Limnological changes in South Carpathian glacier-formed lakes (Retezat Mountains, Romania) during the Late Glacial and the Holocene: a synthesis

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Abstract

Remains of aquatic biota preserved in mountain lake sediments provide an excellent tool to study lake ecosystem responses to past climate change. In the PROLONG project a multi-proxy study was performed on sediments of glacier-formed lakes from the Retezat Mountains, Southern Carpathians (Romania). The studied lakes (Lake Brazi and Gales) are situated on the northern slope of the mountain at different altitudes (1740 m and 1990 m a.s.l.). Our main objectives were 1) to describe the main limnological changes in these lakes during the last ca. 15,000 years and 2) to summarize the environmental history of the studied lakes based on taxonomical and functional patterns of the biological proxies. For this synthesis we used the results of diatom and chironomid analyses, and indirect biotic and abiotic parameters, including sediment organic matter (LOI) content, geochemical element concentrations (Al, Ca, S, Sr) and biogenic silica content. Using multivariate numerical approaches we analysed changes in the assemblage structure of siliceous algae and chironomids, compared temporal patterns among proxies, examined the relationship between potential driving factors, chironomid and diatom assemblage changes and identified paleolimnological phases of the lake successions. Changes in assemblage composition and aquatic ecosystem state apparently followed summer insolation, local climatic conditions and local productivity changes driven by these. Diatom and chironomid assemblages generally changed in a similar direction and at a similar time within a lake, but differed to some extent between Lake Brazi and Gales. At both lakes the strongest variations were observed in the Late Glacial and the first half of the Holocene. The strongest Holocene assemblage changes took place in the earliest Holocene in Lake Brazi, but extened into the mid-Holocene in Lake Gales, following long-term insolation changes and climatic changes. In addition, three common zone boundaries were identified: at ca. 14,200 and at ca. 6500 cal yr BP for every records and at ca. 3100 cal yr BP for diatom records in both of the lakes and for the chironomid record of Lake Brazi. This multi-proxy

synthesis provides comprehensive data that increase our understanding of the past variability of lake ecosystem functioning and biodiversity in East-Central Europe.

Keywords: Chironomidae; Diatoms; geochemical elements; multi-proxy; paleolimnology

Introduction

Lake sediments and the fossils preserved in them are important archives of past environmental, limnological and climatic events and thereby provide us the possibility to understand the natural development of lake ecosystems as well as regional climatic and ecological processes on historic and prehistoric time scales (Battarbee, 2000). Detailed knowledge on recent patterns of species-environment and assemblage-environment relationships may allow inferences about the past environmental circumstances based on biotic assemblages in lake sediment records, and in some cases to establish modern calibration-based quantitative reconstructions of certain environmental variables (e.g. Birks et al., 1990; Walker et al., 1997; Heiri et al., 2011). In order to obtain the most complete and balanced interpretation, many proxy records combined in a multi-proxy study are the most advantageous to evaluate alternative hypotheses and explanations (Birks et al., 1990; Birks and Birks, 2006). Moreover, several proxies are sensitive to human impact, and thus paleoecological records may also supplement the available archaeological information on land use development as well as its effects on terrestrial and aquatic ecosystems (Birks et al., 2014).

In this study we present a paleolimnological synthesis of environmental changes in and around two glacial lakes in the Retezat Mountains (Southern Carpathians) covering the Late Glacial and Holocene. The South Carpathian Mountains received relatively little attention in paleolimnological studies until recently when both local (e.g. Magyari et al., 2009a) and larger scale projects (e.g. Catalan et al., 2009; Heiri et al., 2014) started. Within the multi-

proxy paleoecological project PROLONG (Magyari et al., 2009a) several biotic and abiotic proxies have been studied on sediment cores of four mountain lakes including sediment organic matter (as loss on ignition) and biogenic silica content, geochemical element concentrations, diatoms, chrysophycean cysts, cladocera, ostracods and chironomids (Korponai et al., 2011; Braun et al., 2012; Buczkó et al., 2012; Iepure et al., 2012; Tóth et al., 2012; Buczkó et al., 2013; Soróczki-Pintér et al., 2014; Tóth et al., 2015). In this study we concentrate on proxy records from two lakes on the northern slopes of the Retezat Mountains. We primarily discuss proxies that are available from both lakes and provide information about past limnological changes. These are loss on ignition, biogenic silica content, selected major element concentrations, as well as diatom and chironomid assemblages. A wide range of biotic and abiotic proxies have been analysed from the same sediment cores from two lakes with contrasting hydromorphology and environment. This study therefore provides the opportunity to compare the different proxies and develop a holistic interpretation of the limnological changes during the Late Glacial and Holocene.

Our specific objectives are 1) to describe the most important limnological changes and 2) to summarize the environmental histories of the studied lakes.

Study sites

The Retezat Mountains, located in the South Carpathians, are among the wettest massifs (annual rainfall 1400 mm yr^{-1} at 1500–1600 m a.s.l.) in Romania due to vapour supply by both Mediterranean and Atlantic air masses (Jancsik, 2001; Magyari et al., 2013). The climate of the Retezat is temperate continental modified by a distinct mountain mesoclimate (Spinoni et al., 2015). The mean annual temperature is around +6°C in the foothill zone and -2°C at the top of the mountains (2500 m a.s.l.). At present, July is the warmest and January the coldest

month characterized by mean temperatures of 11.9°C and -5.9°C around Lake Brazi at 1740 m a.s.l. (calculated using CARPATCLIM data for the period 1961–2010, Spinoni et al., 2015). At the elevation of Lake Gales (1990 m), mean July and January temperatures are 10.1 and -6.8°C respectively.

In this study, the multi-proxy results of two sediment profiles are compared. The first was obtained from Lake Brazi (Tăul dintre Brazi, 1740 m, 45°23'47"N, 22°54'06"E; Fig. 1), a small and shallow lake with maximum water depth of 1.1 m and a surface area of 0.4 ha (Magyari et al., 2009a). Nowadays, the lake is oligotrophic, its summer pH ranges between 6.1–6.7 and its conductivity between 10–16 µS cm^{-1} (Magyari et al., 2013; Kövér, 2016). The lake is situated in the subalpine belt, on the western marginal side of the Galeş glacial valley, in a mixed Norway spruce (*Picea abies)* and stone pine *(Pinus cembra)* forest.

Lake Gales (Lacul Galeş, 45°23'6"N, 22°54'33"E) is located in the same valley, but at higher altitude (1990 m a.s.l.), *ca.* 150 m above the timberline in the dwarf pine (*Pinus mugo*) zone. Lake Gales is deeper than Lake Brazi with a maximum depth of 20 m and a surface area of 3.68 ha (Magyari et al., 2009a). Nowadays, the lake is oligotrophic, its summer pH is between 7.1–7.67 and its conductivity is about 16.2–16.4 µS/cm (Magyari et al., 2013; Kövér, 2016). This higher lake has a small inflow and a relatively large outflow.

Methods

Fieldwork and sediment description

From Lake Brazi a 490-cm long sediment core (TDB-1; 111–600 cm depth measured from the water surface) was taken in the central part of the lake (water depth 1.1 m) in August 2007 with a modified Livingstone piston corer (diameter 7 cm). From Lake Gales a 328-cm sediment core (Gales-3; 0–328 cm, measured from the sediment surface) was taken in the

central part of the lake (water depth 19.5 m) using a modified Kullenberg corer (diameter 7 cm; Emery and Broussard, 1954). Gales-3 was drilled in one section using a 4-m long plastic pipe supplied with a piston; therefore, correlation problems between core sections were avoided.

The sediment stratigraphy and organic content record of the lakes investigated were described in detail in Magyari et al. (2009a, 2012), Buczkó et al. (2013) and Hubay et al. (2016).

Chronology

The chronological framework of TDB-1 was established using 21 AMS ^{14}C dates, and suggests that sediment accumulation started prior to 15,000 cal yr BP (at 490 cm sediment depth) and was continuous throughout the Late Glacial and the Holocene (Hubay et al., 2016; and Supplementary Fig. 1).

The chronological framework of Gales-3 was established using 20 AMS ^{14}C dates and relative chronological marker points via the comparison of the Lake Gales and Lake Brazi pollen diagrams (Hubay et al., 2016). The bottom layer at 328 cm is also estimated to be >15,000 cal yr BP old in Lake Gales using a smooth spline age-depth model (see Hubay et al., 2016; and Supplementary Fig. 1). From the Holocene part of this lake a *Pinus* twig dated to *ca*. 2060 cal yr BP at 15 cm sediment depth suggests that the coring started below the sediment surface and therefore, the Gales-3 sediment core likely does not represent the last *ca.* 1800 years (see Hubay et al., 2016).

Loss-on-ignition and geochemical analyses

The total organic matter of the sediment was determined by loss-on-ignition (LOI) at 550°C for 4 hours following Heiri et al. (2001).

For the elemental analyses 1 cm^3 dried samples were digested with 5 mL HNO$_3$ (65%) and 2 mL H$_2$O$_2$ (30%). Acid-soluble element concentrations were determined by inductively coupled plasma optical emission spectrometry (Spectroflame ICP-OES). In a preliminary Principal Components Analysis (PCA) including all of the measured acid-soluble element concentrations, Al, Ca, S and Sr explained the largest amount of variance in the studied lakes. Therefore in the statistical analyses we used these four geochemical elements as potential explanatory variables. Aluminium (Al) is mostly used to indicate intensifying chemical weathering and soil development (podsolization). Calcium (Ca) and sulphur (S) concentrations correlated positively with organic matter content and in association with LOI their increase was used to infer increasing productivity and in case of S, increasing productivity coupled with anoxic environment, mostly increased algal production and peat accumulation (Urban, 1994; Drevnick et al., 2010; Magyari et al., 2009b). Strontium (Sr) accumulates selectively in the needle leaves of Norway spruce (*Picea abies*) (Hubay et al., unpublished data from the Retezat), therefore its concentration increase was used to infer increasing abundance of Norway spruce around the lakes.

For analyses of the biogenic silica (BiSi) fraction, dried and homogenized sediment samples (20 mg) were suspended in 10 cm^3 0.2 mol dm^{-3} sodium hydroxide at 90°C for 2 hours. Silica and aluminium were measured by ICP-OES in case of TDB-1, and aluminium correction was not applied. In Gales-3 aluminium was measured by Microwave Plasma Atomic Emission Spectrometry (4100 MP-AES), while silica content was determined by colorimetry (DR Hach 2000 Spectrophotometer) using the molybdenum blue method (Iler, 1979). Measured silica content was corrected with aluminium in Gales-3 due to the generally low organic content of the sediment that resulted in significant dissolution of the non-biogenic silica in the sodium hydroxide solution.

