VWC) optima for many of the terrestrial diatoms of their list (Supplementary material Table 2).

An essential point for the present paper was the designation of "trivial" species. These were defined as "common, widespread, often eutrathentic and abundant species which often replace characteristic and specialized species during biotic homogenization". They were designated in Supplementary material Table 2 by MC based on experience and the literature and then carefully validated and integrated by KM and RS. MC was the lead Editor of the *Freshwater Benthic Diatoms of Central Europe: Over 800 Common Species Used in Ecological Assessment*, an identification text that includes ecological preferences based on a

dataset resulting from analyses carried out on samples from the ca. 11.000 stations of the monitoring network of the German Environmental Agencies. Our approach to the designation of “trivial” species is therefore similar to what is commonly done in the USA for the development and calibration of a Biological Condition Gradient (BCG) models for macroinvertebrates, fishes or algae (Charles et al., 2021), which is a collective exercise among biologists to assign sites to BCG levels, and then to develop rules to make assignments of new sites (Hausmann et al., 2016; Paul et al., 2020).

Multiple statistical comparisons were performed to determine if the diatom community changed from 2010 to 11 to 2020–22 using Mann-Whitney *U* Tests with Statistica 7.0 (StatSoft, Inc., Tulsa, OK USA). To test these changes in diatoms communities, some species have been considered (e.g., “trivial”) as well as some biological metrics (i.e., species richness and community diversity calculated using OMNIDIA software version 6.0.8, Lecoigne et al., 1993, 1999).

Agglomerative hierarchical cluster analysis (Kaufman and Rousseeuw, 1990) was applied using the *Agnes* function in the R package *Cluster* (Maechler et al., 2005) using an unweighted pair group method with arithmetic averages (UPGMA). The agglomeration coefficient was computed as it provides a measure of the average height of the mergers in a dendrogram. An internal validation approach was used to select the number of clusters to be retained (Handl et al., 2005). Further validation was provided by the metaMDS R function of the *vegan* package (Oksanen et al., 2019), which uses multiple analyses to assess the stress value associated with the number of groups selected.

Potential indicator taxa of the different clusters were identified using the Indicator Value (*IndVal*) (Dufrene and Legendre, 1997) method, using the *duleg* function in the *labdsv* package in R (Roberts, 2016). This analysis provides a qualitative insight into the composition of the different clusters; consideration of indicator value significance would be inappropriate due to circularity (i.e., the clusters were observed within the same set of biological observations).

Stepwise ordinations were conducted to identify the environmental variables responsible for the patterns in the biological data using the *vegan* package in R version 3.1.0 (Oksanen et al., 2019; R Core Team, 2019). The forward stepwise ordination regression ran through permutations. Only significant environmental variables were used for the subsequent variance partitioning analysis. Before variance partitioning, all variables were assessed for collinearity to ensure that the statistical outputs were accurate and stable. A variance inflation factor (VIF) >5 was used to determine if the variables were collinear ($VIF_x = 1/1-R_x^2$). The procedure was performed in R using the *vif.cca* function (R Core Team, 2019) for each group of environmental variables. The variance partitioning was then conducted separately for three groups of environmental variables: river type, hydrology, and season. Variance partitioning was used to determine the relative amount of variance in the diatom assemblage that each group of variables explained. The analysis

was conducted using redundancy analysis (RDA: Boccard et al., 2011) in R, using the *vegan* package (Oksanen et al., 2019), to quantify the individual contribution that each variable group had in shaping the diatom assemblage, along with the contributions from interactions among the environmental variables.

Based on the output of the variance partitioning, the environmental variables selected were used to build a multiple discriminant function (DF) modelling procedure using the *Mass* package in R version 3.1.0 (R Core Team, 2019; Venables and Ripley, 2002). Group size was a prior probability in predicting group membership probabilities from the DF model (Clarke et al., 2003).

3. Results

3.1. Morphological, physical, and chemical characteristics of the Cypriot streams in 2010–11 and 2020–22

Supplementary material Table 1 provides a list of the sampling sites along with their main characteristics: typological attribution, whether a reference site or not; drainage area and elevation; physical and chemical characteristics for 2010–11 and 2020–22. Table 1 summarizes all sites' main physical and chemical characteristics, focussing on the determinants most relevant to diatoms. Instant discharge values are relatively low, ranging from 0 to 3.8 m³/s in 2010–11 and to 4.25 m³/s in 2020–22, with an average of 0.16 m³/s in 2010–11 and 0.21 m³/s in 2020–22. Water temperature and conductivity increased in average and max values from 2010–11 to 2020–22, while the primary algal nutrients (N and P) concentrations decreased.

3.2. Diatom assemblages of Cypriot streams in 2010–11 and 2020–22

Table 2 lists the 50 species with the highest maximum relative abundances, ranked in decreasing order, in 2010–11 and 2020–22, respectively. Also, the number of occurrences (frequency) in the samples taken in the two periods is provided.

In the upper positions, there are classical organic pollution/eutrophication indicators (e.g., *Nitzschia inconspicua*, *Amphora pediculus*), which occupy lower positions (= lower maximum relative abundance) in 2010–11. Some species are characteristic of the diatom microflora of the Mediterranean streams in Cyprus (e.g., *Ulnaria monodii*, *Gomphonema pumilum* var. *rigidum*, *Gomphonema rosenstockianum*).

Some qualitative observations are worth reporting. Reference (least-impacted) sites in 2010–11 hosted the following sensitive species, missing in 2020–22: - some *Delicatophycus* species (including comparatively large-celled species); - several species of *Epithemia* (capable of N₂-fixation via cyanobacterial endosymbionts); - *Frustulia spicula* subsp. *judaica*; - occasional cells of large Alpine species (*Cymbella helvetica*, *Surirella helvetica*). *Crenotia rumrhorum* was relatively frequent in

Table 1
Main physical and chemical characteristics of all sampling sites in 2010–11 and 2020–22.

