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PRIMARY RESEARCH PAPER

Topographically shaded lakes may provide refugia for cold-adapted aquatic fauna threatened by climate change

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Abstract Understanding the structure and diversity of high-altitude lake communities and the patterns of their altitudinal changes is important for predicting their response to ongoing climate change.
We analysed littoral benthic communities of 18 mountain lakes of glacial origin distributed along a 500-m altitudinal gradient and characterized by differing topographic shading levels: unshaded lakes and shaded lakes with a substantially lower (by 1151 h) mean annual duration of direct solar radiation. We hypothesized that local topographic shading modifies diversity–altitude relationships and affects the pattern of community turnover along the altitudinal gradient.
We found a decreasing trend in diversity with increasing altitude and a significant deviation from that pattern in shaded lakes. Investigated lake groups supported distinct communities in lower altitudes. However, their community composition converged towards higher altitudes in communities typical for a greater abundance of cold stenotherms. The proportion of cold-stenothermal species increased with increasing altitude in shaded lakes and was notably greater than that in unshaded lakes along the

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studied altitudinal gradient. The lower temperatures of shaded lakes and different temperature variabilities of the two groups of lakes likely explain the observed patterns. We hypothesize that topographically shaded lakes may provide refugia for cold-stenothermal communities threatened by ongoing global warming.

Keywords Macrozoobenthos · High-elevation · Stenotherms · Tatra Mountains · Central Europe · Global warming

Introduction

Mountain lakes are inherently sensitive to both direct and indirect effects of climate change (Sommaruga, 2001; Weckström et al., 2016, Maberly et al. 2020) because air temperature increases faster in mountain regions than in adjacent lowland sites (Mountain Research Initiative EDW Working Group, 2015). For example, in the Tatra Mts. (the West Carpathians, Central Europe), a particularly steep increase in air temperature was evident from 1980 onwards, with an average linear increase of 0.05°C yr^{-1} (Łupikasz & Szypuła, 2019; Svitok et al., 2021). Lake responses are generally most intense at 1500–2000 m a.s.l. due to the strongest impact of air temperature changes on lake temperature and ice cover duration at these altitudes (Thompson et al., 2005). However, the character and intensity of an individual response of a lake to climate variability can vary considerably regionally, depending on geographic position, catchment characteristics, and lake morphology, which strongly affect the thermal cycles of the lake (Soranno et al., 1999; Bleckner, 2005; Brodersen & Anderson, 2000; Novikmec et al., 2013; Szumny et al., 2022).

Altitude is certainly the most distinguishing and fundamental factor determining mountain climate characteristics (Beniston, 2006). Altitudinal control on mountain climates also significantly influences the distribution of aquatic ecosystems, their temperature, and the conditions of their environment (Beniston, 2006; Moser et al., 2019). Water temperature is a crucial factor affecting the function of mountain lakes, controlling lake ecosystems directly but also indirectly through its effect on physicochemical conditions and the distribution of aquatic organisms (Regier et al., 1990; Winder & Hunter, 2008; Gudasz et al., 2010; Svitok et al., 2021). As the water temperature characteristics of mountain lakes vary closely with air temperature (Livingston & Lotter, 1998; Livingstone et al., 2010; Alcocer et al., 2021), the temperature and ice cover duration of mountain lakes are generally also related to elevation, and lakes at higher altitudes are cooler than those at lower altitudes (Livingstone et al., 1999; Šporka et al., 2006). Nonetheless, beyond the main altitudinal gradient, local catchment conditions (Sabás et al., 2021), wind speed (Magee & Wu, 2017) but particularly topographic shading, may be significantly involved in the modification of lake temperature and the response of mountain lake temperature to large-scale temperature signals (Novikmec et al., 2013).

Due to the combination of short growing seasons and limited energy and nutrient resources, lakes at high altitudes generally experience harsh conditions (Füreder et al., 2006) and are inhabited by benthic fauna consisting of few, mostly rare and sensitive species. All these organisms are well adapted to extreme conditions but are also particularly vulnerable to environmental changes (Lencioni, 2004; de Mendoza & Catalan, 2010; Boggero et al., 2019). In the Tatra Mts., the macroinvertebrate fauna of lakes of glacial origin is characterized by species-poor communities dominated by chironomids. The communities primarily comprise very typical taxa, with their present distribution representing a remnant of that in historical periods when this fauna inhabited all Tatra lakes irrespective of altitude (Krno et al., 2006; Bitušík et al., 2006, 2017; Dvorak et al., 2024).

Climate change, however, is likely to induce changes in the living conditions of the occurring species (Beniston et al., 1997; Walther et al., 2002; Niedrist et al., 2018; Hock et al., 2019) and a variety of species responses (Velthuis et al., 2017; Hansen et al., 2017). Currently, for example, the rising temperatures of the Tatra lakes are already affecting the structure of benthic communities through upward shifts in the distribution ranges of more thermophilous species from lower altitudes (Svitok et al., 2021). The generally predicted response of cold-stenothermal species to warming is either migration to higher altitudes or extinction (Woodward et al., 2010; Rosset & Oertli, 2011; Domisch et al., 2013; Giersch et al., 2015), although taxonomically distinct groups differ in their vulnerability, and they are threatened differently by climate change effects (warming waters, changing food resources) (Hotaling et al., 2020; Niedrist &

Füreder, 2023). In addition, the responses of benthic communities may also differ due to locally induced differences in lake thermal characteristics. Based on our previous study (Novikmec et al., 2013), we can assume that some topographically shaded lakes can be less sensitive to climate signals and may provide an environment allowing the existence of taxa requiring cold conditions under continuously rising temperatures (Hamerlík et al., 2017).

Studies on the diversity–altitude relationship in European mountain lakes have shown a variety of patterns, including a decrease in diversity with increasing altitude, a hump-shaped pattern, or even no clear relationship (Catalan et al., 2009; de Mendoza & Catalan, 2010; Martínez-Sanz et al., 2012). This heterogeneity may arise from differences in scales among surveys (Rahbek, 2005; Motta et al., 2019) and taxonomic resolution (Hamerlík et al., 2017), or it may be related to local or regional peculiarities not associated with increasing altitude (Körner, 2007).

A thorough understanding of the structure and diversity of high-altitude lake communities, the patterns of their changes along altitudinal gradients, and the factors driving these patterns is of particular relevance for predicting communities' responses to ongoing environmental changes. Furthermore, the identification of sites and communities that deviate from the conventional altitudinal scheme may help define and apply conservation measures and monitoring programmes for mountain lakes. Identifying the peculiarities of community–altitudinal gradient relationships at the regional scale is also important because various ecoregions, for example, differ in their species pools that possess distinct proportions of species vulnerable to climate change (Niedrist & Füreder, 2023).

In this study, we analysed littoral benthic communities of 18 mountain lakes of glacial origin distributed along a 500-m altitudinal gradient consisting of two groups: (i) unshaded lakes with significantly greater amounts of possible solar radiation than (ii) topographically shaded lakes. Our objectives were (1) to compare the altitudinal patterns of invertebrate diversity between shaded and unshaded lakes and (2) to assess the altitudinal turnover of community composition between the two lake groups. We hypothesized that local topographic shading could modify patterns of species richness and composition, as well as the proportion of cold-stenothermal species along the altitudinal gradient. Consequently, we also assumed that topographically shaded lakes would serve as more suitable environments for cold-adapted species, which are among the most sensitive to the effects of climate change.

Material and methods

Study area

The Tatra Mts. are the highest part of the Carpathian mountain system (20°10' E, 49°10' N). The average annual air temperature decreases with increasing altitude by 0.6 °C per 100 m (Konček & Orlicz, 1974). The annual amount of precipitation varies from 1000 to 1600 mm (but can reach 2000 mm in some valleys) (Chomitz & Šamaj, 1974). Snow cover usually lasts from October to June at altitudes above 2000 m.

For the purposes of this study, we selected 18 lakes with contrasting local topographic shading (9 shaded and 9 unshaded lakes) situated along a ~ 500-m altitudinal gradient (Fig. 1). Our selection was based on the outputs of the insolation model that considered atmospheric effects, latitude, elevation, slope, aspect, seasonal sun angle shifts, and topographic shadows using 20 × 20 m digital elevation model (see Novikmec et al. (2013) for details) The lakes are soft-water, oligotrophic, and fishless and lack any direct anthropogenic influence. We also excluded lakes affected by anthropogenic acidification in the past (Kopáček et al., 2015). The catchments of the lakes are dominated by granodiorite bedrock. The most common soils are undeveloped podsols, leptosols, and regosols. The vegetation of the catchments is formed mainly by dwarf pine (*Pinus mugo* Turra) shrubs (between 1550 and 1800 m a.s.l.) and, in the alpine zone (above 1800 m a.s.l.), dry alpine meadows, rush-heaths, or lichen in scree areas. The lakes are situated above the present-day timberline. A detailed description of the lakes can be found in Novikmec et al. (2013).