Diatom analysis

For analyses of the siliceous algae, samples were prepared using standard digestion procedures (Battarbee, 1986). Approximately 350 valves were counted from each sample using a light microscope (LEICA DM LB2 with 100 HCX PLAN APO objective). In this paper, we worked with an amalgamated diatom record. Altogether 46 taxonomical units are used for numerical comparison. Taxa were grouped together mainly on species level *sensu lato*: for some species their varieties and close relatives were regarded as a species complex. Some taxa were merged at the genus level. For more details about the taxonomic harmonization and the diatom flora of Lake Brazi see Buczkó et al. (2012, 2013). The diatom record of Lake Gales is introduced in detail the first time within this issue (Buczkó et al., this issue).

Diatoms were classified into four life form groups: aerophytic (colonizing subaerial or terrestrial habitats); benthic (living at the bottom or shore of the lake, but not attached to living organisms); periphytic (diatoms attached to surfaces) and planktonic taxa.

The diatom records presented here cover a time interval between *ca.* 14,500 cal yr BP and 2007 AD for Lake Brazi and between *ca.* 11,000–1800 cal yr BP for Lake Gales. Diatom remains from samples older than 11,000 cal yr BP had very poor preservation and occurred sparsely in Lake Gales, therefore we did not use this part of the record (for more detail see Buczkó et al., this issue).

Chironomid analysis

Chironomid analysis of Lake Brazi was described in detail by Tóth et al. (2012, 2015). From Lake Gales 2 cm^3 sediment was analysed at 4 cm intervals between 0 and 153 cm and at 2 cm intervals between 153 and 190 cm. Because of the low chironomid head capsule concentration in the Late Glacial section, 2–15 cm^3 sediment were investigated between 190 and 328 cm at

2–8 cm intervals. With this increased sample volume most samples contained > 45 head capsules (except 5 and 20 bottom layers in Lake Brazi and Gales respectively), so they provided representative counts for the quantitative analyses (Heiri and Lotter, 2001). The bottom samples with low chironomid head capsule counts were also included in the analyses since the low number of chironomid remains also provides ecological information (unfavourable conditions for chironomid growth and survival).

Sample preparation followed Walker (2001), while identification of the chironomid head capsules followed Wiederholm (1983), Rieradevall and Brooks (2001) and Brooks et al. (2007).

The chironomid records cover a time interval between *ca*. 15,700 cal yr BP and 2007 AD in Lake Brazi and between *ca*. 15,000–1800 cal yr BP in Lake Gales. The chironomid record of Lake Brazi has been published already (Tóth et al., 2012, 2015), while the record of Lake Gales is presented here for the first time. The chironomid relative abundance diagram of Lake Gales was plotted using the program psimpoll 4.27 (Bennett, 2007). At Lake Gales a July air temperature (T_{VII}) reconstruction calculated on the basis of the available chironomid-temperature inference models from Central Europe (i.e. Alps; Heiri and Lotter, 2010; Heiri et al., 2011) would be strongly affected by edge effects because of the high elevation of the lake. Furthermore, the thermal limits of two dominant chironomids in this record (*Micropsectra radialis*-type and *Pseudodiamesa*) cannot be clearly delimited at the cold end of the temperature gradient in the currently available calibration data (see discussion in Ilyashuk et al., 2011). Therefore, we did not manage to produce a meaningful chironomid-based T_{VII} reconstruction for this lake. On the other hand, a chironomid-inferred T_{VII} reconstruction from Lake Brazi (based on the merged Norway-Swiss calibration dataset) is available (Tóth et al., 2012, 2015), and was included in the numerical analyses.

Plotting and statistical analyses

Due to limited sediment volume, the investigated proxies were sampled from alternating sediment depths in some cases. In order to make them comparable, all proxy records were recalculated to a constant time interval prior to the statistical analyses (Birks and Birks, 2006). A new data set was generated by interpolating the original data to 100 years intervals with the psimpoll 4.27 software (linear fitting; Bennett, 2007). The age gap between the neighbouring sample-pairs in the original data was longer than 100 years only in 20% of the cases, so the chosen 100 years interval resulted in a similar sampling resolution as in the original proxy datasets.

To address study aim 1, diatom and chironomid relative abundance data (without any data transformation) were plotted for each lake and divided into local assemblage zones using psimpoll 4.27 (Bennett, 2007). In order to establish a consistent stratigraphical zonation scheme, the same zonation method was used for the various proxies. This method was CONISS (stratigraphically constrained cluster analysis). All taxa reaching 1% relative abundance at least in one sample were included in the zonation (Grimm, 1987). The significance of each zone was tested using the broken-stick model (Bennett, 2007).

To address study aim 2, we performed partial direct gradient analysis followed by variance partitioning (Cushman and McGarigal, 2002; Peres-Neto et al., 2006) to evaluate the extent that each environmental factor can explain variability in the diatom and chironomid assemblages. Rare taxa with <1% relative abundance were excluded to reduce their disproportionate effect in the multivariate analyses (Legendre and Legendre, 2012). For the statistical analyses diatom and chironomid percentage data were arcsin√x transformed according to the recommended method of handling proportional data ranging between 0 and 1 in ecological studies (Podani, 2000). Proportional environmental variables such as LOI and BiSi were also arcsin√x transformed, while element concentrations (Al, Ca, S, Sr) were lnx

transformed prior to the analyses. Additionally, we used the chironomid-inferred T_{VII} data from Lake Brazi (Tóth et al., 2012, 2015) and the summer insolation data for 45°N (Laskar et al., 2004) as environmental variables, but these data were not transformed. A Detrended Correspondence Analysis (DCA) was used to summarize the major changes in the diatom and chironomid assemblages. DCAs indicated relatively long gradient length (> 2 SD units) in both of the investigated lakes; therefore, we chose Canonical Correspondence Analysis (CCA) for direct gradient analyses (Lepš and Šmilauer, 2003). Altogether four CCAs were run using the diatom and chironomid data sets in Lake Brazi and Gales, respectively. Potential explanatory variables were subjected to a forward stepwise selection procedure (at p <0.05) based on Monte Carlo randomization test with 9,999 unrestricted permutations under the full model. Chironomid-inferred T_{VII} from Lake Brazi (Tóth et al., 2012, 2015) was used as explanatory variable in CCAs using the diatom data, while it was added as a supplementary variable to the CCA plots of the chironomid data in order to see its direction in the ordination space and possible effect without using it in the calculations. Then, a series of CCA and partial CCAs were conducted to partition the effects of significant environmental variables on the diatom and chironomid assemblages (Cushman and McGarigal, 2002). DCA and CCA were performed with CANOCO version 4.5 (ter Braak and Šmilauer, 2002).

To summarize and compare major changes in the diatom and chironomid assemblages of the studied lakes Detrended Canonical Correspondence Analysis (DCCA; ter Braak, 1986) was applied using age as the only constraint. Changes in the first axis scores of DCCA, expressed in standard deviation (SD) units, indicated the amount of taxonomic turnover and allowed the direct comparison of the biotic assemblages (Birks, 2007). DCCA was performed using CANOCO version 4.5 (ter Braak and Šmilauer, 2002).

Results

1. Diatom assemblage zones

Stratigraphically constrained cluster analysis (CONISS) indicated 12 and 7 significant diatom assemblage zones in Lake Brazi (Table 1) and Lake Gales (Table 2), respectively.

We found three common zone boundaries for diatoms in the two lakes around 8900–8700, 6600–6500 cal yr BP and 3100 cal yr BP. Of these, two were accompanied by largely synchronous assemblage changes in the chironomid records of the two lakes at 6900–6300 cal yr BP and in the chironomid record of Lake Brazi at 3200 cal yr BP (Figs 3–4).

In addition to these floristic changes, diatom life forms showed significant shifts in Lake Brazi at *ca*. 9000 cal yr BP (Fig. 3), when the relative abundance of the formerly dominant benthic life forms started to decrease, while planktonic diatoms showed an increasing trend. However, planktonic diatoms became dominant much later, from *ca*. 5900 cal yr BP onwards (Fig. 3). In Lake Gales benthic life forms were dominant until *ca*. 7200 cal yr BP, followed by the relative abundance increase of planktonic life forms (Fig. 4). In addition to the planktonic and benthic diatoms, periphytic life forms reached relatively high abundance in Lake Gales.

2. Chironomid assemblage zones

Altogether 24 chironomid taxa (more than 15,800 head capsules) and 43 chironomid taxa (overall 9200 head capsules) were identified in Lake Brazi (Tóth et al. 2012, 2015) and Lake Gales (Fig. 2), respectively. CONISS indicated 7 significant chironomid assemblage zones in Lake Brazi and 5 in Lake Gales (Tables 1–2). Two common significant zone boundaries were found at 14,200 and at 6900–6300 cal yr BP (Figs 3–4).

3. Diatom and chironomid assemblages - environment relationships

Forward selection resulted in eight environmental variables explaining 46.1% of the total variance, and four environmental variables explaining 33.2% of the total variance in the final

CCA model for the diatom assemblages in Lake Brazi and Gales, respectively (Table 3). For the chironomid records, forward selection resulted in seven selected environmental variables explaining 52.7% of total variance, and six variables explaining 43.5% of total variance in the final CCA model for Lake Brazi and Gales, respectively (Table 3). The analyses suggest that slightly different processes were responsible for the assemblage changes in the two lakes. Most of the investigated environmental variables had significant explanatory power in Lake Brazi (explained variations in either the diatom or chironomid assemblages), while BiSi did not contribute to our models in Lake Gales, and Al and LOI had significant explanatory power only for the chironomid assemblages (Table 3 and Figs 5–6).

Based on the variance partitioning, LOI (total explained variance 24.4%), S (19.4 %) and Al (17.3%) explained the highest amount of variance in the chironomid assemblages in Lake Brazi (Table 3). The CCA biplot indicates that variations in these three variables also correlate with changes in chironomid-inferred temperature from lake Brazi (added as a passive variable; Fig. 5). Al (total explained variance 30.4%), S (29.0%) and LOI (28.2%) had the largest explanatory value in Lake Gales (Table 3). Again, variations in these variables are correlated with July air temperatures from Lake Brazi in the correlation biplot (Fig. 6). 0he highest amount of variance in the diatom assemblages was explained by BiSi (total explained variance 18.9%), summer insolation (17.5%) and Al (14.4%) in Lake Brazi; and by summer insolation (total explained variance 19.4%) in Lake Gales (Table 3). In most cases, the unique effect of the selected variables was relatively low in either the diatom or chironomid assemblages in comparison with the shared effects (Table 3).