	2010–11				2020–22			
	Average	Min	Max	Median	Average	Min	Max	Median
Instant discharge (m ³ /s)	0.16	0.00	3.80	0.04	0.21	0.00	4.25	0.05
pH	8.30	6.05	9.75	8.33	8.56	3.65	10.95	8.61
EC field_Us (μS/cm)	853	103	6030	680	1090	114	9634	748
DO% field (%)	93.42	14.00	153.00	96.70	94.43	6.54	167.50	95.40
Temp_water (°C)	14.62	6.30	28.10	13.70	15.41	4.20	38.50	14.60
Turb_field (NTU)	6.53	0.01	571.40	1.91	5.11	0.05	84.97	3.99
SO ₄ ²⁻ (mg/L)	78.76	2.27	430.17	53.60	136.85	2.50	1019.00	64.00
Cl ⁻ (mg/L)	95.12	11.35	1390.00	44.09	61.78	16.00	338.00	41.00
Na ⁺ (mg/L)	68.63	6.66	857.00	38.90	47.64	11.00	170.00	35.00
BOD ₅ (mg/L O ₂)	2.00	0.50	71.00	0.50	0.78	0.00	6.00	0.50
COD (mg/L O ₂)	7.78	0.00	187.00	3.00	6.38	0.00	28.00	5.00
N_total (mg/L N)	2.94	0.01	124.00	1.00	1.43	0.25	13.40	0.25
NO ₃ -N (mg/L N)	1.74	0.00	60.77	0.56	1.08	0.02	13.07	0.23
P_total (mg/L P)	0.06	0.00	2.63	0.00	0.02	0.00	1.00	0.00

Table 2

Composition (50 species with highest MRA in decreasing order) of the diatom assemblages in Cypriot streams in 2010–11 and 2020–22. NO = number of occurrences, MRA = maximum relative abundance.

2010–11			2020–22		
Species names	NO	MRA	Species names	NO	MRA
<i>Cocconeis euglypta</i> + <i>C. placentula</i> var. <i>placentula</i>	79	73.1	<i>Cocconeis euglypta</i> + <i>C. placentula</i> var. <i>placentula</i>	104	87.4
<i>Achnanthyidium minutissimum</i>	76	70.4	<i>Achnanthyidium minutissimum</i>	103	86.6
<i>Planothidium victorii</i>	74	68.5	<i>Nitzschia inconspicua</i>	84	70.6
<i>Ulnaria monodii</i>	74	68.5	<i>Amphora pediculus</i>	83	69.7
<i>Nitzschia inconspicua</i>	61	56.5	<i>Ulnaria monodii</i>	77	64.7
<i>Navicula veneta</i>	60	55.6	<i>Achnanthyidium lineare</i>	75	63.0
<i>Amphora pediculus</i>	59	54.6	<i>Gomphonema pumilum</i> var. <i>rigidum</i>	75	63.0
<i>Nitzschia linearis</i>	58	53.7	<i>Planothidium victorii</i>	68	57.1
<i>Achnanthyidium jackii</i>	54	50.0	<i>Encyonopsis minuta</i>	67	56.3
<i>Gomphonema pumilum</i> var. <i>rigidum</i>	52	48.1	<i>Gomphonema rosenstockianum</i>	62	52.1
<i>Gomphonema rosenstockianum</i>	52	48.1	<i>Diatoma moniliformis</i>	57	47.9
<i>Navicula cryptotenella</i>	51	47.2	<i>Amphora micra</i>	51	42.9
<i>Nitzschia dissipata</i>	49	45.4	<i>Navicula cryptotenella</i>	51	42.9
<i>Navicula caterva</i>	45	41.7	<i>Reimeria uniseriata</i>	51	42.9
<i>Reimeria uniseriata</i>	43	39.8	<i>Cocconeis lineata</i>	50	42.0
<i>Amphora micra</i>	41	38.0	<i>Cocconeis pediculus</i>	50	42.0
<i>Diatoma moniliformis</i>	41	38.0	<i>Navicula tripunctata</i>	49	41.2
<i>Nitzschia liebetruithii</i> + <i>N. pseudalpina</i>	40	37.0	<i>Nitzschia palea</i>	45	37.8
<i>Encyonopsis minuta</i>	38	35.2	<i>Cymbella affinis</i>	43	36.1
<i>Gomphonema tergestinum</i>	38	35.2	<i>Navicula cryptotenelloides</i>	43	36.1
<i>Navicula tripunctata</i>	38	35.2	<i>Halumphora veneta</i>	42	35.3
<i>Halumphora veneta</i>	37	34.3	<i>Navicula veneta</i>	41	34.5
<i>Fragilaria recapitellata</i> + <i>F. deformis</i>	36	33.3	<i>Cymbella kolbei</i>	40	33.6
<i>Gomphonemaparvulum</i>	36	33.3	<i>Nitzschia fonticola</i>	40	33.6
<i>Navicula cryptotenelloides</i>	32	29.6	<i>Achnanthyidium jackii</i>	39	32.8
<i>Planothidium lanceolatum</i>	32	29.6	<i>Nitzschia linearis</i>	39	32.8
<i>Achnanthyidium minutissimum</i> sensu lato	31	28.7	<i>Gomphonema tergestinum</i>	37	31.1
<i>Nitzschia soratensis</i>	31	28.7	<i>Cymbella vulgata</i>	35	29.4
<i>Cymbella kolbei</i>	30	27.8	<i>Encyonopsis subminuta</i>	35	29.4
<i>Cymbella vulgata</i>	30	27.8	<i>Nitzschia dissipata</i>	35	29.4
<i>Gomphonema micropus</i>	29	26.9	<i>Gomphonemaparvulum</i>	33	27.7
<i>Navicula radiosa</i>	29	26.9	<i>Navicula reichardtiana</i>	33	27.7
<i>Nitzschia communis</i>	29	26.9	<i>Nitzschia communis</i>	32	26.9
<i>Achnanthyidium ertzii</i>	27	25.0	<i>Nitzschia amphibia</i>	31	26.1
<i>Adlafia minuscula</i> var. <i>muralis</i>	27	25.0	<i>Planothidium frequentissimum</i>	30	25.2
<i>Navicula moskali</i>	27	25.0	<i>Nitzschia liebetruithii</i> + <i>N. pseudalpina</i>	29	24.4
<i>Nitzschia palea</i>	27	25.0	<i>Planothidium lanceolatum</i>	29	24.4
<i>Tryblionella apiculata</i>	27	25.0	<i>Rhoicosphenia abbreviata</i>	29	24.4
<i>Nitzschia fonticola</i>	26	24.1	<i>Encyonema ventricosum</i>	28	23.5
<i>Cocconeis pediculus</i>	25	23.1	<i>Nitzschia soratensis</i>	28	23.5
<i>Fragilaria vaucheriae</i>	24	22.2	<i>Fragilaria recapitellata</i> + <i>F. deformis</i>	27	22.7
<i>Ulnaria acus</i> sensu lato (sp. pl.)	24	22.2	<i>Nitzschia frustulum</i>	27	22.7
<i>Rhoicosphenia abbreviata</i>	23	21.3	<i>Diploneis separanda</i>	25	21.0
<i>Meridion circulare</i>	22	20.4	<i>Encyonopsis microcephala</i>	23	19.3
<i>Cymbella affinis</i>	21	19.4	<i>Navicula radiosa</i>	23	19.3
<i>Cymbella tumidula</i>	20	18.5	<i>Ulnaria ulna</i>	23	19.3
<i>Diploneis separanda</i>	20	18.5	<i>Achnanthyidium straubianum</i>	22	18.5
<i>Navicula antonii</i>	20	18.5	<i>Nitzschia archibaldii</i>	21	17.6
<i>Nitzschia adamata</i>	19	17.6	<i>Achnanthyidium minutissimum</i> sensu lato	19	16.0
<i>Nitzschia amphibia</i>	19	17.6	<i>Adlafia minuscula</i> var. <i>minuscula</i>	19	16.0

2010–11 and absent in 2020–22. *Gogorevia exilis* appeared in 2020–22 but was absent in 2010–11.