The lakes were selected randomly with the restriction that lakes of similar morphometries but various shading levels (shaded *vs.* unshaded) were included within each altitudinal belt of approximately 150 m to minimize correlations between altitude, shading, and lake morphology. On average, unshaded lakes potentially receive 1151 h more of direct solar radiation per year than shaded lakes (Table 1). The groups

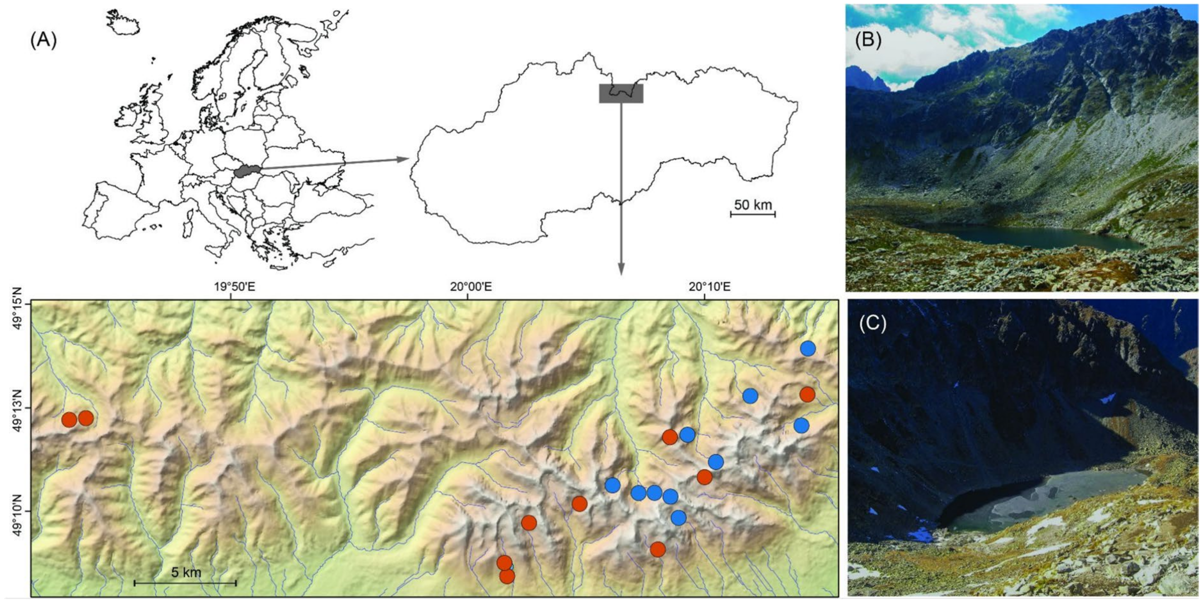

Fig. 1 Map showing the location of studied lakes (A; orange circles—unshaded lakes, blue circle—shaded lakes), and examples of the unshaded (B; Pusté pleso) and shaded (C; Zamrznuté pleso) lakes, the highest located representatives of studied groups of lakes. Pictures were taken the same day (October, 12th, 2010)

Table 1 Basic characteristics of shaded and unshaded Tatra Mountain lakes

	Shaded lakes			Unshaded lakes				
Variable	Mean (SD)	Min	Max	Mean (SD)	Min	Max	*t*	*P*
TDDSR (hours/year)	1708 (244)	1436	2170	2859 (485)	2155	3418	–	–
Altitude (m)	1767 (174)	1565	2040	1780 (174)	1562	2056	0.16	0.873
Area (ha)	1.3 (0.8)	0.2	2.5	1.3 (1.0)	0.2	3.5	0.02	0.988
Maximum depth (m)	8.3 (6.4)	1.2	19.1	5.8 (4.3)	0.8	12.6	0.95	0.356
Avg. annual temperature (°C)	3.0 (0.9)	2.1	4.2	4.3 (1.3)	2.8	6.1	2.37	0.033
Annual temp. variability (°C)	3.4 (0.6)	2.6	4.4	4.6 (1.1)	3.1	6.1	2.78	0.016
Avg. July temperature (°C)	6.3 (1.7)	4.1	9.1	9.7 (2.6)	6.0	13.3	3.16	0.007
July temp. variability (°C)	2.3 (0.5)	1.7	3.0	2.9 (0.5)	2.2	3.4	2.82	0.013
Water pH	7.0 (0.3)	6.5	7.3	6.8 (0.2)	6.5	7.2	1.76	0.098
Total nitrogen (μg dm^{-3})	443 (71)	315	551	436 (117)	290	683	0.16	0.878
Total phosphorus (μg dm^{-3})	2.3 (0.3)	1.8	2.6	2.7 (0.9)	1.1	3.9	1.54	0.158
Dissolved organic carbon (mg dm^{-3})	0.3 (0.1)	0.2	0.5	0.6 (0.4)	0.1	1.5	2.10	0.065

The table shows the mean values, standard deviations (SD), and minimum and maximum values for each variable

The test statistics (*t*) and associated probabilities (*P*) of Welch's t-tests testing for the differences between shaded and unshaded lakes are displayed. Differences in the potential total duration of direct solar radiation (TDDSR) were not tested to avoid circular reasoning

Note that temperature variability was quantified using standard deviations of daily temperatures

of lakes with contrasting shading do not differ significantly in terms of area, depth, altitude, and chemistry (Table 1). However, the unshaded lakes have significantly higher mean annual and mean July water temperatures than the shaded lakes (Table 1, Fig. 2). In addition, the surface water temperature variability of the unshaded lakes is significantly higher than that of the shaded lakes. The altitudinal gradient

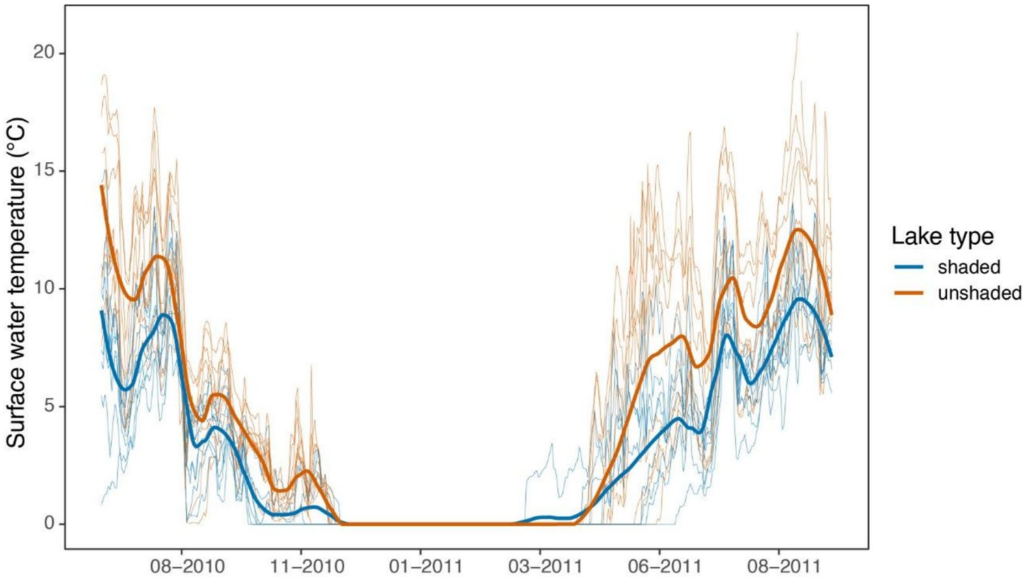

Fig. 2 Mean daily lake surface water temperatures (at 5 cm depth) of shaded and unshaded Tatra Mountains lakes measured from July 2010 to September 2011. General trends are depicted by locally weighted regression smoothing (LOESS) with a span of 20% (thick lines)

covered in our study was characterized by variations in temperature and nutrient levels (Table S1). Further details on the temperature regimes of lakes can be found in Novikmec et al. (2013). Data on water chemistry (Table S1; average for the 2009–2011 period) come from Kopáček et al. (2015 and unpubl. data).

Benthic macrofauna sampling and processing

Samples of benthic macroinvertebrates were collected during two sampling campaigns in 2009 and 2011. The samples were taken in early autumn when the lakes were free from ice and most insect larvae were in late instars or fully grown. Invertebrates were sampled semiquantitatively with a D-shaped hand net (mesh size 250 µm) using a short series of kicks from different substrate types, disturbing the substrates for 5 min. Dominant substrate types of individual lakes (mostly mineral in all the lakes) were sampled, considering their relative dominance. The littoral was sampled to a depth of ~ 1 m, which was shallow enough to perform thorough sampling and to ensure the representative sample covering the highest number of present macroinvertebrate groups (de Mendoza & Catalan, 2010). Sampled material was placed into polythene bottles and preserved with formalin at a concentration of 4%. In the laboratory, all specimens were removed under a low-power stereomicroscope (mag. 7–40 ×). Chironomids were mounted on slides using Berlese's fluid.