In Lake Brazi the first axis of the CCA based on the forward selected variables accounted for 25.2% and 31.1%, while the second CCA axis accounted for 8.8% and 13.9% of the variance in diatom and chironomid assemblages, respectively (Fig. 5). The diatom and chironomid records are clearly divided into Late Glacial and Holocene assemblages along the first CCA

axes. In case of Lake Brazi this separation coincided with variations in Al, LOI, BiSi and chironomid inferred T_{VII} as well as, for diatoms, with summer insolation (Figs. 3 and 5). In Lake Gales the first CCA axis accounted for 20.2% and 32.8%, and the second axis for 8.7% and 5.4% of the variance in the diatom and chironomid assemblages, respectively (Fig. 6). The chironomid assemblage showed again a separation along the first CCA axis into Late Glacial and Holocene assemblages in relation with changing LOI and T_{VII} as well as Al and S concentrations from the Late Glacial into the Holocene (Figs 4 and 6). The diatom record covered only the Holocene (from *ca.* 11,000 cal yr BP onwards), and was divided into Early and Mid to Late Holocene assemblages along the first axis in relation with changes in summer insolation and chironomid inferred T_{VII} (Figs 4 and 6).

4. Comparison of assemblage changes in Lake Brazi and Lake Gales

The first DCCA axes revealed that taxonomic turnover in the chironomid and diatom assemblages (expressed in SD units) was high during the Late Glacial and in the first half of the Holocene for both lakes. SD values for chironomids and diatoms show very similar and largely simultaneous changes within a lake (Fig. 7). The strongest Late Glacial change in chironomid assemblages occurred *ca.* 14,700–13,700 cal yr BP and in Lake Brazi and *ca.* 14,800–14,000 cal BP in Lake Gales. The most pronounced Holocene shifts for both chironomids and diatoms were recorded between *ca.* 11,500 and 9800 cal yr BP in Lake Brazi. In Lake Gales, strong, largely gradual changes were recorded along axis 1 for both chironomids and diatoms in the first half of the Holocene, with the most pronounced shifts at *ca.* 8600–5500 cal yr BP. A distinct change in SD values is apparent for chironomids in Lake Brazi around 3300 cal yr BP. A similar shift is not apparent for chironomids in Lake Gales or in any of the diatom records (Fig. 7).

At Lake Brazi the first (strongest) axis of the DCA of the chironomid record (Fig. 3) strongly correlated with the chironomid-inferred summer air temperatures (r= -0.961; p<0.001), while the first chironomid DCA axis of Lake Gales (Fig. 4) correlated also significantly with the T_{VII} curve of Lake Brazi (r= -0.794, p<0.001) suggesting a similar temperature-related trend in the chironomid assemblages in the two lakes at the millenial time scales examined in this study.

At Lake Gales rheophilic chironomid taxa (e.g. *Diamesa zernyi*-type, *Eukiefferiella fittkaui*-type, *Tvetenia bavarica*-type) occurred in large numbers, especially in the Holocene section, which complicates chironomid-inferred temperature reconstruction based on lacustrine chironomid assemblages. For this reason, and because we expect assemblages in the lake to be affected by edge effects in the available transfer functions (see in Methods/Chironomid analysis above) we did not manage to produce a meaningful chironomid-based T_{VII} reconstruction for this lake.

Discussion

In this study we present the results of a multi-proxy investigation from two glacier-formed lakes located at different altitudes on the northern slope of the Retezat Mountains (Southern Carpathians). Inferences from the multivariate analyses based on several limnological proxy records are discussed in this section in conjunction with the Cladocera and ostracod records described from the Late Glacial sediment of Lake Brazi (Korponai et al., 2011; Iepure et al., 2012).

As indicated by the local assemblage zones, changes in the diatom flora and the chironomid fauna of Lake Brazi and Lake Gales differed from each other. Altogether 151 diatom taxa (more than 63,700 valves) and 200 taxa (ca 25,500 valves) were identified and *ca*. 3500 and 14,000 stomatocysts were also recorded in Lake Brazi and Lake Gales, respectively (Buczkó

et al., 2013; Buczkó et al., this issue). Moreover, the shallow Lake Brazi in the alpine forest belt was characterized by less (24) chironomid taxa than the deep Lake Gales (40 taxa) above the timberline. The most prominent difference in the composition of the chironomid assemblages was the relatively high taxonomic richness of rheophilic taxa in Lake Gales that was missing from Lake Brazi. High diversity and abundances of rheohilic taxa can be observed in alpine lake sediments in situations when in-lake productivity of chironomid remains is very low compared with head capsules of rheophilic forms washed in from inflowing streams or other habitats. This can occur when the runoff of inflowing streams increases. However, such situations can also develop when in-lake populations of chironomid larvae decrease, e.g. due to low oxygen content (Heiri and Lotter, 2003) or very low in-lake primary productivity. Finally, since many rheophilic taxa can also survive in the shallowest littoral region of high alpine lakes, the observed high abundance of rheophilic chironomids could also be explained by a greater extent of the shallowest littoral zone at Lake Gales if, e.g., the water level of the lake decreased. However, even in this case the littoral habitats in the lake would be very limited due to the steep shores of the lake. Furthermore, diatom and chironomid assemblages do not provide clear indications of a lake level shift and significant water table changes would only be possible if the outlet of the lake was inactive during the summer months.

Direct gradient analyses (CCA) revealed that changes in the biotic proxies (i.e. diatoms and chironomids) were closely associated with variations in the considered explanatory variables, particularly with changes in LOI, Al, S, and summer insolation. Passive or active plotting of reconstructed T_{VII} in the CCA diagrams indicated that major assemblage changes in chironomid and diatom assemblages (that covaried with these explanatory variables) also correlated with chironomid-inferred July air temperatures from Lake Brazi (Figs 5–6). This correlation was weakest for the diatom record of Lake Brazi (Fig. 5).

DCCA analyses also revealed that the timing and direction of shifts in diatom flora and chironomid fauna for a given site were largely similar, at least for the Holocene sections of the records (Fig. 7). Whereas the strongest changes in Lake Brazi took place in the earliest Holocene, shifts in Lake Gales were more delayed and extended into the mid-Holocene. Additionally, we identified zone boundaries at *ca.* 14,200 cal yr BP, 6900–6300 cal yr BP for every records and at *ca.* 3100-3200 cal yr BP for diatom records in both of the lakes and for chironomid record of Lake Brazi, which occurred with a very similar timing in all of the records (Figs 3–4). We suppose that in these time periods assemblage changes were triggered by a common factor.

In the following section we discuss these results in an attempt to determine the driving factors and most important shifts in the limnic ecosystems. We also provide a synthesis of the limnological conditions and their changes in the two lakes.

1. Driving factors for Late Glacial and Holocene aquatic ecosystem states and assemblage shifts

The CCA results suggest that changes in the Late Glacial and Holocene chironomid assemblages were strongly related to local productivity changes that in turn coincide with long-term changes in summer insolation and summer temperature in Lake Brazi and Lake Gales (Table 3, Figs 3, 5–7). These changes were apparently modified by local habitat changes. For example, the high explanatory power of S for changes in chironomid assemblages could be explained by increasing extent of lakeshore mire habitats around the lake and increasing green algal production as we have shown in earlier studies (Urban, 1994; Drevnick et al., 2010; Magyari et al., 2012; Buczkó et al., 2012). Rich sources of labile carbon likely stimulated dissimilatory sulfate reduction and the produced sulphide was trapped in the sediment (Urban, 1994). Chironomid DCA axis 1 scores, Al concentrations, LOI (Fig. 3) and

turnover values along DCCA axis 1 (Fig. 7) for Lake Brazi showed the strongest change between 11,000 and 10,000 cal yr BP, starting synchronously with the strongest increase in chironomid inferred T_{VII} registered in the Holocene. This change occurred about 700 years after the Younger Dryas to Holocene transition (at *ca*. 11,700 cal yr BP; Blockley et al., 2012) when the strongest temperature increase and pronounced changes are usually recorded in Late Glacial to Holocene chironomid records from Europe (e.g. Brooks and Birks, 2000; Ilyashuk et al., 2009; Hájková et al., 2016). Together, these changes suggest that changes in chironomid assemblages and local summer climate were driven by macroclimate, but with some delay (Tóth et al., 2015, 2015). This reorganization of the chironomid fauna continued for ~1000 years coinciding with increasing chironomid-inferred temperatures (Fig. 3) and likely strongly reinforced by biotic forcing (terrestrial vegetation reorganisation and local productivity increase). Similar relationships were found between external variables and DCA axis 1 scores in Lake Gales (Fig. 4). Here Al concentration changes reflect the intensity of chemical weathering, and show a rapid increase in the Early Holocene, which however continues until 7000 cal yr BP (Fig. 4). LOI and turnover values show a similar trend suggesting that productivity increase and related faunistic changes were ongoing in the higher altitude lake until the decrease of summer insolation in the mid-Holocene (Figs 4 and 7). The strong explanatory value of Al and LOI in the CCA of chironomid assemblages (Fig. 6) is thus best interpreted by the gradual increase in biological productivity in this high altitude system lagging the Early Holocene insolation increase, similarly as the local temperature development increase (T_{VII}, Figs 3–4). Similar inferences can be drawn from the DCA and CCA analyses of the diatom assemblages. For Lake Gales, diatom assemblage changes following the long-term trends in summer insolation were clearly indicated by the CCA biplot (Fig. 6). The productivity of diatoms was however not simply temperature (T_{VII}) dependent (see Figs 3–4). Siliceous algae can be competitive in cold oligotrophic environments

(Reynolds, 1984), thus it is not surprising that the BiSi inferred maximum production has an Early and a Late Holocene maximum (10,500-9500 and after 5400 cal yr BP; Fig. 3). In the first case, the Early Holocene warming facilitated the establishment of new taxa and habitat diversification in Lake Brazi (see Magyari et al. 2012; Orbán et al., this issue). These factors certainly favoured increasing diatom productivity. From 5400 cal yr BP the increase of planktonic habitats (either driven by seasonal water-depth increases or increasing wind turbulence, see Buczkó et al., this issue) seemingly led to an overall diatom population growth with related assemblage shifts starting already 6500 cal yr BP (Fig. 3, TDB-d9 and d-10). The driving factors of the diatom assemblage changes in Lake Gales were similar to Lake Brazi during the Holocene. Although this record lacks a meaningful diatom productivity record (BiSi was biased, see Buczkó et al., this issue), assemblage changes related to changes in summer insolation in the CCA (Fig. 6), and diatom assemblage zones also reflected the rapid reorganization of the diatom flora in the Early Holocene (Table 2), until terrestrial ecosystems and slopes stabilized around this high-altitude lake.