The species found also included some new-to-science species. Besides those mentioned in Cantonati et al., 2020a, two new (*Mastogloia cyprica*, *Navicula loumatensis*) and one epitypified (*Craticula simplex*) species were recently published (Cantonati et al., 2024).

Concerning diatom life forms, the total number of high-profile ($U = 2380$, $Z = -8.189$, $p = 0.0000$), motile ($U = 3773$, $Z = -5.369$, $p = 0.0000$), and planktonic ($U = 4372$, $Z = -4.158$, $p = 0.0000$) species increased from 2010–11 to 2020–22 (Fig. 2).

3.3. Changes over time of “trivial” diatom species

We found statistically significant increases (from 2010–11 to 2020–22) in the total number of diatom species designed as “trivial”, the total number of trivial diatom species’ valves, and 38 individual trivial diatom species (Table 3, Fig. 3).

3.4. Changes over time of eutraphentic, aerial/terrestrial, warm-water diatom species

Sixteen species having “eutraphentic” (eu) as their “ecology” in the diatom Red List for Central Europe (Hofmann et al., 2018) turned out to show statistically significant increases from 2010–11 to 2020–22 (Table 4). Moreover, the total number of eutraphentic species also showed a statistically significant increase.

The combined application of Hofmann et al. (2018)/Levkov (in prep.)/Foets et al. (2021) allowed to designate many of the species we found as “aerial” (complete list in Supplementary material Table 2). Twenty-two of these showed statistically significant increases from 2010–11 to 2020–22 (Table 5). Moreover, the total number of “aerial” species also showed a statistically significant increase ($U = 2806$, $Z = -7.327$, $p = 0.0000$). Besides well-known aerophytes, these 22 species include, for instance, *Caloneis lancettula*, *Cocconeis pediculus*, *Fragilaria gracilis*, *Navicula cryptotenella*, and the halophile (Levkov in prep.)

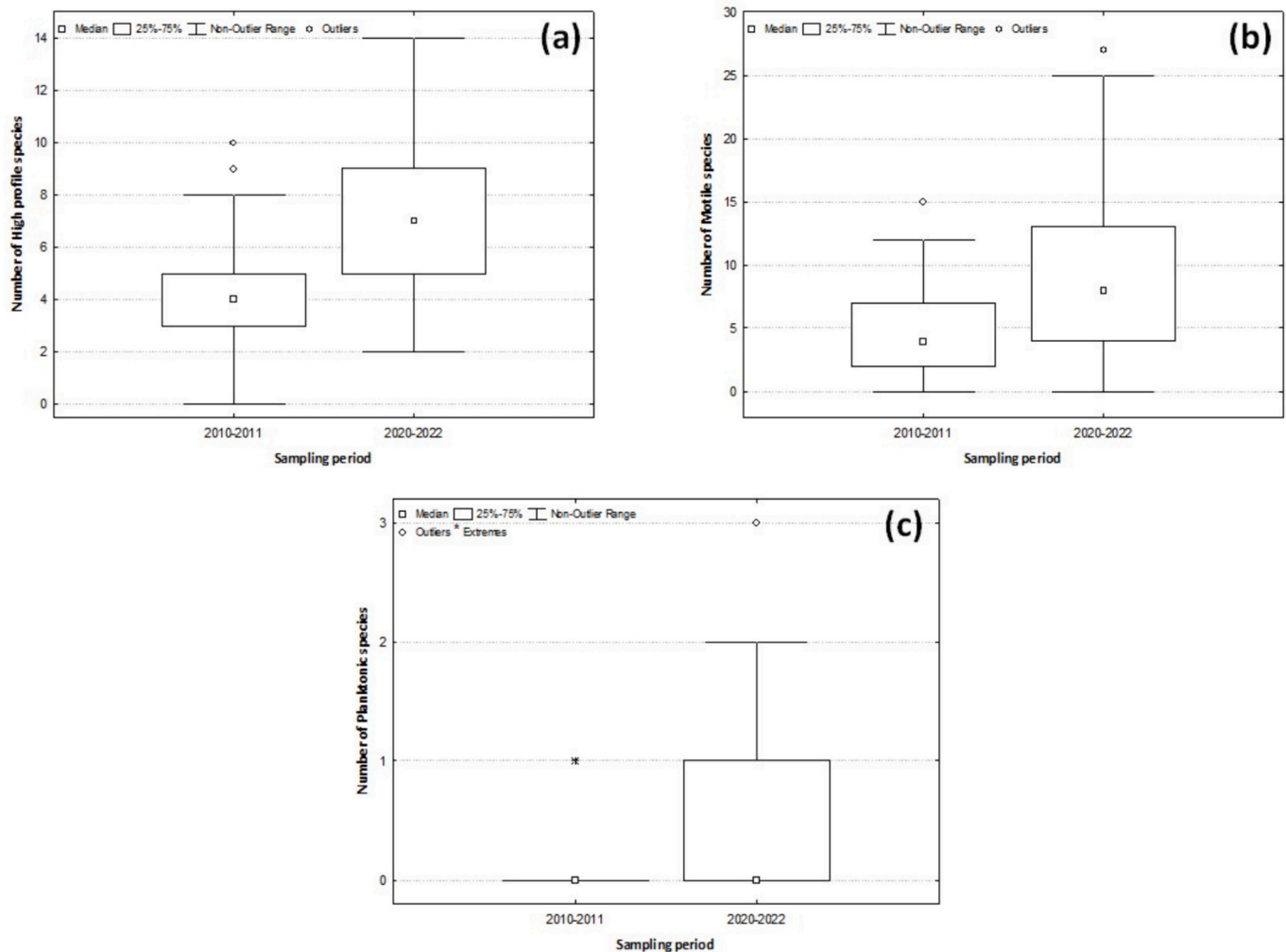


Fig. 2. Boxplots of a total number of high-profile (a), motile (b) and planktonic (c) species in 2010–11 and 2020–22.

aerophyte (Hofmann et al., 2018) *Pinnularia kneuckeri* ($U = 5886$, $Z_{adjust.} = -3.074$, $p = 0.0021$).