All the macroinvertebrates were counted and identified to the lowest possible taxonomic level. The identification of chironomids was performed under high magnification (400 ×) following the keys of Bitušík (2000), Stur & Ekrem (2006), Andersen et al. (2013), and Bitušík & Hamerlík (2014). The identification of other macroinvertebrate groups was based on Rozkošný et al. (1980), Bauernfeind and Humpesch (2001), Waringer & Graf (2011) and Krno (2013). For one of the analyses, we classified cold-stenothermal taxa according to the species trait database (Schmidt-Kloiber & Hering, 2015) and available published information (Čiamporová Zaťovičová et al., 2010; Hamerlík et al., 2017).

Data analysis

The data from the two sampling dates were averaged and stored in a species-by-lake matrix. Univariate and multivariate methods were used to assess differences in the altitudinal patterns of benthic communities in shaded and unshaded alpine lakes.

Species richness was analysed using generalized additive models (GAMs), a flexible approach that allows for non-linear responses and non-normal distributions, using the package mgcv (Wood, 2017). The diversity of benthic invertebrates was modelled using Poisson GAM with thin plate regression splines as base functions (Wood, 2003) and double penalty smoothing (Marra & Wood, 2011). The GAM involved an overall smoother for altitude common to both lake types and a smoother representing the deviation from the overall trend in shaded lakes.

GAMs were also used to assess patterns in the proportions of cold-stenothermal species (Table S2). The proportions were calculated as the number of cold-stenothermal species relative to the total number of species recorded in a given lake. We applied the same parameterization as described for the GAM earlier, with the exception that the proportions were represented as beta responses utilizing a logit link function (Ferrari & Cribari-Neto, 2004). The residuals of the GAMs were checked for overdispersion and heteroscedasticity using the package DHARMa (Hartig, 2022); no violations of the assumptions were detected.

To gain insight into the altitudinal changes in species composition, the species-by-lake abundance matrix was converted to Bray–Curtis dissimilarities and analysed using distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999) as implemented in the package vegan (Oksanen et al., 2020). Species abundance data were square-root transformed to downweight the influence of the most abundant species. The ordination model involved the effect of lake type (shaded *vs.* unshaded), altitude, and their interaction. The statistical significance of the model terms was assessed using a randomization test (10,000 unrestricted permutations of residuals).

Since altitude and topographic shading are proxy variables that integrate multiple drivers of aquatic biodiversity (Tab. 1, Table S1), we further explored the processes shaping benthic communities, assuming that lake and basin morphology influences habitat conditions, which, in turn, affect biodiversity. A suite of univariate and multivariate models was formulated to assess the strength of evidence supporting the hypothesized causal relationships.

Morphological characteristics (lake area, depth and topographic shading) were used as explanatory variables to estimate their direct effects on average annual water temperature (hereafter water temperature), water pH (pH), total nitrogen (TN), total phosphorus (TP), and dissolved organic carbon (DOC). Water temperature was also included as a predictor of water chemistry, as it influences key physicochemical processes and nutrient dynamics in alpine lakes (e.g. Sommaruga-Wögrath et al., 1997; Rogora et al., 2003; Baquero et al., 2006). We used generalized linear models (GLMs) with a gamma distribution and a logarithmic link function to fit these non-negative continuous variables (McCullagh & Nelder, 1989). The performance of the GLMs was assessed using diagnostic plots of residual. Lake area and depth were logarithmically transformed to meet the distributional assumptions of the models.

Subsequently, temperature and water chemistry were used as predictors of species richness, the proportion of cold-stenothermal species and community composition. Lake area and depth were also included to account for the potential influence of species-area relationships and littoral-profundal habitat transition, respectively. GAMs and db-RDA, with the same settings as above, were used to model the biodiversity characteristics of benthic communities.

Finally, individual models were integrated into a network of structural equation models (SEMs; Shipley, 2000a) using the package piecewiseSEM (Lefcheck, 2016). Shipley's d-sep tests were used to evaluate the consistency of the data with the hypothesized pathways (Shipley, 2000b). We calculated semi-partial determination coefficients to quantify the relative importance of individual predictors (Ray-Mukherjee et al., 2014).

The analyses were performed in R v.4.1.2 (R Core Team, 2021), and plots were created using the package ggplot2 (Wickham, 2016).

Results

Our sampling of 18 lakes revealed the occurrence of 59 taxa (Table S2). The most diverse and abundant group was Chironomidae (Diptera), which accounted for more than half of the total recorded diversity and abundance. The most abundant and frequent species was *Heterotrissocladius marcidus* (Walker, 1856). The local species richness ranged from 7 to 25 taxa per lake.

Generalized additive models revealed a significant overall trend in diversity along the altitudinal gradient (effective degrees of freedom [edf] = 1.1, $\chi^2 = 5.85$, p = 0.003) and a significant deviation from that trend manifested in shaded lakes (edf = 1.4, $\chi^2 = 4.64$, p = 0.028). Both lake types showed a sigmoidal decrease in species richness with increasing altitude; however, the pattern was more pronounced in shaded lakes than in unshaded lakes (Fig. 3a). At lower altitudes, the lake types were distinct in diversity, while the difference gradually diminished as altitude increased, eventually reaching a point of statistical indistinguishability around 1800 m a.s.l. and beyond. The model displayed a reasonably close fit to the observed data (adjusted $R^2 = 0.64$).

The relative proportion of cold-stenothermal species within aquatic communities showed a significant correlation with altitude (edf = 2.3, $\chi^2 = 32.0$, $p < 0.001$). Shaded lakes exhibited a substantial departure from this overall trend (edf = 2.1, $\chi^2 = 21.3$, $p < 0.001$). The proportion of cold-stenothermal species was notably greater in shaded lakes and displayed a consistent increase with increasing altitude (Fig. 3b). In contrast, following an initial rise, the proportion of cold-adapted species reached saturation in unshaded lakes beyond an altitude of approximately 1850 m. The model demonstrated a good match with the observed data, as evidenced by an adjusted R^2 value of 0.75.

Also, species composition showed significantly different altitudinal trends in shaded and unshaded lakes (db-RDA; altitude × lake type: pseudo-F = 1.54, $p = 0.032$, $R^2 = 0.49$).

The investigated lake groups hosted distinct invertebrate communities at lower altitudes (Fig. 4). The communities of unshaded lakes had greater abundances of *Psectrocladius limbatellus* group, *Sialis lutaria* (Linnaeus 1758), and *Microtendipes pedellus* group, while the shaded lakes were typical for *Micropsectra notescens* (Walker 1856), *Micropsectra lindrothi* Goetghebuer 1931, *Drusus trifidus* McLachlan 1868, and *Nemurella pictetii* (Klapálek 1900). However, the community composition of shaded and unshaded lakes converged towards higher altitudes (> 1800 m a.s.l.) in communities typical for a higher abundance of *Leuctra rosinae* Kempny 1900 and *Capnia vidua* Klapálek 1904. The ordination model explained 28.5% of the variation in the community dissimilarity data.

Since altitude and topographic shading serve as proxy variables that encompass multiple drivers of aquatic biodiversity, we investigated the processes shaping benthic communities using a network of structural equation models. SEMs revealed that topographic

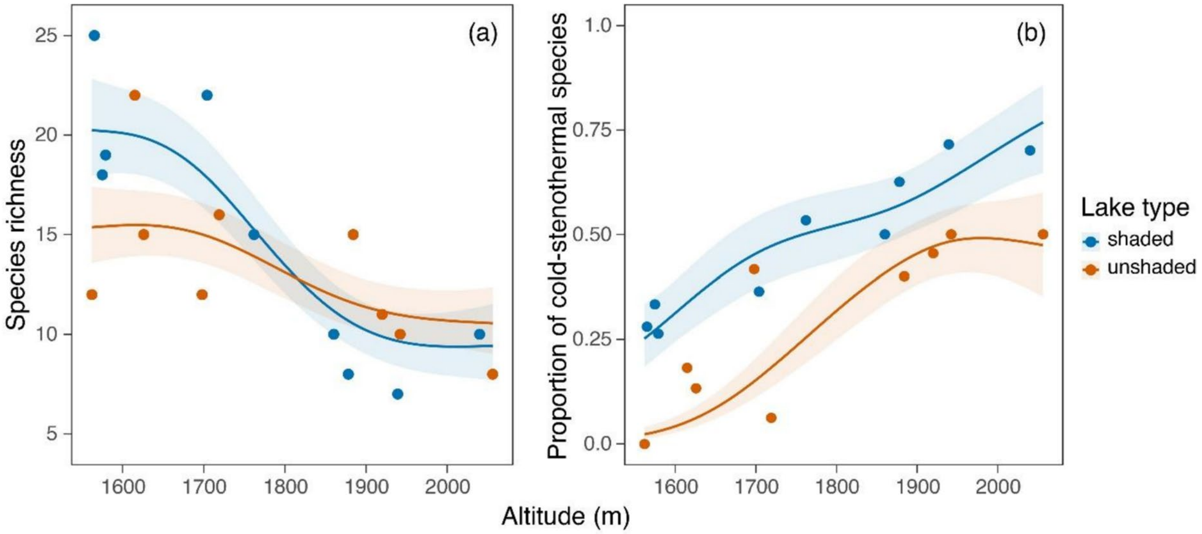

Fig. 3 Significant differences in the altitudinal patterns of species richness (**a**) and the proportion of cold-stenothermal species (**b**) in the shaded and unshaded Tatra lakes. GAM-based predictions (lines) and their standard error bands are shown along with the observed values (dots)