Overall, we conclude that changes in the studied aquatic proxies mainly followed summer insolation in both mountain lakes in the Retezat Mountains but with some delays in the early part of the Holocene also reflected in the local summer temperature development as reconstructed by chironomids (Tóth et al., 2012, 2015). Two further important shifts in the aquatic systems were identified between 6900–6300 cal yr BP and between 3300–3000 cal yr BP (Figs 3–4 and 7). Both of these may be connectable to the decreasing summer insolation driven ecosystem reorganizations that in the Southern Carpathians exerted the strongest change in the aquatic ecosystems at these times. In comparison with the Neoglacial cooling in NW Europe (e.g. Dahl-Jensen et al., 1998), the 3000 cal yr BP dates compares well with the onset of rapid advances and retreats of sea ice at the continental margin of West Spitsbergen (Müller et al., 2012) but lags the Greenland temperature curve (Dahl-Jensen et al., 1998) and

the earliest indication of neoglaciation in the Alps (e.g. Leemann and Niessen, 1994; Ivy-Ochs et al., 2009), by several centuries.

A further important shift in the lake ecosystems occurred between 14,700–14,500 cal yr BP associated with the beginning of the Late Glacial Interstadial. This change is well-expressed in the chironomid DCA axis 1 scores in both of the lakes and in the chironomid-inferred T_{VII} reconstruction from Lake Brazi (Figs 3–4). This time period is related to the transition from GS-2 to GI-1 in the Greenland ice core $\delta^{18}O$ record (Björck et al., 1998; Rasmussen et al., 2006) and it has been noted in various other proxy records (e.g. Andric et al., 2009; Płóciennik et al., 2011; Lotter et al., 2012). Before 14,700 cal yr BP only a few biological remains (both diatoms and chironomids) were found. This observation could be related to very low organic matter content and extremely cold temperature (Figs 3–4). After *ca.* 14,500 cal yr BP the number of remains started to increase in parallel with gradually increasing summer insolation and increasing chironomid-inferred summer temperatures that indicated altering environment in the lakes (Figs 3–4).

2. Succession of the aquatic systems

2.1. 15,700–14,200 cal yr BP: cold oligotrophic lake conditions

All of the examined biological remains were characterized by very small concentrations and especially the diatoms with poor preservation in the sediments suggesting that Lake Brazi may have been a temporal pond after its formation until *ca*. 14,500 cal yr BP (Figs. 3–4; Buczkó et al., 2013).

A prominent change was observed in the lakes around 14,700–14,500 cal yr BP, when the concentration and preservation of the biological remains started to increase, indicating more stable conditions. The most probable driving factor of the changes at *ca.* 14,700 cal yr BP was climatic warming coinciding with the beginning of the Late Glacial Interstadial (or

Bølling/Allerød) as defined in Central Europe (e.g. Lotter et al., 1992) as well as the GS-2/GI-1 transition apparent in the Greenland ice core records (Björck et al., 1998; Fig. 3). This warming is also clearly apparent in the chironomid-inferred T_{VII} record from Lake Brazi (Fig. 3).

The scarcity of biological remains together with low organic content of the sediment and dominance of cold stenothermic chironomid taxa typical for nutrient poor environments (*Pseudodiamesa*, *Diamesa zernyi*- and *Micropsectra radialis*-type support cold oligotrophic conditions) in the studied lakes until *ca.* 14,200 cal yr BP. The dominance of benthic and alkalophil diatoms indicates shallow and slightly alkaline conditions prevailed in Lake Brazi (Buczkó et al., 2013).

2.2. 14,200–11,700 cal yr BP: seasonality changes

This time interval covers the younger part of the Bølling/Allerød interstadial (correlated with GI-1 in the Greenland ice core records; Björck et al., 1998) and the Younger Dryas (or GS-1 in the Greenland ice core records; Björck et al., 1998) until the onset of the Holocene. Dominant chironomid taxa (Table 1) indicate warmer but still cool and oligotrophic lake conditions and the reconstructed T_{VII} at Lake Brazi shows an increasing trend until *ca.* 13,700 cal yr BP followed by stagnant temperatures (at around 8.3°C) until *ca.* 11,700 cal yr BP (Tóth et al., 2012; Fig. 3).

One of the most characteristic events at this time is the well-defined cooling at the Younger Dryas (GS-1; Björck et al., 1998). In Lake Brazi a clear faunistic turnover was detected in the chironomid assemblages between *ca.* 12,800–11,500 cal yr BP (Fig. 7; dominance of *Micropsectra insignilobus*-type), but this change appeared just weakly in the inferred July air temperatures (by *ca.* 1°C; Tóth et al., 2012). Additionally, analysis of Late Glacial treelines (Magyari et al., 2009b) suggests that Lake Brazi remained within the treeline ecotone during

the Younger Dryas, also indicating only moderate cooling. In Lake Gales we did not find any clear change in the chironomid assemblages during GS-1 (Table 2), also supporting relatively minor climatic impacts on the lake during this time. Similarly, the GS-1 stadial did not appear clearly in the cladoceran record of Lake Brazi. However, assemblage changes and increased ostracod abundance indicate increasing productivity and turbidity in the lake during this episode (Korponai et al., 2011; Iepure et al., 2012). A weak response of chironomids to the GS-1 cooling has been reported before from Central Eastern Europe (see Płóciennik et al., 2011) and corresponds well with climate model simulations of Renssen and Isarin (2001). These results as well as supporting proxy evidence (Renssen and Isarin, 2001; Heiri et al. 2014) suggest that the amplitude of summer cooling was highest along the North Atlantic margin of Europe and towards the north and decreased towards the interior of the European continent and towards the south. A recently published multi-proxy study from Eastern Slovakia (49°N) indicates that in more northerly localities in the Carpathians a distinct warming at the Younger Dryas to Holocene transition occurred (Hájková et al., 2016).

In contrast with the relatively weak response of cladocerans and chironomids, the acidophilous diatom *Stauroforma exiguiformis* showed a rapid increase in the diatom assemblages of Lake Brazi between *ca.* 12,900 and 12,500 cal yr BP (onset of GS-1), on the basis of which decreasing pH values were reconstructed (Fig. 3; Buczkó et al., 2012). This abrupt decrease in inferred pH was most likely the result of a seasonality shift, which caused longer and colder winters and thus prolonged winter ice cover for the first half of GS-1, while summer temperature conditions changed only slightly in the South Carpathians (Buczkó et al., 2012) and in Central Eastern Europe (Heiri et al., 2014; Renssen et al., 2015). In the second part of the GS-1 cooling episode, between *ca.* 12,500–11,200 cal yr BP, the diatom assemblages changed again (Table 1), and indicated cold and slightly alkaline shallow water conditions with increasing diatom-inferred pH. This likely mark a decrease in winter ice-

cover length and moderate increase in lake productivity (Buczkó et al., 2012, 2013).

Additionally, the largest Al concentration was observed during the second part of the GS-1

stadial (Fig. 3) suggesting enhanced clastic inwash at Lake Brazi. A similar division of the

GS-1 cooling with changing climatic conditions in the second half of the event was described

from Western and Northern Europe (e.g. Birks et al., 2000, 2012) and from the Eastern

Carpathians (Hájková et al., 2016).

2.3. Between ca. 11,700–10,350 cal yr BP: increasing productivity with general warming

At the onset of the Holocene, the diatom assemblages did not show any significant floristic

change, but diatom productivity (BiSi) and LOI increased gradually indicating increasing

productivity in and around Lake Brazi (Buczkó et al., 2013). This productivity increase was

supported also by a cladoceran increase (*Alona affinis*), chironomid assemblage changes (first

appearance of Chironomini) and by an increase in the abundance of green algae (*Pediastrum*

spp.) reflecting warmer water and summer air temperatures (Korponai et al., 2011; Tóth et al.,

2015). Similarly, the chironomid record of Lake Gales changed also notably. The decreasing

and disappearing cold-stenothermic taxa (*Pseudodiamesa* and *Micropsectra radialis*-type) at

ca. 11,800 cal yr BP indicate a remarkable alteration in the lake's condition likely due to

warming and/or to productivity increase reflected in slightly increasing LOI values.

Moreover, Al concentrations started to increase in Lake Gales also at the onset of the

Holocene (Fig. 4) and showed strong positive correlation with organic matter content (r=0.94,

p<0.001), while in the sediment of Lake Brazi Al concentration dropped at *ca.* 11,000 cal yr

BP notably (with sharply increasing LOI values in this lake). Al concentrations likely

increased in Lake Gales due to intensifying chemical weathering, soil development

(podzolisation) and Al-leaching at this high altitude during the Holocene, while at lower

altitude (at Lake Brazi) soil development started earlier and the diluting effect of the organic content resulted in the lower concentrations (see Figs 3–4; Hubay et al., 2016).

In summary, the marked changes at *ca.* 11,700-10,350 cal yr BP, appeared in most of the available proxy records from the lakes and were apparently driven by changing climatic conditions: At ca. 11,700 cal yr BP changes were most likely due to temperatures during seasons other than summer and/or hydrology and from *ca.* 11,000 cal yr BP onwards also due to a distinct increase in summer temperature. In the quantitative analyses (zonation, DCCA, DCA) the above summarized changes in the aquatic biota mainly appear as significant variations in DCA axis 1 scores, several assemblage zones within this period (especially in Lake Brazi), and major increases in the DCCA axis 1 turnover values (Figs 3–4).

2.4. Between ca. 10,350–9000 cal yr BP: generally warm conditions

It is now well-recognized that the climate of the Holocene also featured significant climatic events (e.g. Bond et al., 1997; Wanner et al., 2011). However, after the rapid warming of the end of the Younger Dryas, climatic variations in the Holocene were more muted than during the Lateglacial period. Since Holocene climate changes were characterized by relatively small amplitudes, several other environmental (limnological) factors (e.g. pH, trophic conditions, water depth, etc.) could have stronger effect on the lake ecosystems than temperature (e.g. Brooks, 2006; Velle et al., 2010). Therefore, mid to late Holocene assemblage changes in mid-latitude mountain lakes may be related to different and multiple local and regional factors.

The zone boundary at *ca.* 10,350 cal yr BP appears only in Lake Brazi, where the occurrence of acidophilous diatoms (e.g. *S. exiguiformis*, *Eunotia exigua*) and *Sphagnum*-bog associated plant macrofossils indicated decreasing pH and bog-expansion on the lakeshore until *ca.* 9700 cal yr BP (Buczkó et al., 2013). Decreasing pH was also supported by the cladoceran

assemblages via the notable decrease of daphnids (Korponai et al., 2011). From *ca.* 10,350 cal yr BP warm stenothermous chironomid taxa characterized this lake and lake productivity apparently increased as indicated by chironomid assemblages, Ca and S concentration peaks and high LOI values. At the same time, relative abundances of ostracods decreased notably, while *Chaoborus* mandibles reached relatively high concentrations indicating shallow and dystrophic environment in Lake Brazi (Korponai et al., 2011; Iepure et al., 2012). Similarly, in the higher lake, Lake Gales, diatom assemblages (e.g. high relative abundance of *Humidophila schmassmannii*) together with increasing LOI values indicate relatively warm conditions for this period, with low, but increasing nutrient content and with the prevalence of benthic taxa. Additionally, increasing Sr concentration apparently reflect increasing abundance of *Picea abies* around the lake as is supported by the plant macrofossil record (Orbán et al., this issue).