The compelling first colonizer, *Achnanthyidium tepidaricola* ($U = 5847$, $Z_{adjust.} = -2.721$, $p = 0.0065$), and the osmotic stress resistant (desiccation, salinity) *Craticula simplex* ($U = 5724$, $Z_{adjust.} = -3.529$, $p = 0.0004$) increased significantly their relative abundances.

Two species known to be distributed particularly in warm waters increased significantly also from 2010-11 to 2020–22: *Cymbella kappii* ($U = 5670$, $Z_{adjust.} = -3.670$, $p = 0.0002$) and *Ulnaria monodii* (presence/absence based, $U = 5183$, $Z = -2.514$, $p = 0.0120$).

3.5. Changes over time in diversity

We could show a statistically significant decrease in β -diversity and an increase in nestedness from 2010-11 to 2020–22 (Table 6, Fig. 4).

On the contrary, species richness (S) and the Shannon-Wiener Index (α -diversity, H) increased (Table 7, Fig. 5).

3.6. Relationships with environmental variables

A Redundancy Analysis (RDA) carried out to explore the influence of different environmental factors on diatom communities allowed us to identify the following drivers as significant: year, river type (largely hydrology-based), conductivity (these three significant with the usual threshold $p = 0.05$), water temperature, and discharge (significant adopting a p threshold of 0.09) (Table 8).

3.7. IndVal indicators 2010–11 and 2020–22

The agglomerative cluster analysis of all the diatom samples allowed to identify three groups: Group 1 and Group 2 with median in 2011, and Group 3 with median in 2020 (Fig. 6).

The IndVal analysis confirmed the presence of significant indicators for these groups, and those exclusive of each group are listed in Table 9.

4. Discussion

In particular in the face of climate change, biotic homogenization has become a phenomenon of ever increasing importance worldwide (Baiser et al., 2012). In a previous paper (Cantonati et al., 2020a), we described the diatom communities of Cypriot streams, providing a robust ecological, as well as taxonomic, characterization of the assemblages, and highlighted the overwhelming importance of hydro(geo)logy in shaping the diatom assemblages of stream sites on the Island of Cyprus, particularly the least-impacted ones. Here, we show that, over the last ten years, in response to climate-change effects (seen mainly in increased water temperature, conductivity, and discharge variability), Cypriot stream diatom communities include a higher number of trivial (= common, widespread, often eutraphentic and abundant species which often replace characteristic and specialized species during biotic homogenization), aerial, terrestrial, planktonic, motile, and thermophilic species, have reduced β -diversity, and increased nestedness. Tornés et al. (2022) considered climate change impacts on stream benthic diatoms in

Table 3

Results of the statistical comparisons (Mann-Whitney U Tests) performed to detail the occurrence and abundance of species designed as “trivial” in 2010–11 and 2020–22. Only statistically significant ($p < 0.05$) or close-to-significant changes in individual species and groups are listed. Significant probabilities are in bold, and close-to-significant probabilities are in italics. The complete list of trivial species is available in the Supplementary material Table 2. Comparisons were made using the relative abundances except for rows highlighted in light grey, where values are based on presence/absence.

Comparison 2010-11 and 2020-22:	U	Z	p	Z _{adjust.}	p
- Individual trivial species					
<i>Achnanthydium lineare</i>	2647	-7.647	0.0000	-8.927	0.0000
<i>Achnanthydium minutissimum</i>	5148	-2.586	0.0100	-3.5531	0.0003
<i>Adlafia minuscula</i> var. <i>muralis</i>	5773	1.322	0.1860	2.157	0.0310
<i>Amphora indistincta</i>	5886	-1.093	0.2745	-3.073	0.0021
<i>Amphora pediculus</i>	5038	-2.809	0.0050	-2.911	0.0036
<i>Caloneis lancetula</i>	5688	-1.494	0.1351	-2.913	0.0036
<i>Cocconeis euglypta</i> + <i>C. placentula</i> var. <i>placentula</i>	5073	-2.739	0.0062	-2.758	0.0058
<i>Cocconeis lineata</i>	3954	-5.002	0.0000	-6.749	0.0000
<i>Cocconeis pediculus</i>	4904	-3.081	0.0021	-3.823	0.0001
<i>Craticula buderi</i>	6002	-0.858	0.3909	-2.413	0.0158
<i>Cymbella affinis</i>	4714	-3.465	0.0005	-4.708	0.0000
<i>Diatoma moniliformis</i>	4992	-2.903	0.0037	-3.394	0.0007
<i>Encyonema ventricosum</i>	5048	-2.790	0.0053	-4.742	0.0000
<i>Fistulifera saphophila</i>	6102	-0.656	0.5120	-2.360	0.0183
<i>Fragilaria gracilis</i>	5616	-1.639	0.1012	-3.592	0.0003
<i>Gomphonema parvulum</i>	5656	-1.559	0.1189	-2.172	0.0298
<i>Halamphora veneta</i>	5436	-2.004	0.045	-2.557	0.0106
<i>Mayamaea permitis</i>	6021	-0.820	0.4125	-1.749	<i>0.0802</i>
<i>Melosira varians</i>	6048	-0.765	0.4443	-2.554	0.0106
<i>Navicula cryptotenella</i>	4931	-3.026	0.0025	-3.639	0.0003
<i>Navicula cryptotenelloides</i>	5347	-2.185	0.0289	-2.753	0.0058
<i>Navicula radiosa</i>	5472	-1.931	0.0535	-3.381	0.0007
<i>Navicula reichardtiana</i>	4927	-3.034	0.0024	-4.720	0.0000
<i>Navicula tripunctata</i>	5084	-2.716	0.0066	-3.308	0.0009
<i>Nitzschia amphibia</i>	5071	-2.743	0.0061	-4.316	0.0000
<i>Nitzschia archibaldii</i>	5354	-2.170	0.0300	-4.228	0.0000
<i>Nitzschia communis</i>	5528	-1.817	<i>0.0692</i>	-2.614	0.0089
<i>Nitzschia dissipata</i> var. <i>media</i>	5828	-1.210	0.2262	-2.268	0.0233
<i>Nitzschia fonticola</i>	5365	-2.148	0.0317	-2.822	0.0048
<i>Nitzschia frustulum</i>	5464	-1.947	<i>0.0516</i>	-3.098	0.0019
<i>Nitzschia incospicua</i>	5156	-2.569	0.0102	-2.664	0.0077
<i>Nitzschia palea</i>	4843	-3.204	0.0014	-4.184	0.0000
<i>Nitzschia palea</i> var. <i>tenuirostris</i>	6210	-0.437	0.6620	-1.918	<i>0.0551</i>
<i>Nitzschia supralitorea</i>	5886	-1.093	0.2745	-3.074	0.0021
<i>Planothidium frequentissimum</i>	4806	-3.278	0.0010	-5.571	0.0000
<i>Rhoicosphenia abbreviata</i>	5506	-1.863	0.0625	-2.809	0.0050
<i>Tryblionella apiculata</i>	5965	-0.934	0.3503	-1.751	<i>0.0799</i>
<i>Ulnaria ulna</i>	5437	-2.001	0.0454	-3.560	0.0004
- Total number of trivial diatom species	2644	-7.655	0.0000	-7.664	0.0000