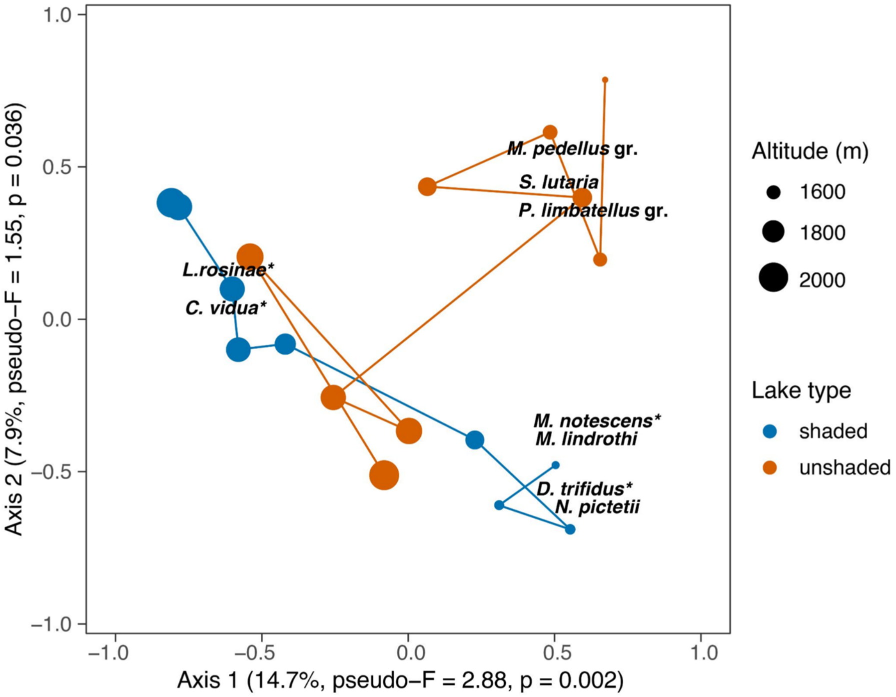

Fig. 4 Ordination plot of db-RDA showing differences in the community composition of shaded and unshaded lakes along the altitudinal gradient in the Tatra Mts. Variation in community dissimilarity accounted for the ordination axes is displayed in parentheses along with test statistics (pseudo-F) and probabilities (*P*) of the randomization tests (10,000 permutations). Note that the trajectories connect lakes along the altitudinal gradient. The ordination scores of the best-fitting species are shown in italics. Asterisks indicate cold-stenothermal species

shading plays a pivotal role by strongly influencing water temperature, which mediates its effects on water chemistry and, ultimately, benthic communities (Fig. 5). Specifically, topographic shading significantly reduced water temperature, which in turn affected TP and DOC concentrations (Table S3, Fig. S1a−c). These temperature-driven changes had cascading effects on benthic communities, as water temperature directly influenced species richness, the proportion of cold-stenothermal species and community composition (Table S4, Fig. S1d, g, i). Additionally, water temperature acted indirectly through its influence on DOC variation (Fig. S1f). While temperature-mediated effects of topographic shading were dominant, other environmental factors such as lake depth, TN and pH also contributed to shaping benthic communities (Fig. S1e, h, i). The observed patterns closely aligned with the pathways hypothesized in the SEMs, as supported by non-significant results of Shipley's d-sep tests (Fig. 5).

Discussion

Communities of the studied lakes along the altitudinal gradient

The community composition of the surveyed lakes, dominated by Chironomidae (Diptera) in terms of both abundance and species number, is typical for high-altitude lakes in Europe (e.g. Fjellheim et al., 2009; de Mendoza & Catalan, 2010; Lods-Crozet et al., 2012; Bertoli et al., 2023) and has also been found in previous studies from the Tatra Mts. (Bitušík et al., 2006; Krno et al., 2006; Novikmec et al., 2015).

Both shaded and unshaded lakes showed a distinct sigmoidal decrease in species richness with increasing altitude. The observed shape of the diversity curves diverges somewhat from the monotonic or unimodal patterns usually observed (Rahbek, 2005; de Mendoza et al., 2017). However, it is recognized

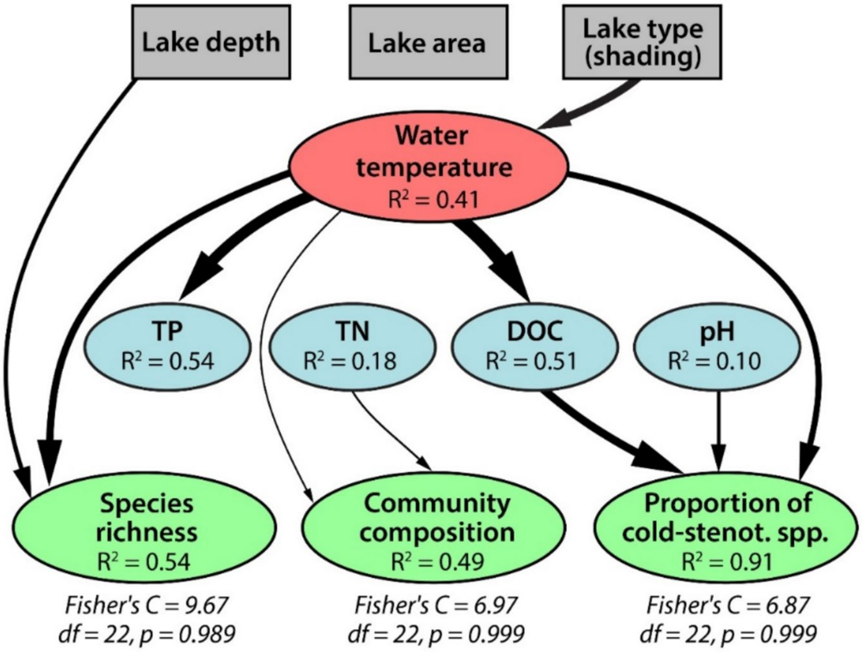

Fig. 5 Structural equation models linking lake and basin morphometry (grey), water temperature (red), and water chemistry (blue) with diversity and composition of benthic communities (green). Arrows indicate significant relationships ($p < 0.05$) while the width of the lines is proportional to the variation in a response explained by each predictor. Overall variation explained by the models is given for each response (R^2). Test statistics of Shipley's d-sep test (Fisher's C), along with the associated degrees of freedom (df) and probabilities (P), are displayed for each SEM. Numeric details are provided in Tab. S.3 and Tab. S.4

that the relationship between species richness and altitude depends on the scale or length of the gradient (Jankowski & Weyhenmeyer, 2006; Werenkraut and Ruggiero, 2014; Motta et al., 2019) and also on the location of the studied gradient at particular altitudes (de Mendoza & Catalan (2010). Additionally, the sigmoidal shape of the diversity curve observed in our study would likely become smoother with the inclusion of additional lakes (Colwell et al., 2004; Bartels et al., 2021).

The altitudinal decline in the number of species in the studied lakes can be attributed to the harshening of in-lake environmental conditions when moving upslope (Moser et al., 2019) and corroborates previous studies from the Tatra Mts. (Krno et al., 2006; Čiamporová et al., 2010; Hamerlík et al., 2014, 2017). With increasing altitude, various factors contribute to the harshening of in-lake conditions, including decreasing water temperatures, shorter ice-free periods, alterations in nutrient concentration and the availability of food resources, among others (Table S1; Kopáček et al., 2000; Luoto et al., 2013; Novikmec et al., 2013). These physiologically demanding conditions, coupled with the smaller geographic extent of higher altitudes, lead to a reduction in the regional species pool to a low number of taxa capable of tolerating these conditions (Clarke & Gaston, 2006; Romdal & Grytnes, 2007).