All of the changes mentioned above coincide with the summer insolation maximum at 45°N at *ca.* 9000 cal yr BP (Fig. 3) and with the Holocene Summer Thermal Maximum, which dates between *ca.* 9400–8900 cal yr BP at Lake Brazi (Tóth et al., 2015). These high summer temperatures were likely driving the temperature and productivity increase in the lakes and are probably also responsible for the decreasing water levels in the Carpathian Mountains (e.g. Feurdean et al., 2008; Magyari et al., 2009b) and in the Carpathian basin as well (Jakab and Sümegi, 2007).

2.5. Between ca. 9000–6500 cal yr BP: increasing productivity

From *ca.* 9000 cal yr BP the chironomid record suggests warm conditions with increasing lake productivity (Table 1), which coincided with increasing LOI values and increasing Ca and S concentrations in Lake Brazi. Moreover, diatoms show gradually decreasing water

depth until *ca.* 8400 cal yr BP and slightly increasing productivity in the lake (Buczkó et al., 2013).

At 8150 cal yr BP a distinct lake-level rise was described by diatoms, most likely associated with the 8.2 ka event (Buczkó et al., 2013). This short-term cooling is well-documented in the Carpathian region (Płóciennik et al., 2011; Feurdean et al., 2008; Hájková et al., 2016). However, the chironomid records of the investigated lakes did not show any responses to the 8.2 ka event which may be associated with the more southerly location of these lakes in comparison with other studied localities. In Lake Gales the diatom and chironomid assemblages indicated deep and oligotrophic conditions for this tine, while LOI reached relatively high values but was generally lower than in Lake Brazi. The chironomid taxonomic richness reached the highest values from *ca.* 8400 cal yr BP onwards in Lake Gales, due to the appearance of several Orthocladiinae taxa that occur often in the surf zone of lake littorals (Table 2). This could be related to increase in runoff of inflowing stream and thus increased water current at Lake Gales.

2.6. Between ca. 6500–3100 cal yr BP: decreasing productivity

Between *ca.* 6500 and 3100 cal yr BP increasing planktonic diatom relative abundances (mainly of *Aulacoseira* taxa) with slightly increasing BiSi values support increasing water level and/or water turbulence in Lake Brazi. At the same time, LOI and diatom-inferred total phosphorous (Buczkó et al., 2013) started to decrease indicating a drop in lake productivity that coincided with slightly decreasing summer air temperatures inferred by chironomids (Fig. 3; Tóth et al., 2015). In Lake Gales planktonic diatoms did not increase notably at 6500 cal yr BP, but the relative abundance of benthic diatoms decreased, leading to similar abundances of planktonic and benthic life forms (Fig. 4). Altogether the diatom (increasing *Aulacoseira* taxa abundance) and the chironomid (increase in *Heterotrissocladius marcidus*-type) record are in

agreement with deep, cool and oligotrophic lake conditions in Lake Gales (Table 2). Increasing lake levels or increased water turbulence in the investigated lakes would agree with summer cooling and increased moisture in the Eastern Carpathians (e.g. Schnitchen et al., 2006; Magyari et al., 2009b) and in the Carpathian basin (e.g. Jakab and Sümegi, 2007) during this mid Holocene period.

2.7. From ca. 3100 cal yr BP until present: increasing human impact

A significant zone boundary was found at *ca.* 3100 cal yr BP based on the diatom records in both of the lakes and the chironomid record of Lake Brazi (Figs 3–4). At Lake Gales chironomid assemblages were dominated by the same taxa as in the previous phase and together with diatoms (mainly planktonic *Aulacoseira* taxa) supported continuous deep oligotrophic lake conditions. In addition, rheophilic chironomid taxa were present continuously (since *ca.* 10,000 cal yr BP) and possibly indicated stronger water currents from the inflows that may also have increase transport of rheophilic remains to the lake. Higher precipitation would also agree with increased water level as suggested by the diatom flora. During the last 1500–2000 years, diatoms of Lake Brazi indicate eutrophication (Buczkó et al., 2013) that was supported by the chironomid assemblage as well (Tóth et al., 2015). At Lake Gales our sediment record stopps at *ca.* 1800 cal yr BP and does not cover this interval. Generally, in the last 2000 years intensified human land use is reported from the Carpathian region (Feurdean et al., 2008) and the pollen records from both lakes support also intensified land-use in the Retezat Mountains (Orbán et al., this issue). On the souther slope, of these mountains signs of human activity appeared even earlier, from *ca.* 4200 cal yr BP onwards as registered by pollen, macrofossil, and stomata records (Orbán et al., this issue; Vincze et al., in press). Changes of the terrestrial vegetation indicate that humans started to use the alpine meadows at Lake Bucura for pasturing from *ca.* 4200 cal yr BP (Orbán et al., this issue;

Vincze et al., in press). Recent studies revealed that spreading of human land use was a slow process in the region. Its earliest evidences appeared in the alpine area of the Retezat Mountains at Lake Bucura (2040 m a.s.l.) and at Lake Gales (at 1990 m a.s.l.; Orbán et al., this issue). At Lake Lia (at 1910 m a.s.l. on the southern slope), human land-use was detected later, from *ca.* 2700 cal yr BP and was associated with intensified burning of the open shrubland around the lake (Vincze et al., in press). At the subalpine Lake Brazi (at 1740 m a.s.l.), human impact was only detected in the last 1500 years when occasional cutting of the local spruce forests was evidenced. Moreover, pasturing of domesticated animals (sheep, cattle, horse) in the nearby Gales valley has also been reported (Maderspach, 1986). These human activities apparently also influenced limnological processes in the studied lakes; however, aquatic indicators marked this effect only in the last 2000 years when human impact reached its highest intensity.

Conclusions

In this study we present a paleolimnological synthesis from the northern slope of the Retezat Mountains (South Carpathians). Our results indicated that the most important changes in lake conditions and the succession of the aquatic ecosystems followed summer insolation, local climatic conditions and local productivity changes driven by these. At the formation of the investigated lakes (at *ca.* 15,700 and 15,000 cal yr BP) sporadic and poor preservation of the biotic proxies indicated unfavourable lake conditions. The lake and its environment changed substantially between *ca.* 14,700–14,500 cal yr BP when the proxy records indicated cool and oligotrophic lake conditions during the Late Glacial. One of the most prominent events of the Late Glacial is the Younger Dryas cooling (between *ca.* 12,900–11,700 cal yr BP) that showed a clear seasonal shift in the South Carpathians. Our data suggest that it was manifested primarily in longer and colder winters, while summer temperatures changed only

slightly. From the onset of the Holocene (*ca.* 11,700 cal yr BP) onwards the investigated lakes showed general warming and increasing productivity until the Late Holocene when (during the last *ca.* 2000 years) slightly increasing human impact affected the natural lake successions.

The available proxy records suggest that although the fossil flora and fauna of the two lakes differed, they still changed in the common general direction but with differences in timing of the environmental changes. This common pattern is likely related to long-term insolation-driven changes in climatic conditions that are difficult to separate from the limnological processes driven by in-lake processes. All together four major shifts aquatic ecosystem state were observed: at *ca.* 14,700–14,500; 11,000–10,000; 6900–6300 and 3300–3000 cal yr BP.

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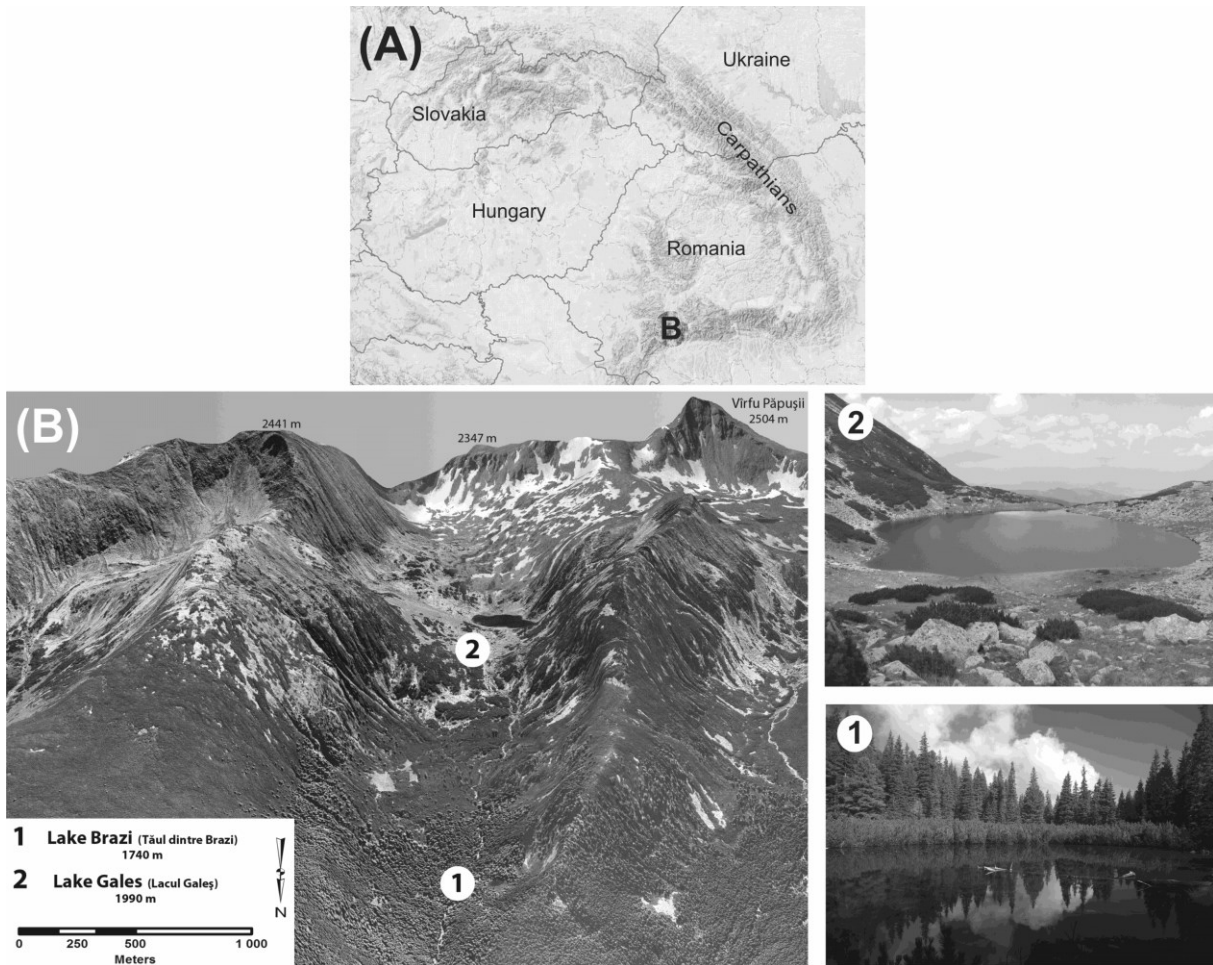
Fig. 1. The location of the Retezat Mountains (B) in the Southern Carpathians (A) and location and view of (1) Lake Brazi (1710 m a.s.l.) and (2) Lake Gales (1990 m a.s.l.) on the northern slope of the Retezat Mountains (B). http://maptive.com/

Fig. 2. Chironomid relative abundance diagram (including selected chironomid taxa with relative abundances > 1%) with chironomid concentration (remains cm^{-3}), and significant zones for the chironomid stratigraphy of Lake Gales (Southern Carpathians).