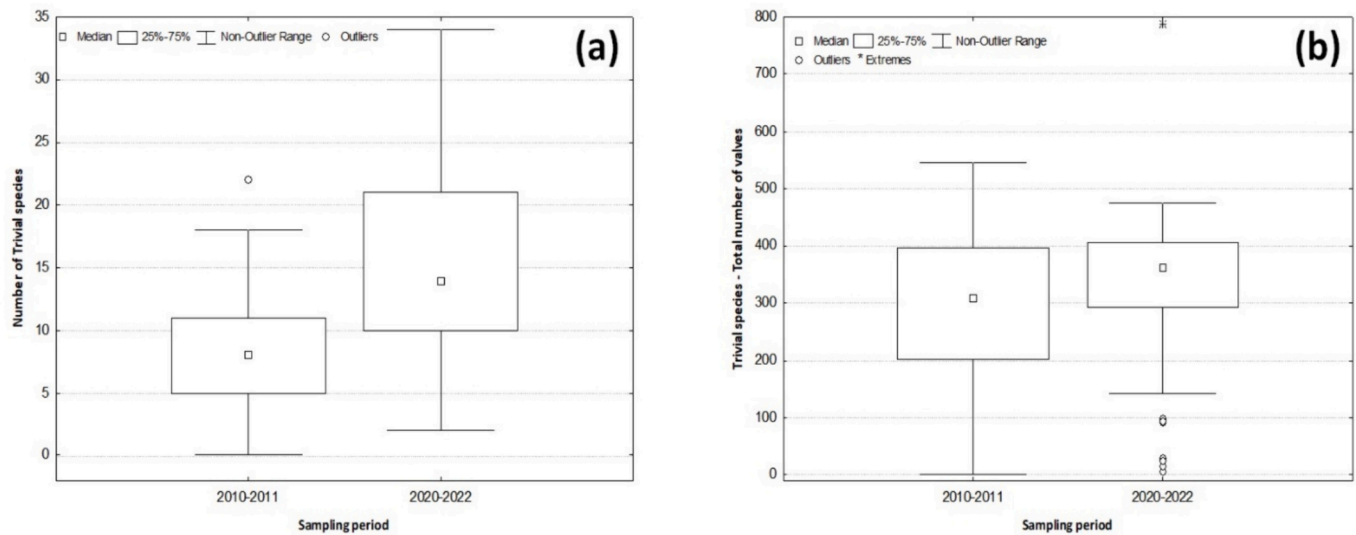


Fig. 3. Boxplots of the total number of trivial species (a) and the total number of trivial diatom species valves (b) in 2010–11 and 2020–22.

Table 4

Results of the statistical comparisons (Mann-Whitney U Tests) performed to detail the occurrence and abundance of species having “eutraphentic” (eu) as their “ecology” in the diatom Red List for Central Europe (Hofmann et al., 2018) in 2010–11 and 2020–22. Only statistically significant ($p < 0.05$) or close-to-significant changes in individual species and groups are listed. Significant probabilities are in bold, and close-to-significant probabilities are in italics. The complete list of “eutraphentic” species, according to Hofmann et al. (2018), is available in the Supplementary material Table 2. Comparisons were made using the relative abundances except for rows highlighted in light grey where values are based on presence/absence.

Comparison 2010-11 and 2020-22:	U	Z	p	Z _{adjust.}	p
- Individual eutraphentic, pollution indicator species					
<i>Amphora pediculus</i>	5038	-2.809	0.0050	-2.911	0.0036
<i>Caloneis lancettula</i>	5688	-1.494	0.1351	-2.913	0.0036
<i>Cocconeis pediculus</i>	4904	-3.081	0.0021	-3.823	0.0001
<i>Craticula buderi</i>	6002	-0.858	0.3909	-2.413	0.0158
<i>Encyonema ventricosum</i>	5048	-2.790	0.0053	-4.742	0.0000
<i>Fistulifera saprophila</i>	6102	-0.656	0.5120	-2.360	0.0183
<i>Gomphonema parvulum</i>	5655	-1.559	0.1189	-2.172	0.0298
<i>Halamphora veneta</i>	5436	-2.004	0.0450	-2.557	0.0106
<i>Kolbesia ploenensis</i>	5994	-0.874	0.3820	-2.737	0.0062
<i>Mayamaea permitis</i>	6021	-0.819	0.4130	-1.749	<i>0.0803</i>
<i>Navicula cryptotenelloides</i>	5347	-2.184	0.0290	-2.753	0.0059
<i>Navicula tripunctata</i>	5084	-2.716	0.0066	-3.308	0.0009
<i>Nitzschia amphibia</i>	5071	-2.743	0.0061	-4.316	0.0000
<i>Nitzschia dissipata</i> var. <i>media</i>	5828	-1.210	0.2262	-2.268	0.0233
<i>Nitzschia inconspicua</i>	5157	-2.569	0.0102	-2.664	0.0077
<i>Nitzschia palea</i>	4843	-3.204	0.0014	-4.184	0.0000
- Total number of eutraphentic species	5437	-2.002	0.04524	-2.004	0.0451

Table 5

Results of the statistical comparisons (Mann-Whitney *U* Tests) performed to detail the occurrence and abundance of species having “aerial”/“terrestrial” distribution in 2010–11 and 2020–22. Only statistically significant ($p < 0.05$) or close-to-significant changes in individual species and groups are listed. Significant probabilities are in bold, and close-to-significant probabilities are in italics. The complete list of “aerial”/“aerophytes”/“terrestrial” species, according to Hofmann et al. (2018)/Levkov (in prep.)/Foets et al. (2021), is available in the Supplementary material Table 2. Comparisons were made using the relative abundances except for rows highlighted in light grey where values are based on presence/absence.