At an altitude of approximately 1800 m, a noticeable shift in the diversity and community composition of the surveyed lakes occurred. This altitude corresponds to the subalpine–alpine boundary in the Tatra Mountains. At this boundary line, the decrease in vegetation and soil cover proportion in the catchments is linked to a reduction in nutrients (especially phosphorus), dissolved organic carbon, and lake productivity (Bitušík et al., 2006; Kopáček et al., 2015). Low production rates and lower terrestrial export of nutrients and organic carbon from catchments above this line lead to restricted food availability for benthic invertebrates, resulting in species-poorer communities with similar compositions (Bitušík et al., 2006; Füreder et al., 2006). Such sudden altitudinal transitions in the environmental conditions, community composition, and diversity of mountain lakes have been reported in other mountain areas (Heegaard et al., 2006; Catalan et al., 2009; de Mendoza & Catalan, 2010; Motta et al., 2019), although the exact altitudinal position of these ecological thresholds may vary depending on latitude and climate (Hamerlík et al., 2017).

Effect of topographic shading

We have demonstrated that topographic shading is a key driver, significantly affecting water temperature, which in turn shapes water chemistry and ultimately influences benthic communities (Fig. 5). The studied lakes belonging to the shaded lake group had lower year-round temperatures and significantly lower mean annual and mean July water temperatures than the unshaded lakes (Fig. 2, Table 1, Fig. S1a, Novikmec et al., 2013). We observed distinctions in the diversity and composition of communities between shaded and unshaded lakes in the lower part of the studied gradient, but these differences gradually diminished towards higher altitudes. While communities of unshaded lakes had a greater abundance of species that tolerate a broad range of temperatures (*S. lutaria*) or taxa typical for lower altitudes (*Psectrocladius limbatellus* group, *Microtendipes pedellus* group, Šporka et al., 2003), shaded lakes were characterized by taxa without strict thermal preferences and a greater abundance of the cold-stenothermal *Drusus trifidus. D. trifidus* was present only in the shaded lakes at the lower part of the studied gradient, which indicates different temperature conditions in the lakes with contrasting local topographic shading (Novikmec et al., 2013; Hamerlík et al., 2017).

Upon passing the ecological threshold at the subalpine–alpine boundary of ~ 1800 m, the communities of both lake types shifted towards higher abundances of the cold-stenothermal stoneflies *L. rosinae* and *C. vidua.* These species generally prefer permanently low temperatures and are restricted to the high alpine zone (Krno et al., 2006; Hamerlík et al., 2014; Novikmec et al., 2015). This is not surprising given the extremely harsh environmental conditions of alpine lakes, characterized by consistently low temperatures, prolonged ice cover (Gądek et al., 2020), and diminishing temperature differences between shaded and unshaded lakes (Novikmec et al., 2013). In such a cold environment, only a limited pool of well-adapted species persists, resulting in species-poor communities that exhibit higher similarity among lakes (Füreder, 2007; Hamerlík et al., 2017; Loria et al., 2020).

In the lower parts of the studied altitudinal range, shaded lakes showed higher diversity than unshaded lakes. The observed significantly higher annual and July temperature variabilities in unshaded lakes (Table 1) are likely responsible for this pattern. In high-altitude lakes, widely fluctuating temperatures may eliminate some taxa because these ecosystems are predominantly occupied by a limited pool of macroinvertebrate species that tolerate a restricted temperature range and are sensitive even to small temperature fluctuations (Bonacina et al., 2023). Indeed, we found significant differences in temperature variability between shaded and unshaded lakes along the entire gradient, with substantially higher variance recorded in unshaded lakes at lower altitudes compared to their counterparts (Fig. S2). In this regard, the stable conditions of shaded lakes in the lower part of the gradient are perhaps more favourable for supporting higher diversity.

In our attempt to find evidence of the topographic shading effect, we also investigated the relative proportion of cold-stenothermal species in the communities of the studied lakes. In shaded lakes, the proportion of cold-stenothermal species continuously increased with increasing altitude. This finding is consistent with strong temperature niche filtering at high altitudes. Individual taxa can respond to increasing altitude by changes in their presence rather than their abundance (e.g. de Mendoza & Catalan, 2010), which may cause the elimination of species with higher temperature requirements (Hamerlík et al., 2017) and a higher proportion of cold-stenothermal species capable of tolerating these conditions (Füreder et al., 2006; Bartels et al., 2021).

Perhaps more importantly, lakes with contrasting topographic shading differed in the proportion of cold-stenothermal taxa along the whole studied gradient, with a consistently lower relative proportion of these taxa in the unshaded lakes. This is not surprising because it likely reflects temperature differences between lakes with contrasting topographic shading. Topographically shaded lakes showed consistently lower temperatures than unshaded but otherwise similar lakes across all the studied altitudinal belts. For example, the summer daily mean lake surface water temperatures of morphologically similar lakes differed by as much as 5°C at the lowest altitude and ~ 2°C at an altitude of ~ 2050 m (Novikmec et al., 2013). The only exception in the observed pattern was the unshaded lake Vyšné Frukotské pleso at an elevation of approximately 1700 m, with a proportion of cold stenotherms similar to shaded lakes at similar elevations. However, this similarity in proportions resulted from the low overall diversity of the lake, rather than specific temperature or topographic conditions, and does not disrupt the overall observed pattern.

Importance of topographic shading

The observed differences in the proportions of cold-stenothermal species could be important considering the ongoing warming of mountain areas. These taxa play a key role as sensitive indicators of climate change, given that they are particularly vulnerable to its effects (Oertli et al., 2008; Domisch et al., 2013; Lindholm et al., 2015; Pallarés et al., 2020). We may assume that populations of cold-stenothermal taxa could survive in topographically shaded lakes despite future increases in ambient temperature; i.e. these lakes could act as refuges for cold-adapted taxa (Fahy et al., 2024). The expected upward movement of cold-stenothermal species (Rosset and Oertli, 2011; Ilg & Oertli, 2014) and thus may not be the general rule since these species could also survive at lower altitudes in topographically induced suitable conditions. This phenomenon has already been documented in cold-stenothermal chironomids in the Tatra Mts. (Hamerlík et al., 2017). Indeed, gradual warming will also impact the temperatures and, consequently, the communities of shaded lakes. However, ecosystems of these lakes might exhibit greater resistance to climate signals. Topographic shading significantly contributes to the lowering of lake water temperature compared to unshaded lakes along the entire studied gradient (Novikmec et al., 2013). Consequently, regardless of their distribution along the elevation gradient, all cold-stenothermal species could benefit from this effect. The efficiency of these cold refugia will also depend on potentially changed species interactions (Owens et al., 2023; Lamouille-Hébert et al., 2024) due to the generally expected shift in species ranges and possible immigration of species from warmed lower altitudes (Hodkinson & Jackson, 2005; Shepard et al., 2021; Svitok et al., 2021).

Conclusions

To the best of our knowledge, this is the first time that topographic shading has been explicitly considered in relation to the structure and distribution of high-altitude aquatic communities. Our study clearly shows that this feature can be substantially involved in the direct and indirect shaping of community composition and diversity patterns along altitudinal gradients, likely primarily through its direct effect on lake temperature characteristics (Novikmec et al., 2013). This finding is an important contribution to understanding the drivers of the composition and distribution of mountain lake communities and is potentially useful for monitoring and predicting their reactions to progressively increasing lake temperatures (Woolway et al., 2017). We showed that topographic shading affects the distribution of cold stenotherms, species especially expected to migrate and change their altitudinal range in response to the adverse effects of climate change. Our study highlights the high potential of topographically shaded lakes to serve as refuges for cold-stenothermal species. This could aid in planning and implementing conservation strategies where feasible and focusing these actions preferably on shaded lakes, especially at lower altitudes.

Despite stressing the importance of lake temperature as a key variable affected by topographic shading, its outcome is more complex than straightforward. Other factors indirectly related to topographic shading (e.g. primary production, processing of allochthonous inputs) may also influence the community assembly of lakes. Further studies encompassing more lakes distributed along larger altitudinal gradients and preferably reflecting a broad gradient of topographic shading are needed for a better understanding of the role of topographic shading in the modification of community and ecosystem process patterns.

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Data availability Data will be made available on reasonable request.

Declarations

Conflict of 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.

References

Alcocer, J., L. A. Oseguera, D. Ibarra-Morales, E. Escobar & L. Garcia-Cid, 2021. Responses of benthic macroinvertebrate communities of two tropical, high-mountain lakes to climate change and deacidification. Diversity 13: 243. https://doi.org/10.3390/d13060243.

Andersen, T., P. S. Cranston & J. H. Epler (Eds), 2013. Chironomidae of the Holarctic Region–Keys and diagnoses–Larvae. Series: Insect Systematics and Evolution Supplements, 66, 573

Baquero, M. R., P. Carrillo, B. J. Arco, P. C. Martinez & V. M. Argaiz, 2006. Climate-driven change on phytoplankton-zooplankton coupling and nutrient availability in high mountain lakes of Southern Europe. Freshwater Biology 51: 989–998. https://doi.org/10.1111/j.1365-2427.2006.01545.x.

Bartels, A., U. G. Berninger, F. Hohenberger, S. Wickham & J. S. Petermann, 2021. Littoral macroinvertebrate communities of alpine lakes along an elevational gradient (Hohe Tauern National Park, Austria). PLOS One 16: e0255619. https://doi.org/10.1371/journal.pone.0255619.