Fig. 3. First DCA axis scores (SD units) and significant assemblage zones of the diatom (TDB-d 1-11) and chironomid (TDB-ch 1-7) records plotted together with selected explanatory variables (Table 3) in Lake Brazi (Southern Carpathians): relative abundance of the dominant (benthic, planktonic and periphytic) diatom life forms, loss-on-ignition (LOI), biogenic silica content (BiSi), Al, Ca and S concentrations, summer insolation at 45°N

(Laskar et al., 2004) plotted together with chironomid-inferred July air temperature based on a merged Norwegian-Swiss training set (black line: temperature reconstruction, grey lines: sample-specific standard errors; Tóth et al., 2012, 2015) and diatom inferred pH and total phosphorous (TP) reconstructions from Lake Brazi (Buczkó et al., 2013).
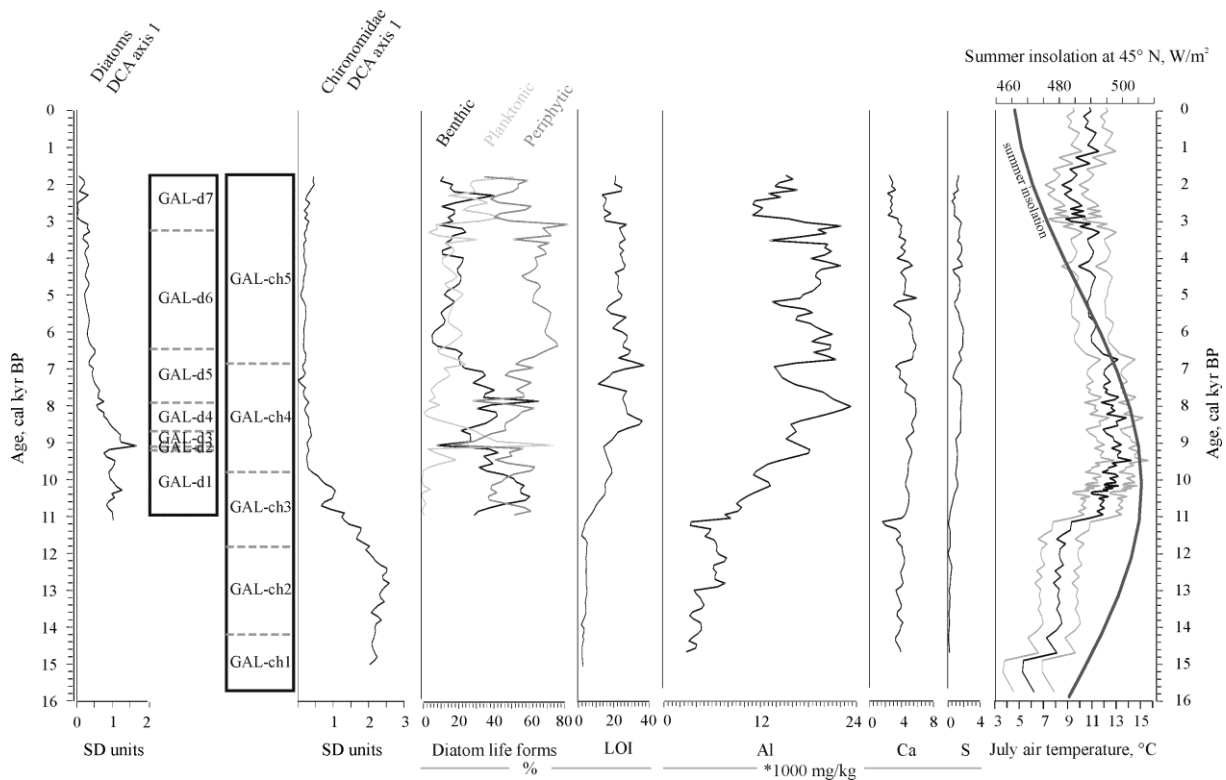

Fig. 4. First DCA axis scores (SD units) and significant assemblage zones of the diatom (GAL-d 1-7) and chironomid (GAL-ch 1-5) records plotted together with selected explanatory variables (Table 3) in Lake Gales (Southern Carpathians): relative abundance of the dominant (benthic, planktonic and periphytic) diatom life forms, loss-on-ignition (LOI), Al, Ca and S concentrations, summer insolation at 45°N (Laskar et al., 2004) plotted together with chironomid-inferred July air temperature from Lake Brazi based on a merged Norwegian-Swiss training set (black line: temperature reconstruction, grey lines: sample-specific standard errors; Tóth et al., 2012, 2015).
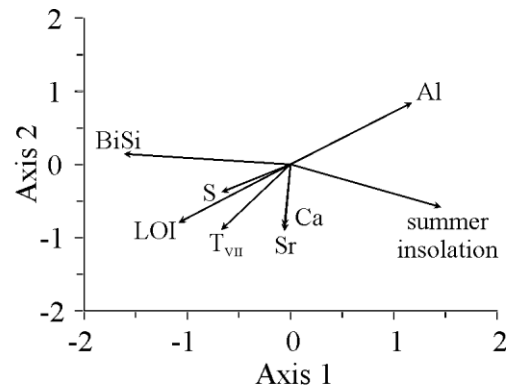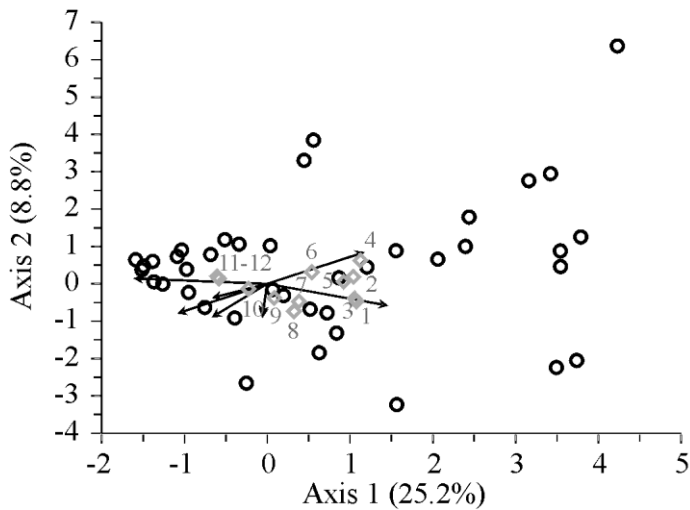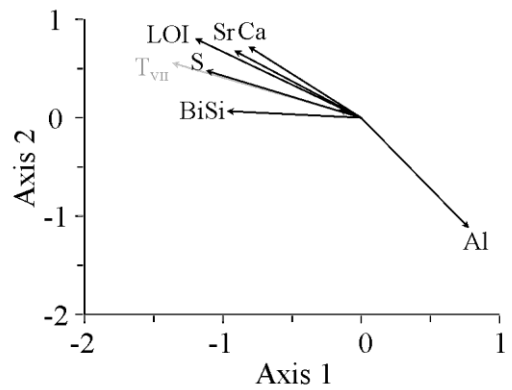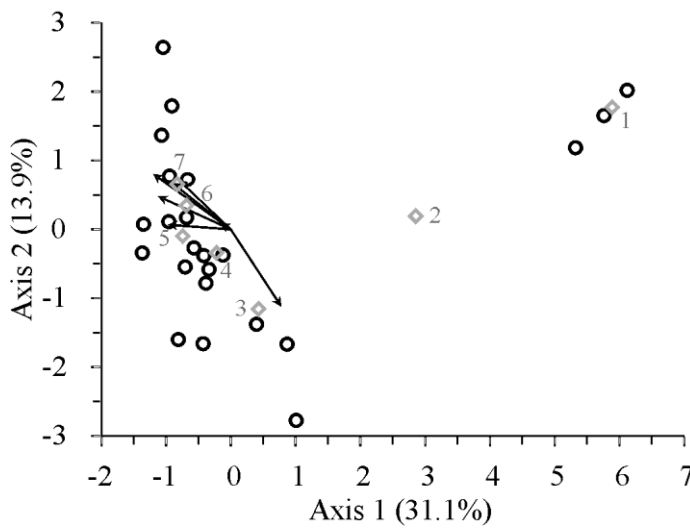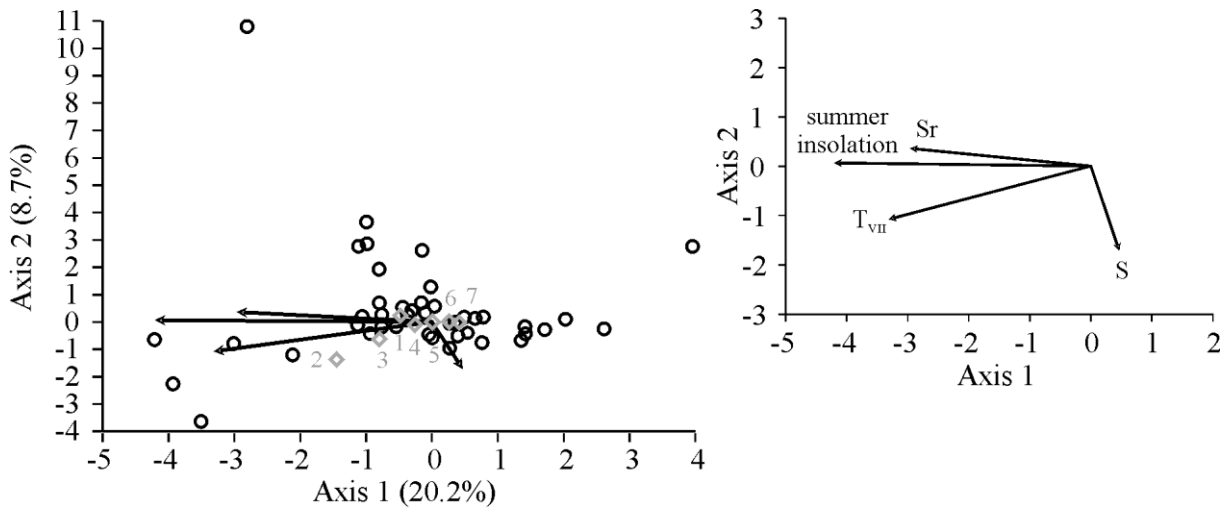
Fig. 5. Results of a canonical correspondence analysis (CCA) describing the relationships between the significant explanatory variables (Table 3) and diatom and chironomid assemblages in Lake Brazi (Southern Carpathians). The grey numbers indicate the centroids of the statistically significant assemblage zones of the diatom and chironomid assemblages, respectively. Percentage variances of species data explained by the axes are indicated in brackets after the axis name. Chironomid-inferred July air temperature reconstruction (T_{VII}) was plotted passively (as supplementary variable) in the chironomid CCA biplot.
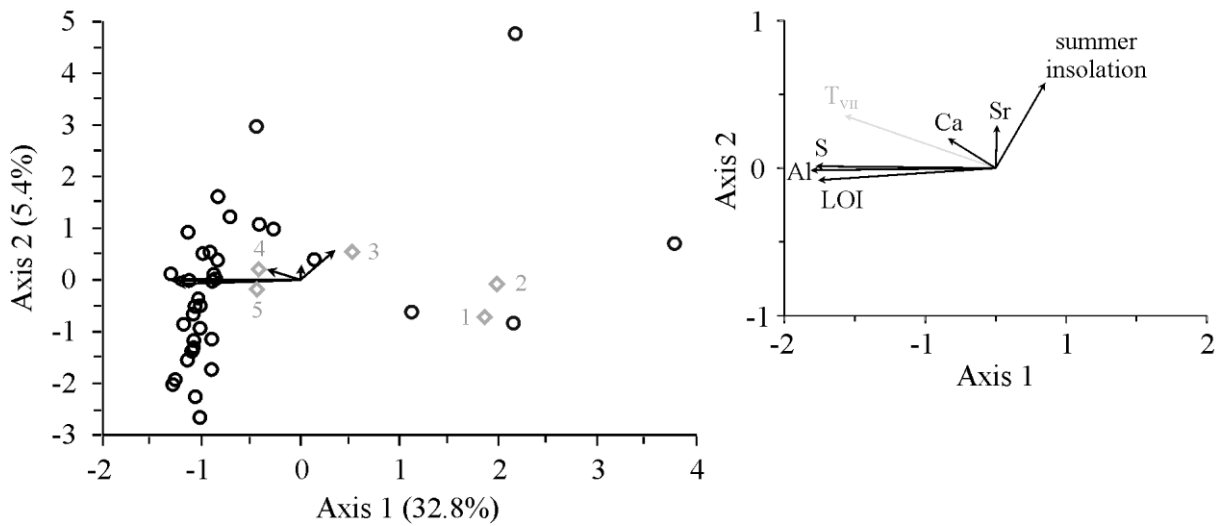
Diatoms