Comparison 2010-11 and 2020-22:	<i>U</i>	<i>Z</i>	<i>p</i>	<i>Z</i> _{adjust.}	<i>p</i>
- Aerial/terrestrial indicator species					
<i>Achnanthydium minutissimum</i>	5148	-2.586	0.0097	-3.553	0.0004
<i>Adlafia minuscula</i> var. <i>minuscula</i>	5400	-2.076	0.0379	-4.323	0.0000
<i>Caloneis lancettula</i>	5692	-1.485	0.1374	-2.899	0.0037
<i>Cavinula cocconeiformis</i>	6069	0.723	0.4700	2.599	0.0093
<i>Cocconeis lineata</i>	3954	-5.002	0.0000	-6.749	0.0000
<i>Cocconeis pediculus</i>	4904	-3.081	0.0021	-3.823	0.0001
<i>Fragilaria gracilis</i>	5616	-1.639	0.1012	-3.592	0.0003
<i>Gomphonema parvulum</i>	5656	-1.559	0.1189	-2.172	0.0298
<i>Mayamaea permitis</i>	6021	-0.820	0.4125	-1.749	<i>0.0802</i>
<i>Navicula cryptotenella</i>	4931	-3.026	0.0025	-3.639	0.0003
<i>Nitzschia acidoclinata</i>	6048	-0.765	0.4443	-2.554	0.0106
<i>Nitzschia amphibia</i>	5071	-2.743	0.0061	-4.316	0.0000
<i>Nitzschia dissipata</i> var. <i>media</i>	5828	-1.210	0.2262	-2.268	0.0233
<i>Nitzschia frustulum</i>	5464	-1.947	0.0516	-3.098	0.0019
<i>Nitzschia palea</i>	4843	-3.204	0.0014	-4.184	0.0000
<i>Nitzschia palea</i> var. <i>tenuirostris</i>	6210	-0.437	0.6620	-1.918	<i>0.0551</i>
<i>Nitzschia solita</i>	6264	-0.328	0.7430	-1.657	<i>0.0974</i>
<i>Nitzschia supralitorea</i>	5886	-1.093	0.2745	-3.074	0.0021
<i>Pinnularia kneuckeri</i>	5886	-1.093	0.2745	-3.074	0.0021
<i>Planothidium frequentissimum</i>	4806	-3.278	0.0010	-5.571	0.0000
<i>Rhoicosphenia abbreviata</i>	5506	-1.863	0.0625	-2.809	0.0050
<i>Sellaphora stroemii</i>	6058	-0.746	0.4558	-2.206	0.0274
- Total number of aerial/terrestrial diatom species	2806	-7.327	0.0000	-7.372	0.0000

Spain. They concluded that the most sensitive stream type to the impacts of climate change would be mineralized rivers, and predicted an increase in diatom assemblage homogenization, and higher proportions of planktonic taxa, terrestrial, and aerophilic diatoms under the pressure of climate change, which is in perfect agreement with the results of our study.

Moreover, IndVal indicators of 2010–11 are characteristic, often relatively rare species (*Achnanthydium ertzii*, *A. tepidaricola*, *Cavinula cocconeiformis*, *Gomphonema pseudotenellum*, *Tryblionella hungarica*) while the indicators of 2020–22 are a group of distinct trivial, eutra-pentic, and thermophilic species (e.g., *Achnanthydium lineare*, *Cocconeis pediculus*, *Cymbella kappii*, *Navicula cryptotenelloides*, *N. tripunctata*, *Rhoicosphenia abbreviata*).

Cavinula cocconeiformis and *Gomphonema pseudotenellum* are category “G” (threat of unknown extent) of the Red List (Hofmann et al.,

2018). *Achnanthydium tepidaricola*, an effective pioneer species (first colonizer) and aerial taxon, originated from the eastern Mediterranean (Van de Vijver et al., 2011).

Cymbella kappii was described from South Africa and originally occurred in subtropical and tropical climates.

Though not captured by the selection of samples we could consider in this study, *Crenotia rumrichorum* was relatively frequent only in 2010–11 (absent in 2020–22), while *Gogorevia exilis*, often occurring in warm and polluted waters, appeared in 2020–22.

Concerning diatom life forms, the total number of high-profile, motile, and planktonic species increased. High-profile species are known to indicate higher nutrients (e.g., Passy, 2007; Cantonati et al., 2021), while motile and planktonic diatom species might be favoured during prolonged droughts (seeking refugia in the surface sediments, developing in the residual pools; e.g., Cantonati et al., 2020b). In

Table 6

The output of an ANOVA performed to test if the differences in Sørensen index, nestedness, and total β -diversity between 2010–11 and 2020–22 are significant. Significant (p) code: “***” 0.001.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
<i>Sørensen index</i>					
Groups	1	0.4719	0.4719	48.732	3.91e-11***
Residuals	207	2.0045	0.00968		
<i>Nestedness</i>					
Groups	1	0.08235	0.082345	23.07	2.994e-06***
Residuals	207	0.73886	0.003569		
<i>Total β-diversity</i>					
Groups	1	0.15515	0.155154	23.505	2.444e-06***
Residuals	207	1.3664	0.006601		

ephemeral habitats, the primary stress factors are desiccation and temperature fluctuations, and resting cells and spores of terrestrial and aquatic diatoms are essential for surviving desiccation (Evans, 1958, 1959). These resting spores are packed with oil droplets and have modified additional intracellular silicon walls. Resting spore formation in diatoms is an effective strategy to survive prolonged periods of stress, such as desiccation (McQuoid and Hobson, 1996; Souffreau et al., 2013). We recorded internal resting spores of *Eunotia soleirolii*, *Meridion circulare*, and *Hantzschia amphioxys* in the streams studied in Cyprus. Previously, the same species were recorded with resting spores in mountain peat bogs in Bulgaria subject to desiccation (Stancheva, 2006). These diatoms were also distributed with resting spores in non-perennial streams in the arid southern California. Due to their relatively large size and chain formation, they may be abundant in the environment but rare in the diatom samples dominated by smaller diatoms.

Our finding of statistically significant increases in salinity indicators (*Diatoma moniliformis*, *Fragilaria famelicata*) matches well the increased conductivity values that emerged as one of the relevant drivers also from the RDA.

The halophile, aerophyte *Pinnularia kneuckeri*, the osmotic stress-resistant (desiccation, salinity) *Craticula simplex*, and the thermophilic *Ulnaria monodii* are characteristic members of the diatom microflora and increased their relative abundance in a statistically significant way from 2010–11 to 2020–22. This is consistent with the increases in temperature, discharge fluctuations, and conductivity we found and discussed in this paper. This could reinforce the presence of some diatom species well-suited with adaptive traits to cope with the selective pressures in Mediterranean streams.