Bauernfeind, E. & U. H. Humpesch, 2001. Die Eintagsfliegen Zentraleuropas (Insecta: Ephemeroptera): Bestimmung und Ökologie, Naturhistorisches Museum, Wien:, 239.

Beniston, M., 2006. Mountain weather and climate: a general overview and a focus on climatic change in the Alps. Hydrobiologia 562: 3–16. https://doi.org/10.1007/s10750-005-1802-0.

Beniston, M., H. F. Diaz & R. S. Bradley, 1997. Climatic change at high elevation sites; a review. Climatic Change 36: 233–251. https://doi.org/10.1023/A:1005380714349.

Bertoli, M., E. Pizzul, S. Basile, S. Perilli, R. Tauler, S. Lacorte, M. Prearo & P. Pastorino, 2023. Littoral macrobenthic invertebrates of two high-altitude lakes in the Alps: a small-scale analysis. Ecohydrology & Hydrobiology 23: 211–223. https://doi.org/10.1016/j.ecohyd.2023.02.003.

Bitušík, P., 2000. Príručka na určovanie lariev pakomárov (Diptera: Chironomidae) Slovenska. Časť I. Buchonomyinae, Diamesinae, Prodiamesinae a Orthocladiinae. [Identification guide of Slovakian chironomid larvae (Diptera: Chironomidae). Part I. Buchonomyinae, Diamesinae, Prodiamesinae a Orthocladiinae]. Vyd. Tech. Univerzity vo Zvolene, Zvolen: 133

Bitušík, P. & L. Hamerlík, 2014. Príručka na určovanie lariev pakomárov (Diptera: Chironomidae) Slovenska. Časť 2. Tanypodinae. [Identification guide of Slovakian chironomid larvae (Diptera: Chironomidae). Part II. Tanypodinae], Belianum, Vydavateľstvo Univerzity Matej Bela v Banskej Bystrici:, 96.

Bitušík, P., M. Svitok, P. Kološta & M. Hubková, 2006. Classification of the Tatra Mountain lakes (Slovakia) using chironomids (Diptera, Chironomidae). Biologia 61(18): 191–201. https://doi.org/10.2478/s11756-006-0131-8.

Bitušík, P., D. Dobríková, R. Pıpík & L. Hamerlík, 2017. Relict chironomid communities surviving in the coldest High Tara Mountain lakes confirmed by a palaeolimnological survey. Biologia 72: 965–969. https://doi.org/10.1515/biolog-2017-0102.

Blenckner, T., 2005. A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533: 1–14. https://doi.org/10.1007/s10750-004-1463-4.

Boggero, A., S. Zaupa, S. Musazzi, M. Rogora, E. Dumnicka & A. Lami, 2019. Environmental factors as drivers for macroinvertebrate and diatom diversity in Alpine lakes: new insights from the Stelvio National Park (Italy). Journal of Limnology 78: 147–162. https://doi.org/10.4081/jlimnol.2019.1863.

Bonacina, L., F. Fasano, V. Mezzanotte & R. Fornaroli, 2023. Effects of water temperature on freshwater macroinvertebrates: a systematic review. Biological Reviews 98: 191–221. https://doi.org/10.1111/brv.12903.

Brodersen, K. P. & N. J. Anderson, 2000. Subfossil insect remains (Chironomidae) and lake water temperature inference in the Sisimiut-Kangerlussuaq region, southern West Greenland. Geology of Greenland Survey Bulletin 186: 78–82. https://doi.org/10.34194/ggub.v186.5219.

Catalan, J., M. Grazia Barbieri, F. Bartumeus, P. Bitušík, I. Botev, A. Brancelj, D. Cogalniceanu, M. Manca, A. Marchetto, N. Ognjanova-Rumenova, S. Pla, M. Rieradevall, S. Sorvari, E. Šťefková, E. Stuchlík & M. Ventura, 2009. Ecological thresholds in European alpine lakes. Freshwater Biology 54: 2494–2517. https://doi.org/10.1111/j.1365-2427.2009.02286.x.

Chomitz, K. & F. Šamaj, 1974. Zrážkové pomery [Precipitation conditions]. in: Konček M. (ed.), Klíma Tatier. Bratislava, Veda: 443–536.

Clarke, A. & K. J. Gaston, 2006. Climate, energy and diversity. Proceedings of the Royal Society B 273: 2257–2266. https://doi.org/10.1098/rspb.2006.3545.

Colwell, R. K., C. X. Mao & J. Chang, 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85: 2717–2727. https://doi.org/10.1890/03-0557.

Domisch, S., M. B. Araújo, N. Bonada, S. U. Pauls, S. C. Jähnig & P. Haase, 2013. Modelling distribution in European stream macroinvertebrates under future climates. Global Change Biology 19: 752–762. https://doi.org/10.1111/gcb.12107.

Dvorak, M., I. L. Dittmann, V. Pedrini-Martha, L. Hamerlík, P. Bitušík, E. Stuchlik, D. Vondrák, L. Füreder & R. Lackner, 2024. Molecular and morphological characterisation of larvae of the genus Diamesa Meigen, 1835 (Diptera: Chironomidae) in Alpine streams (Ötztal Alps, Austria). PLOS One 19: e0298367. https://doi.org/10.1371/journal.pone.0298367.

Fahy, J. C., E. Demierre & B. Oertli, 2024. Long-term monitoring of water temperature and macroinvertebrates highlights climate change threat to alpine ponds in protected areas. Biological Conservation 290: 110461. https://doi.org/10.1016/j.biocon.2024.110461.

Ferrari, S. & F. Cribari-Neto, 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31: 799–815. https://doi.org/10.1080/0266476042000214501.

Fjellheim, A., G. G. Raddum, V. Vandvik, D. Cogalniceanu, A. Boggero, A. Brancelj, J. Galas, F. Šporka, Y. Vidinova, P. Bitušík, E. Dumnicka, N. Galdean, A. Kownacki, I. Krno, E. Preda, G. Risnoveanu & E. Stuchlik, 2009. Diversity and distribution patterns of benthic invertebrates along alpine gradients. A study of remote European freshwater lakes. Advances in Limnology 62: 167–190. https://doi.org/10.1127/advlim/62/2009/167.

Füreder, L., 2007. Life at the edge: habitat condition and bottom fauna of alpine running waters. International Review of Hydrobiology 92: 491–513. https://doi.org/10.1002/iroh.200610987.

Füreder, L., R. Ettinger, A. Boggero, B. Thaler & H. Thies, 2006. Macroinvertebrate diversity in Alpine lakes: effects of altitude and catchment properties. Hydrobiologia 562: 123–144. https://doi.org/10.1007/s10750-005-1808-7.

Giersch, J. J., S. Jordan, G. Luikart, L. A. Jones, F. R. Hauer & C. C. Muhlfeld, 2015. Climate-induced range contraction of a rare alpine aquatic invertebrate. Freshwater Science 34: 53–65. https://doi.org/10.1086/679490.

Gudasz, C., D. Bastviken, K. Steger, K. Premke, S. Sobek & L. J. Tranvik, 2010. Temperature-controlled organic carbon mineralization in lake sediments. Nature 466: 478–481. https://doi.org/10.1038/nature09186.

Gądek, B. A., B. J. Szypuła & M. Szumny, 2020. Classification of the Tatra Mountain lakes in terms of the duration of their ice cover (Poland and Slovakia). Journal of Limnology 79: 70–81. https://doi.org/10.4081/jlimnol.2019.1920.

Hamerlík, L., M. Svitok, M. Novikmec, M. Očadlík & P. Bitušík, 2014. Local, among-site, and regional diversity patterns of benthic macroinvertebrates in high altitude waterbodies: do ponds differ from lakes? Hydrobiologia 723: 41–52. https://doi.org/10.1007/s10750-013-1621-7.

Hamerlík, L., M. Svitok, M. Novikmec, M. Veselská & P. Bitušík, 2017. Weak altitudinal pattern of overall chironomid richness is a result of contrasting trends of subfamilies in high-altitude ponds. Hydrobiologia 793: 67–81. https://doi.org/10.1007/s10750-016-2992-3.

Hansen, G. J. A., J. S. Read, J. F. Hansen & L. A. Winslow, 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology 23: 1463–1476. https://doi.org/10.1111/gcb.13462.

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6.

Heegaard, E., A. F. Lotter & H. J. B. Birks, 2006. Aquatic biota and the detection of climate change: are there consistent aquatic ecotones? Journal of Paleolimnology 35: 507–518. https://doi.org/10.1007/s10933-005-3239-x.

Hock, R., G. Rasul, C. Adler, B. Cáceres, S. Gruber, Y. Hirabayashi, M. Jackson, A. Kääb, S. Kang, S. Kutuzov, A. Milner, U. Molau, S. Morin, B. Orlove & H. Steltzer, 2019. High Mountain Areas. In Pörtner, H. O., D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama & N. M. Weyer (eds), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate Cambridge University Press, Cambridge: 131–202. https://doi.org/10.1017/9781009157964.004.