Chironomidae

Fig. 6. Results of a canonical correspondence analysis (CCA) describing the relationships between significant explanatory variables (Table 3) and diatom and chironomid assemblages in Lake Gales (Southern Carpathians). The numbers indicate the centroids of the statistically significant diatom and chironomid assemblage zones. Percentage variances of species data explained by the axes are indicated in brackets after the axis name. Chironomid-inferred July air temperature reconstruction (T_{VII}) was plotted passively (as supplementary variable) in the chironomid CCA biplot.
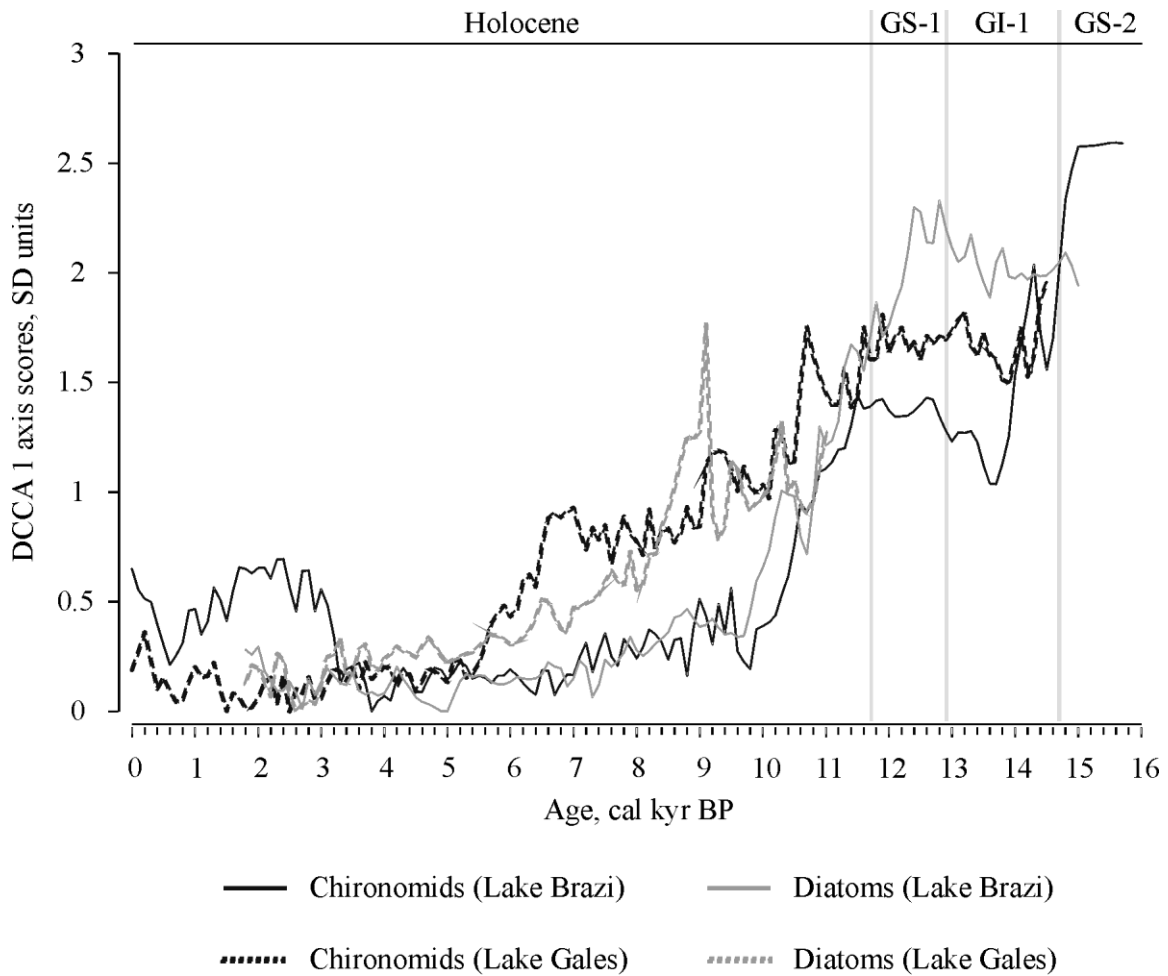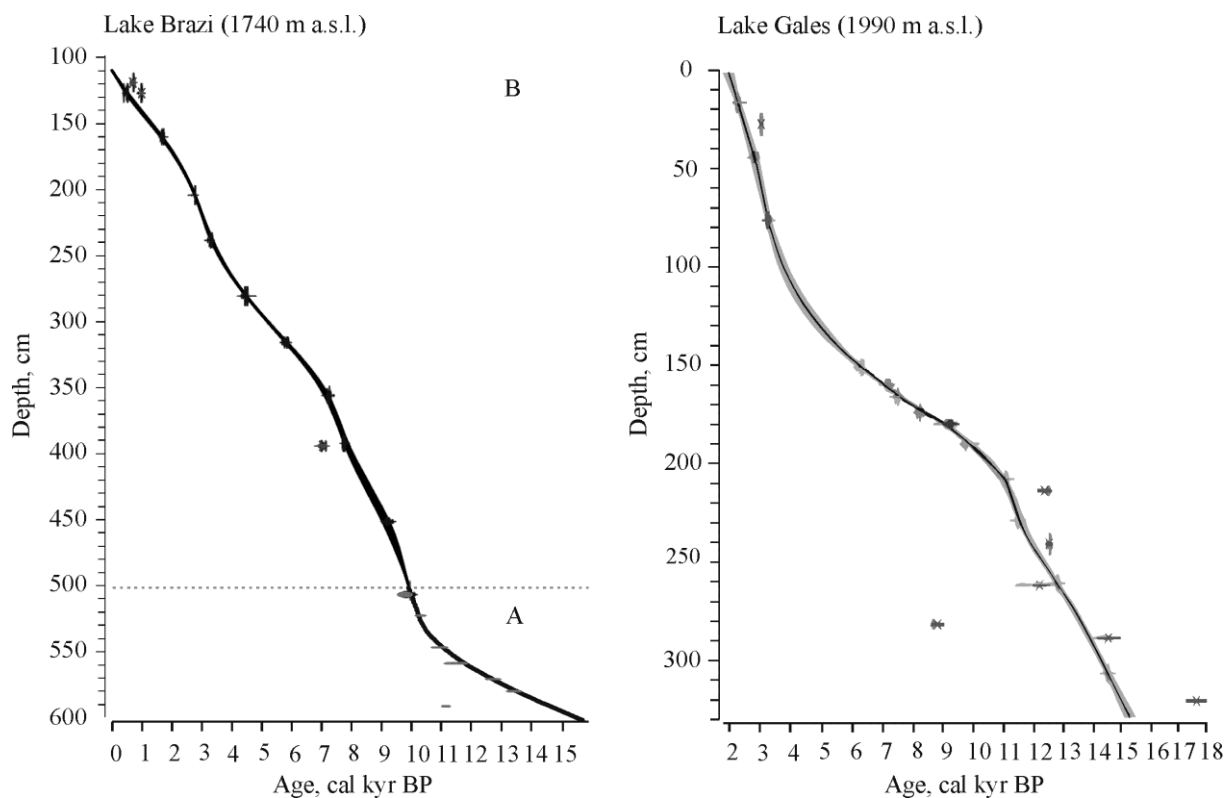
Figure 7. First axis scores (in standard deviation (SD) units) of a DCCA with age (cal kyr BP) as a sole constraining variable caclulated for diatom and chironomid assemblages from Lake Brazi and Lake Gales plotted together with chironomid-inferred July air temperature from Lake Brazi based on a merged Norwegian-Swiss training set (Tóth et al., 2012, 2015).