As it almost always happens, the diatom communities we studied are subjected to multiple stressors, often affecting them in opposite ways. Thus, we detected an increase in trivial species, a reduction in β -diversity, and an increase in nestedness, which we primarily relate to warming, solute concentration, and hydrologic variability due to climate change. However, diatom assemblages experienced a nutrient reduction in several sites at the same time, which could explain the increase in α -diversity. This is in good agreement with the findings of previous biotic homogenization studies. Jiang et al. (2023) analyzed phytoplankton, crustaceans, and rotifers in 28 Adirondack-Park lakes (USA) during 1994–2012, examining the spatiotemporal trends in their α - and β -diversity during recovery from acidification. The spatial mean Bray-Curtis dissimilarities across all lakes decreased over time, increasing spatial homogenization, which, however, co-occurred with overall increasing diversity in this region, which contrasts with the classic view that homogenization is mainly driven by species loss. Lepori and Tolotti (2023) studied the effects of nitrogen on benthic diatom assemblages in high-mountain lakes of the Alps. They could show once more the importance of nitrogen as a driver for diatom-community composition. They could even identify “N-responsive diatoms”, i.e., diatom taxa with nonspurious associations with N. Zorzal-Almeida et al. (2021) studied diatom assemblages in phytoplankton and surface sediment from 12 tropical reservoirs with different trophic levels. They found an increase in nestedness, a decrease in α -diversity, and the development of tolerant species, suggesting that biotic homogenization is leading to a simplification, making assemblages from eutrophic and hypereutrophic reservoirs a subset of assemblages from oligotrophic and mesotrophic ones.

While analysing the samples, we noted several times that slides particularly rich in characteristic and sensitive taxa that were more common in 2010–11 came from sites close to high-ecological-integrity ecosystems such as springs, waterfalls, and dripping rock walls. These freshwater ecosystems, in particular springs that were shown to be excellent hydrologic refugia in climates heavily affected by climate

Table 7

Results of the statistical comparisons (Mann-Whitney U Tests) performed to test if there are significant differences in species richness and Shannon-Wiener diversity in 2010–11 and 2020–22. Statistically significant probabilities ($p < 0.05$) are in bold.

Comparison 2010–11 and 2020–22	U	Z	p	$Z_{adjust.}$	p
Species richness (S)	2668	−7.535	0.000000	−7.541	0.0000
Shannon-Wiener diversity (H)	4258	−4.295	0.000017	−4.295	0.0000

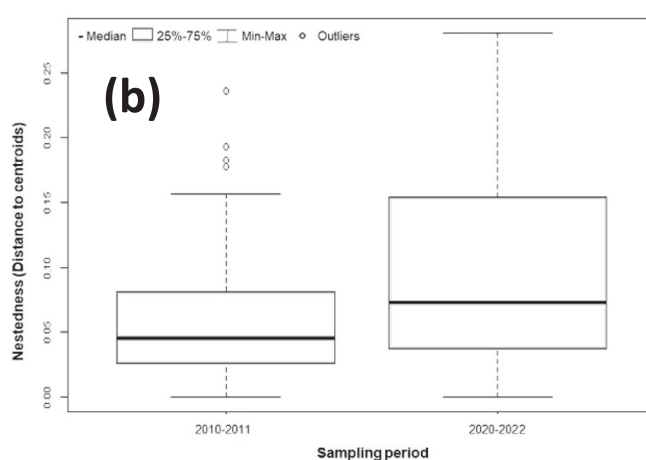
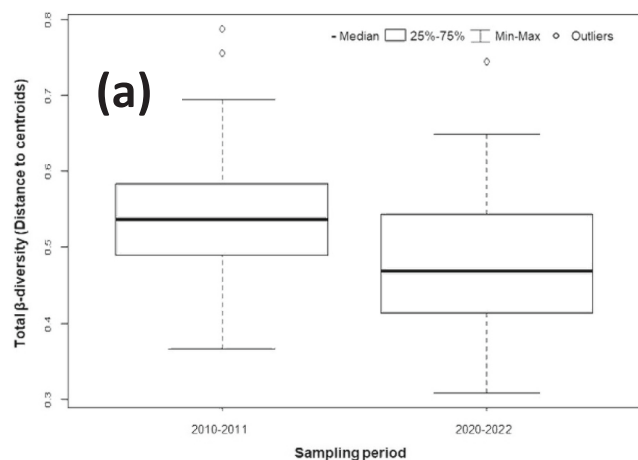


Fig. 4. Boxplots of total β -diversity (a) and its nestedness component (b) in 2010–11 and 2020–22.

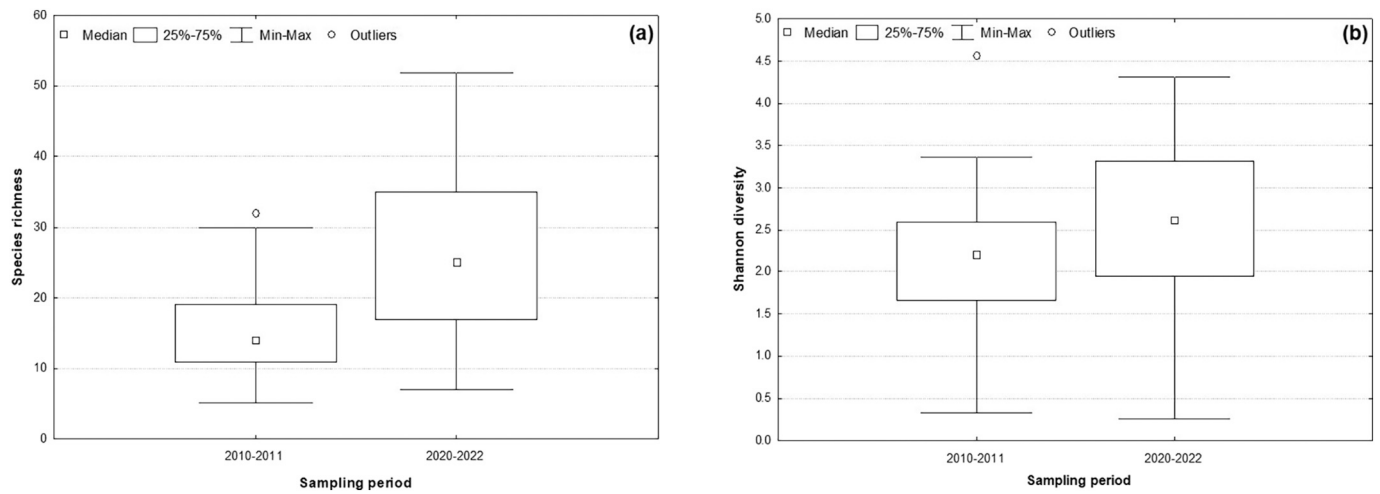


Fig. 5. Boxplots of species richness (a) and Shannon-Wiener diversity (b) in 2010–11 and 2020–22.