Hodkinson, I. D. & J. K. Jackson, 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. Environmental Management 35: 649–666. https://doi.org/10.1007/s00267-004-0211-x.

Hotaling, S., A. A. Shah, K. L. McGowan, L. M. Tronstad, J. J. Giersch, D. S. Finn, H. A. Woods, M. E. Dillon & J. L. Kelley, 2020. Mountain stoneflies may tolerate warming streams: evidence from organismal physiology and gene expression. Global Change Biology 26: 5524–5538. https://doi.org/10.1111/gcb.15294.

Ilg, C. & B. Oertli, 2014. How can we conserve cold stenotherm communities in warming Alpine ponds? Hydrobiologia 723: 53–62. https://doi.org/10.1007/s10750-013-1538-1.

Jankowski, T. & G. A. Weyhenmeyer, 2006. The role of spatial scale and area in determining richness-altitude gradients in Swedish lake phytoplankton communities. Oikos

115: 433–442. https://doi.org/10.1111/j.2006.0030-1299.15295.x.

Konček, M. & M. Orlicz, 1974. Teplotné pomery [Temperature conditions] in: Konček, M. (ed.), Klíma Tatier. Bratislava, Veda: 89–179.

Kopáček, J., S. Bičárová, J. Hejzlar, M. Hynštová, J. Kaňa, M. Mitošinková, P. Porcal, E. Stuchlík & J. Turek, 2015. Catchment biogeochemistry modifies long-term effects of acidic deposition on chemistry of mountain lakes. Biogeochemistry 125: 315–335. https://doi.org/10.1007/s10533-015-0127-y.

Kopáček, J., E. Stuchlík, V. Straškrabová & P. Pšenáková, 2000. Factor governing nutrient status of mountain lakes in the Tatra Mountains. Freshwater Biology 43: 369–383. https://doi.org/10.1046/j.1365-2427.2000.00569.x.

Krno, I., 2013. Determinačný kľúč pre hydrobiológov. Časť II. Pošvatky (Plecoptera). [Identification guide for hydrobiologists. Part II. Stoneflies (Plecoptera)], Výskumný ústav vodného hospodárstva, Bratislava:, 64.

Krno, I., F. Šporka, J. Galas, L. Hamerlík, Z. Zaťovičová & P. Bitušík, 2006. Littoral benthic macroinvertebrates of mountain lakes in the Tatra Mountains (Slovakia, Poland). Biologia 61(18): 147–166. https://doi.org/10.2478/s11756-006-0127-4.

Körner, C., 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22: 569–574. https://doi.org/10.1016/j.tree.2007.09.006.

Lamouille-Hébert, M., F. Arthaud & T. Datry, 2024. Climate change and the biodiversity of alpine ponds: challenges and perspectives. Ecology and Evolution 14: e10883. https://doi.org/10.1002/ece3.10883.

Lefcheck, J. S., 2016. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7: 573–579. https://doi.org/10.1111/2041-210X.12512.

Legendre, P. & M. J. Anderson, 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69: 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.

Lencioni, V., 2004. Survival strategies of freshwater insects in cold environments. Journal of Limnology 63(1): 45–55. https://doi.org/10.4081/jlimnol.2004.s1.45.

Lindholm, M., D. O. Hessen, P. J. Færøvig, B. Rognerud, T. Andersen & F. Stordal, 2015. Is distribution of cold stenotherms constrained by temperature? The case of the Arctic fairy shrimp (Branchinecta paludosa O. F. Müller 1788). Journal of Thermal Biology 53: 46–52. https://doi.org/10.1016/j.jtherbio.2015.08.005.

Livingstone, D. M., R. Adrian, L. Arvola, T. Blenckner, M. T. Dokulil, R. E. Hari, G. George, T. Jankowski, M. Järvinen, E. Jennings, P. Nõges, T. Nõges, D. Straile & G. A. Weyhenmeyer, 2010. Regional and Supra-Regional Coherence in Limnological Variables. In George, G. (ed), The Impact of Climate Change on European Lakes. Aquatic Ecology Series Springer, Dordrecht: 311–337. https://doi.org/10.1007/978-90-481-2945-4_17.

Livingstone, D. M. & A. E. Lotter, 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. Journal of Paleolimnology 19: 181–198. https://doi.org/10.1023/A:1007904817619.

Livingstone, D. M., A. E. Lotter & I. R. Walker, 1999. The decrease in summer surface temperature with altitude in Swiss alpine lakes: a comparison with air temperature lapse rates. Arctic, Antarctic, and Alpine Research 31: 341–352. https://doi.org/10.1080/15230430.1999.12003319.

Lods-Crozet, B., B. Oertli & C. T. Robinson, 2012. Long-term patterns of chironomid assemblages in a high elevation stream/lake network (Switzerland)–Implications to global change. Fauna Norvegica 31: 71–85. https://doi.org/10.5324/fn.v31i0.1361.

Loria, K. A., D. McKnight, D. M. Ragar & P. T. J. Johnson, 2020. The life aquatic in high relief: shifts in the physical and biological characteristics of Alpine lakes along an elevation gradient in the Rocky Mountains, USA. Aquatic Sciences 82: 11. https://doi.org/10.1007/s00027-019-0684-6.

Luoto, T. P. & L. Nevalainen, 2013. Climate-driven limnological changes determine ecological thresholds in an alpine lake. Aquatic Biology 18: 47–58. https://doi.org/10.3354/ab00487.

Maberly, S. C., R. A. O'Donnell, R. I. M. E. J. WoolwayCutler, M. Gong, M. I. D. Jones, C. H. J. Merchant, A. C. A. Miller, E. Politi, E. M. Scott, S. J. Thackeray & A. N. Tyler, 2020. Global lake thermal regions shift under climate change. Nature Communications 11: 1232. https://doi.org/10.1038/s41467-019-13993-7.

Magee, M. R. & C. H. Wu, 2017. Response of water temperatures and stratification to changing climate in three lakes with different morphometry. Hydrology and Earth System Sciences 21: 6253–6274. https://doi.org/10.5194/hess-21-6253-2017.

Marra, G. & S. N. Wood, 2011. Practical variable selection for generalized additive models. Computational Statistics & Data Analysis 55: 2372–2387. https://doi.org/10.1016/j.csda.2011.02.004.

Martinez-Sanz, C., C. Fernández-Aláez & F. García-Criado, 2012. Richness of littoral macroinvertebrate communities in mountain ponds from NW Spain: what factors does it depend on? Journal of Limnology 71: 154–163. https://doi.org/10.4081/jlimnol.2012.e16.

McCullagh, P. & J. A. Nelder, 1989. Generalized Linear Models, 2nd ed. Chapman and Hall/CRC, Boca Raton: https://doi.org/10.1007/978-1-4899-3242-6.

de Mendoza, G. & J. Catalan, 2010. Lake macroinvertebrates and the altitudinal environmental gradient in the Pyrenees. Hydrobiologia 648: 51–72. https://doi.org/10.1007/s10750-010-0261-4.

de Mendoza, G., W. Traunspurger, A. Palomo & J. Catalan, 2017. Nematode distributions as spatial null models for macroinvertebrate species richness across environmental gradients: a case from mountain lakes. Ecology and Evolution 7: 3016–3028. https://doi.org/10.1002/ece3.2842.

Moser, K. A., J. S. Baron, J. Brahney, I. A. Oleksy, J. E. Saros, E. J. Hundey, S. Sadro, J. Kopáček, R. Sommaruga, M. J. Kainz, A. L. Strecker, S. Chandra, D. M. Walters, D. L. Preston, N. Michelutti, F. Lepori, S. A. Spaulding, K. R. Christianson, J. M. Melack & J. P. Smol, 2019. Mountain lakes: Eyes on global environmental change. Global and

Planetary Change 178: 77–95. https://doi.org/10.1016/j.gloplacha.2019.04.001.

Motta, L., A. Ruggiero, G. de Mendoza & J. Massaferro, 2019. The species richness-elevation relationship: global patterns of variation in chironomid richness in mountain lakes. Insect Conservation and Diversity 12: 339–350. https://doi.org/10.1111/icad.12341.

Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate* Change 5: 424–430. https://doi.org/10.1038/nclimate2563

Niedrist, G. H. & L. Füreder, 2023. Disproportional vulnerability of mountain aquatic invertebrates to climate change effects. Arctic, Antarctic, and Alpine Research. https://doi.org/10.1080/15230430.2023.2181298.

Niedrist, G. H., R. Psenner & R. Sommaruga, 2018. Climate warming increases vertical and seasonal water temperature differences and inter-annual variability in a mountain lake. Climatic Change 151: 473–490. https://doi.org/10.1007/s10584-018-2328-6.