Supplementary Figure 1. Age-depth models of the sediment records of Lake Brazi (1740 m a.s.l.) and Lake Gales (1990 m a.s.l.), Retezat Mts. (Southern Carpathians). For Lake Brazi (A) weighted non-linear polynominal regression was used for modelling the age-depth relationship in the Late Glacial and Early Holocene part of the sediment record (600–502cm) and (B) a smoothing spline function in the Holocene part (505–111.14 cm). For Lake Gales a combination of the ^{14}C dates of the Holocene sediment and the relative pollen stratigraphy dates of the Late Glacial section were used together (model based on the smooth-spline function in CLAM v2.1). The x symbols show the ^{14}C dates with 95% highest posterior density and the greyscale shows 95% confidence intervals (see Hubay et al., 2016).

Table 1. The most important assemblage changes in the chironomid and diatom records and inferred environmental changes in Lake Brazi (Retezat Mts., Southern Carpathians).

Chironomid assemblage zones	Diatom assemblage zones	Inferred environmental conditions
TDB-ch1 (15,700-14,900 cal yr BP): *Pseudodiamesa, Micropsectra radialis*- and *Diamesa zernyi*-type dominate		cold and oligotrophic lake conditions
TDB-ch2 (14,900-14,200 cal yr BP): *M. radialis*-, *Tanytarsus lugens*-type and *Procladius* dominate	TDB-d1 (14,600-14,200 cal yr BP): *Pinnularia* spp. and *Encyonema gracile* dominated, fragilaroid taxa, *Tabellaria flocculosa* and *Stauroforma exiguiformis* reach high relative abundance	cool but increasing temperature with oligotrophic shallow and slightly alkaline lake conditions
TDB-ch3 (14,200-11,000 cal yr BP): *Micropsectra insignilobus*-type reaches maximum abundance and *T. lugens*-type dominates further	TDB-d2 (14,200-12,900 cal yr BP): fragilaroid taxa dominate with *E. gracile* and *T. flocculosa*	cool lake conditions and slightly increasing diatom productivity
	TDB-d3 (12,900-12,500 cal yr BP): *S. exiguiformis* and fragilaroid taxa dominate	moderate summer air temperature with low lake water pH and decreasing TP level, likely due to prolonged winter ice cover
	TDB-d4 (12,500-11,200 cal yr BP): next to fragilaroid taxa and *S. exiguiformis*, *Genkalia* spp., *Sellaphora* spp. and *Navicula* spp. (s.l.) reach high relative abundance	moderate summer air temperature and relatively low nutrient level with increasing diatom productivity and diatom-inferred pH
TDB-ch4 (11,000–10,300 cal yr BP): increasing relative abundance of *Psectrocladius sordidellus*-, *Chironomus anthracinus*-, *Tanytarsus pallidicornis*-, *Paratanytarsus austriacus*-type and *Zavrelimyia* type A first appearance of other Chironomini (*Endochironomus*	TDB-d5 (11,200-10,600 cal yr BP): fragilaroid taxa, *S. exiguiformis*, *Navicula* spp (s.l.). dominate	warmer summer air temperatures; cold and slightly alkaline lake conditions

impar-, *Microtendipes pedellus*-type) and *Cricotopus* taxa	TDB-d6 (10,600-10,400 cal yr BP): fragilaroid taxa and *Sellaphora* spp. dominate, with high relative abundance of *Navicula* spp. and *S. exiguiformis*	
	TDB-d7 (10,400-9800 cal yr BP): *S. exiguiformis*, fragilaroid taxa, *E. gracile* and *Sellaphora* spp. dominate	gradually decreasing pH and bog-expansion on the lake-shore
	TDB-d8 (9800-8900 cal yr BP): *S. exiguiformis* dominate	gradually decreasing pH
TDB-ch5 (10,300-6300 cal yr BP): *Tanytarsus mendax*- and *C. anthracinus*-type dominate	TDB-d9 (8900-6600 cal yr BP): *S. exiguiformis*, fragilaroid taxa and *Aulacoseira alpigena* dominate with *T. flocculosa*, *Brachysira brebissonii* and *E. gracile*	warm summer air temperatures with slightly increasing lake productivity and shallow lake conditions
	TDB-d10 (6600-5700 cal yr BP): fragilaroid and *Aulacoseira* taxa become dominant	slightly decreasing summer air temperature with increasing pH
TDB-ch 6 (6300-3200 cal yr BP): *P. sordidellus*-, *T. mendax*- and *P. austriacus*-type dominate	TDB-d11 (5700-3100 cal yr BP): *Aulacoseira* taxa dominate	slightly decreasing summer air temperature and increasing nutrient content
TDB-ch 7 (3200-0 cal yr BP): *T. lugens*-, *P. sordidellus*-type, *Zavrelimyia* type A, *T. mendax*-type dominate with the first stable appearance of *Heterotrissocladius marcidus*-type	TDB-ch12 (3100-0 cal yr BP): *Aulacoseira* spp., fragilaroids, *Sellaphora* spp. and *S. exiguiformis* dominate	meso-, eutrophic conditions; likely increasing human impact in the region

Table 2. The most important assemblage changes in the chironomid and diatom records and inferred environmental changes in Lake Gales (Retezat Mts., Southern Carpathians).

Chironomid assemblage zones	Diatom assemblage zones	Inferred environmental conditions
GAL-ch1 (15,000-14,200 cal yr BP): *Pseudodiamesa* and *Diamesa zernyi*-type dominate	Poor diatom preservation, not suitable for statistical analysis	cold and oligotrophic lake conditions
GAL-ch2 (14,200-11,800 cal yr BP): *Pseudodiamesa* remains abundant, while *Micropsectra radialis*- and *M. insignilobus*-type become dominant		
GAL-ch3 (11,800-9800 cal yr BP): *M. radialis*-type disappears, while *M. insignilobus*-type remains dominant	GAL-d1 (11,000-9200 cal yr BP): benthic fragilaroid taxa, *Sellaphora* spp., *Humidophila schmassmannii*, *Genkalia* spp. and *Achnanthidium minutissimum* dominate	warmer than earlier conditions, permanent lake
GAL-ch4 (9800-6900 cal yr BP): dominated by *M. insignilobus*-, *Paratanytarsus austriacus*-, *Psectrocladius sordidellus*-type, *Zavrelimyia* type A and *Procladius*; appearance of several Orthocladiinae taxa (e.g. *Corynoneura* spp., *Cricotopus intersectus*-, *Eukiefferiella fittkaui*-type, *Orthocladius* spp. and *Parametriocnemus)*	GAL-d2 (9200-9100 cal yr BP): benthic fragilaroid taxa, *H. schmassmannii*, *Genkalia* spp., *Sellaphora* spp. and *A. minutissimum* dominate	warm (or moderate) oligo- to mesotrophic conditions; and likely increased outlet overflow
	GAL-d3 (9100-8700 cal yr BP): *Fragilaria gracilis* dominance C:D ratio low	short term increase in lake level and/or water turbulence with decreasing productivity and increasing erosion from the lake shore
	GAL-d4 (8700-7900 cal yr BP): benthic fragilaroid taxa dominate with decreasing *F. gracilis* abundance, *A. minutissimum*, *Psammothidium curtissimum*, *P.subatomoides H. schmassmannii*, and *Genkalia* spp.	decreasing lake level, warm (or moderate) oligo- to mesotrophic conditions; stream overflow through the lake
GAL-ch5 (6900-1700 cal yr BP): dominated by *M. insignilobus*-, *P.*	GAL-d5 (7900-6500 cal yr BP): in addition to benthic fragilaroid taxa, *Aulacoseira valida*, *P. curtissimum*, *Diatoma* spp., *Stauroforma exiguiformis*, *A. minutissimum* and *P. subatomoides* dominate	decreased lake level with slowly changing diatom flora; and increasing water turbulence

sordidellus-, *Zavrelimyia* type A, *Procladius* and *Heterotrissocladius marcidus*-type;several Orthocladiinae taxa occurr as well (e.g. *Tvetenia bavarica*-, *Thienemanniella clavicornis*-, *Eukiefferiella claripennis*-type, *Chaetocladius* spp., *Limnophyes, Smittia)*	GAL-d6 (6500-3100 cal yr BP): *Aulacoseira* spp., (esp. *A. valida)*, *Diatoma* spp. and benthic fragilaroid taxa dominate with *P. curtissimum*, *Eunotia* spp., *Karayevia oblongella* and *A. minutissimum*	deep cool oligotrophic lake conditions with permanent stream overflow or wind turbulence (turbulent water)
	GAL-d7 (3100-1700 cal yr BP): *Aulacoseira* taxa dominate with fragilaroid taxa, *Encyonema gracile* and *Diatoma* spp.	

Table 3. Percentage variance explained by the selected effective variables in the canonical correspondence analyses exploring patterns in the chironomid and diatom records of Lake Brazi and Lake Gales (Retezat Mts., Southern Carpathians).

Lake Brazi – Chironomidae data

Selected variables	Explained variance (%)			Total variance	
	pure	shared	total	F	p
LOI	2.7	21.7	24.4	50.33	<0.001
S	1.9	17.5	19.4	37.46	<0.001
Al	12.0	5.3	17.3	32.66	<0.001
Sr	1.7	14.0	15.7	29.11	<0.001
BiSi	4.5	10.1	14.6	26.66	<0.001
Ca	2.0	11.8	13.8	24.88	<0.001
summer insolation	1.7	3.0	4.7	7.68	<0.001
All variables			55.7	26.90	<0.001

Lake Brazi – Diatom data

Selected variables	Explained variance (%)			Total variance	
	pure	shared	total	F	p
BiSi	1.9	17.0	18.9	33.52	<0.001
summer insolation	3.4	14.1	17.5	30.62	<0.001
Al	2.3	12.2	14.4	24.26	<0.001
LOI	1.9	10.9	12.8	21.08	<0.001
T_{VII}	1.0	8.4	9.4	14.84	<0.001
S	3.8	4.1	7.9	12.31	<0.001
Sr	0.7	4.7	5.4	8.30	<0.001
Ca	1.2	3.7	4.9	7.48	<0.001
All variables			46.1	14.63	<0.001

Lake Gales – Chironomidae data

Selected variables	Explained variance (%)			Total variance	
	pure	shared	total	F	p
Al	2.8	27.6	30.4	57.22	<0.001
S	1.3	27.7	29.0	53.41	<0.001
LOI	1.2	27.0	28.2	51.59	<0.001
summer insolation	5.0	1.5	6.5	9.01	<0.001
Ca	1.1	3.4	4.5	6.16	<0.001
Sr	1.3	1.3	2.6	3.55	0.006
All variables			43.5	16.2	<0.001

Lake Gales – Diatom data

Selected variables	Explained variance (%)			Total variance	

	pure	shared	total	F	p
summer insolation	5.5	13.9	19.4	21.98	<0.001
Sr	5.3	6.1	11.4	11.75	<0.001
T_{VII}	2.0	11.5	13.5	14.25	<0.001
S	4.3	1.2	5.5	5.28	0.001
All variables			33.2	10.96	<0.001