Table 8

Results of a multivariate analysis (RDA) performed to test the influence of different environmental variables on diatom communities. Significant (*p*) codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.09.

	Df	Variance	F	Pr(>F)
Season	1	0.01885	6.6148	0.001***
Year	1	0.0135	4.7361	0.001***
River type	1	0.00532	1.8648	0.016*
Reference	1	0.01085	3.8052	0.001***
Elevation	1	0.00364	1.2784	0.161
Drainage area	1	0.00401	1.407	0.11
T water	1	0.00426	1.4935	0.078*
Turbidity	1	0.00342	1.1989	0.25
Instantaneous observed flow	1	0.00415	1.4576	0.085*
DO %	1	0.00264	0.9264	0.515
Conductivity	1	0.00659	2.3108	0.004**
pH	1	0.00261	0.914	0.54
Residual	196	0.55868		

Table 9

IndVal results for key indicator species for the different biological groups identified with the agglomerative analysis of the diatom matrix for all the diatom samples. Significant (*p*) codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05. ‘A’ is the specificity of the species as an indicator of the site group, while ‘B’ is the fidelity or sensitivity of the species as an indicator of the group.

Species name	A	B	Stat	<i>p</i> value
Group 1				
<i>Achnanthydium minutissimum</i> sensu lato	0.7283	0.3889	0.532	0.001***
<i>Achnanthydium ertzii</i>	0.8024	0.3519	0.531	0.001***
<i>Gomphonema pseudotenellum</i>	0.694	0.1296	0.3	0.022*
Group 2				
<i>Achnanthydium tepidaricola</i>	0.86856	0.11111	0.311	0.008**
<i>Cavinula cocconeiformis</i>	0.90541	0.06944	0.251	0.022*
<i>Tryblionella hungarica</i>	1	0.05556	0.236	0.018*
Group 3				
<i>Cocconeis pediculus</i>	0.7785	0.61446	0.692	0.001***
<i>Navicula tripunctata</i>	0.75528	0.61446	0.681	0.001***
<i>Achnanthydium lineare</i>	0.73697	0.60241	0.666	0.001***
<i>Reimeria uniseriata</i>	0.6372	0.56627	0.601	0.001***
<i>Navicula cryptotenelloides</i>	0.71312	0.49398	0.594	0.001***
<i>Cymbella kolbei</i>	0.70158	0.45783	0.567	0.001***
<i>Rhoicosphenia abbreviata</i>	0.74793	0.3012	0.475	0.001***
<i>Navicula capitatoradiata</i>	0.86766	0.19277	0.409	0.001***
<i>Cymbella kappii</i>	1	0.13253	0.364	0.001***
<i>Kolbesia ploenensis</i>	1	0.09639	0.31	0.002**
<i>Nitzschia oligotrappenta</i>	1	0.09639	0.31	0.003**
<i>Nitzschia lacuum</i>	1	0.08434	0.29	0.003**
<i>Brachysira vitrea</i>	0.91785	0.07229	0.258	0.025*
<i>Nitzschia acidoclinata</i>	0.89745	0.07229	0.255	0.024*
<i>Cymbopleura citrus</i>	1	0.06024	0.245	0.023*
<i>Delicata verena</i> var. <i>sandrae</i>	1	0.06024	0.245	0.031*

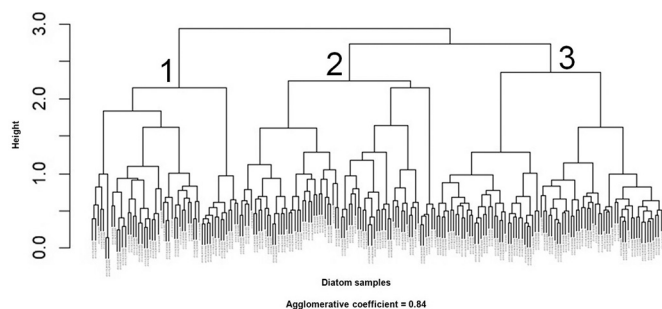


Fig. 6. Dendrogram showing the results of the agglomerative cluster analysis of all the diatom samples. Groups 1 and 2 have the median in 2011 and comprise mainly samples from 2010–11, while Group 3 has the median in 2020 and is mainly composed of samples collected in 2020–22.

change (Cartwright et al., 2020), and the stream sites close to them should be carefully protected as they can be refugia for sensitive and characteristic species that can recolonize the adjacent streams after adverse climatic events.

5. Conclusions

Biotic homogenization has become a global phenomenon (Baiser et al., 2012). Here we show that, over the last ten years, in response to

increased water temperature, conductivity, and discharge variability due to climate-change, Cypriot stream diatom communities include a higher number of trivial (= common, widespread, typically eutrappentic and abundant species which often replace characteristic and specialized species during biotic homogenization), aerial, and thermophilic species, have reduced β -diversity and increased nestedness. Moreover, IndVal indicators of 2010–11 are characteristic, often relatively rare species, while the indicators of 2020–22 are a group of typical trivial, eutrappentic, and thermophilic species. As is almost always the case, the diatom communities we studied are subjected to multiple stressors, often affecting them in opposite ways. Besides the increase in trivial species, the reduction in β -diversity, and the increase in nestedness mentioned above, the diatom assemblages we studied also showed an

increase in α -diversity that could be due to a moderate reduction in nutrients in several sites.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.174495>.

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CRedit authorship contribution statement

Marco Cantonati: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **David G. Armanini:** Writing – review & editing, Formal analysis. **Daniele Demartini:** Writing – review & editing, Formal analysis. **Athina Papatheodoulou:** Writing – review & editing, Investigation. **Olena P. Bilous:** Writing – review & editing, Writing – original draft, Investigation. **Federica Colombo:** Writing – review & editing, Formal analysis. **Nicola Angeli:** Visualization, Investigation, Data curation. **Rosalina Stancheva:** Writing – review & editing, Validation, Data curation. **Gerald Dörflinger:** Writing – review & editing, Validation, Data curation. **Kalina M. Manoylov:** Writing – review & editing, Validation, Data curation.

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.

Data availability

Data will be made available on request.

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