Novikmec, M., M. Svitok, D. Kočický, F. Šporka & P. Bitušík, 2013. Surface water temperature and ice cover of Tatra Mountains lakes depend on altitude, topographic shading, and bathymetry. Arctic, Antarctic, and Alpine Research 45: 77–87. https://doi.org/10.1657/1938-4246-45.1.77.

Novikmec, M., M. Veselská, P. Bitušík, L. Hamerlík, Z. Matúšová, B. Reduciendo-Klementová & M. Svitok, 2015. Checklist of benthic macroinvertebrates of high altitude ponds of the Tatra Mountains (Central Europe) with new records of two species for Slovakia. Check List 116: 1522. https://doi.org/10.15560/11.1.1522.

Oertli, B., N. Indermuehle, S. Angelibert, H. Hinden & A. Stoll, 2008. Macroinvertebrate assemblages in 25 high alpine ponds of the Swiss National Park (Cirque of Macun) and relation to environmental variables. Hydrobiologia 597: 29–41. https://doi.org/10.1007/s10750-007-9218-7.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs & H. Wagner, 2020. vegan: Community Ecology Package. R package version 2.5–7.

Owens, C. H., M. J. Lee, M. Grim, J. Schroeder & H. S. Young, 2023. Interactions between temperature and predation impact insect emergence in alpine lakes. Ecosphere 14: e4619. https://doi.org/10.1002/ecs2.4619.

Pallarés, S., A. Millán, J. M. Mirón, J. Velasco, D. Sánchez-Fernández, M. Botella-Cruz & P. Abellán, 2020. Assessing the capacity of endemic alpine water beetles to face climate change. Insect Conservation and Diversity 13: 271–282. https://doi.org/10.1111/icad.12394.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8: 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x.

Ray-Mukherjee, J., K. Nimon, S. Mukherjee, D. W. Morris, R. Slotow & M. Hamer, 2014. Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. Methods in Ecology and Evolution 5: 320–328. https://doi.org/10.1111/2041-210X.12166.

Regier, H. A., J. A. Holmes & D. Pauly, 1990. Influence of temperature changes on aquatic ecosystems: an interpretation of empirical data. Transactions of the American Fisheries Society 119: 374–389. https://doi.org/10.1577/1548-8659.

Rogora, M., R. Mosello & S. Arisci, 2003. The effect of climate warming on the hydrochemistry of alpine lakes. Water, Air, and Soil Pollution 148: 347–361. https://doi.org/10.1023/A:1025489215491.

Romdal, T. S. & J. A. Grytnes, 2007. An indirect area effect on elevational species richness patterns. Ecography 30: 440–448. https://doi.org/10.1111/j.0906-7590.2007.04954.x.

Rosset, V. & B. Oertli, 2011. Freshwater biodiversity under climate warming pressure: identifying the winners and losers in temperate standing waterbodies. Biological Conservation 144: 2311–2319. https://doi.org/10.1016/j.biocon.2011.06.009.

Rozkošný, R. (ed.), 1980. Klíč vodních larev hmyzu. [Identification guide of aquatic insects larvae]. Academia, Praha, 521 pp.

Sabás, I., A. Miró, J. Piera, J. Catalan, L. Camarero, T. Buchaca & M. Ventura, 2021. Factors of surface thermal variation in high-mountain lakes of the Pyrenees. PLOS One 16(e0254702): 2. https://doi.org/10.1371/journal.pone.0254702.

Schmidt-Kloiber, A. & D. Hering (Eds.): www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 8.0 (accessed on 05.02.2024).

Shepard, I. D., S. A. Wissinger & H. S. Greig, 2021. Elevation alters outcome of competition between resident and range-shifting species. Global Change Biology 27: 270–281. https://doi.org/10.1111/gcb.15401.

Shipley, B., 2000a. Cause and correlation in biology: a user's guide to path analysis, structural equations, and causal inference, Oxford University Press, Oxford: https://doi.org/10.1017/CBO9780511605949.

Shipley, B., 2000b. A new inferential test for path models based on directed acyclic graphs. Structural Equation Modeling 7: 206–218. https://doi.org/10.1207/S15328007SEM0702_4.

Sommaruga, R., 2001. The role of UV radiation in the ecology of alpine lakes. Journal of Photochemistry and Photobiology b: Biology 62: 35–42. https://doi.org/10.1016/S1011-1344(01)00154-3.

Sommaruga-Wögrath, S., K. A. Koinig, R. Schmidt, R. Sommaruga, R. Tessadri & R. Psenner, 1997. Temperature effects on the acidity of remote alpine lakes. Nature 387: 64–67. https://doi.org/10.1038/387064a0.

Soranno, P. A., K. E. Webster, J. L. Riera, T. K. Kratz, J. S. Baron, P. A. Bukaveckas, G. W. Kling, D. S. White, N. Caine, R. C. Lathrop & P. R. Leavitt, 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. Ecosystems 2: 395–410. https://doi.org/10.1007/s100219900089.

Stur, E. & T. Ekrem, 2006. A revision of Western Palaearctic species of the *Micropsectra atrofasciata* species group

(Diptera: Chironomidae). Zoological Journal of the Linnean Society 146: 165–225. https://doi.org/10.1111/j.1096-3642.2006.00230.x.

Svitok, M., V. Kubovčík, J. Kopáček & P. Bitušík, 2021. Temporal trends and spatial patterns of chironomid communities in alpine lakes recovering from acidification under accelerating climate change. Freshwater Biology 66: 2223–2239. https://doi.org/10.1111/fwb.13827.

Szumny, M., B. Gądek, M. Laska & M. Ciepły, 2022. Thermal sensitivity of high mountain lakes: the role of morphometry and topography (The Tatra Mts., Poland). Water 14: 2704. https://doi.org/10.3390/w14172704.

Thompson, R., C. H. Kamenik & R. Schmidt, 2005. Ultra-sensitive Alpine lakes and climate change. Journal of Limnology 64: 139–152. https://doi.org/10.4081/jlimnol.2005.139.

Velthuis, M., L. N. de Senerpont Domis, T. Frenken, S. Stephan, G. Kazanjian, R. Aben, S. Hilt, S. Kosten, E. van Donk & D. B. Van de Waal, 2017. Warming advances topdown control and reduces producer biomass in a freshwater plankton community. Ecosphere 2017: 8. https://doi.org/10.1002/ecs2.1651.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg & F. Bairlein, 2002. Ecological responses to recent climate change. Nature. 2002(416): 389–395. https://doi.org/10.1038/416389a.

Waringer, J. & W. Graf, 2011. Atlas der mitteleuropäischen Köcherfliegenlarven-Atlas of Central European Trichoptera Larvae, Erik Mauch Verlag, Dinkelscherben, 468 pp.

Werenkraut, V. & A. Ruggiero, 2014. The richness and abundance of epigaeic mountain beetles in north-western Patagonia, Argentina: assessment of patterns and environmental correlates. Journal of Biogeography 41: 561–573. https://doi.org/10.1111/jbi.12210.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis, Springer-Verlag, Berlin.

Winder, M. & D. A. Hunter, 2008. Temporal organization of phytoplankton communities linked to chemical and physical forcing. Oecologia 156: 179–192. https://doi.org/10.1007/s00442-008-0964-7.

Wood, S. N., 2003. Thin-plate regression splines. Journal of the Royal Statistical Society (b) 65: 95–114. https://doi.org/10.1111/1467-9868.00374.

Wood, S. N., 2017. Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC.

Woodward, G., D. M. Perkins & L. E. Brown, 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B 365: 2093–2106. https://doi.org/10.1098/rstb.2010.0055.

Woolway, R. I., M. T. Dokulil, W. Marszelewski, M. Schmid, D. Bouffard & C. J. Merchant, 2017. Warming of Central European lakes and their response to the 1980s climate regime shift. Climatic Change 142: 505–520. https://doi.org/10.1007/s10584-017-1966-4.

Čiamporová-Zaťovičová, Z., L. Hamerlík, F. Šporka & P. Bitušík, 2010. Littoral benthic macroinvertebrates of alpine lakes (Tatra Mts.) along an altitudinal gradient: a basis for climate change assessment. Hydrobiologia 648: 19–34. https://doi.org/10.1007/s10750-010-0139-5.

Łupikasza, E. & B. Szypuła, 2019. Vertical climatic belts in the Tatra Mountains in the light of current climate change. Theoretical and Applied Climatology 136: 249–264. https://doi.org/10.1007/s00704-018-2489-2.

Šporka, F., D. M. Livingstone, E. Stuchlík, H. Turek & J. Galas, 2006. Water temperatures and ice cover in lakes of the Tatra Mountains. Biologia 61(18): 77–90. https://doi.org/10.2478/s11756-006-0121-x.

Šporka, F. (Ed.), 2003. Slovak Aquatic Macroinvertebrates. Checklist and Catalogue of Autecological Notes. Slovenský hydrometeorologický ústav, Bratislava, 590.