Long term trends in diatom diversity and palaeoproductivity: a 16,000-year multidecadal study from Lake Baikal, southern Siberia

Anson W. Mackay[1*], Vivian A. Felde[2], David W. Morley[1], Natalia Piotrowska[3], Patrick Rioual[4], Alistair W.R. Seddon[2], George E.A. Swann[5]

[1]Anson W. Mackay*
Environmental Change Research Centre, Department of Geography, UCL, London UK, WC1E 6BT.
ans.mackay@ucl.ac.uk
*Corresponding Author

[2]Vivian Astrup Felde
Department of Biological Sciences, and Bjerknes Centre of Climate Research, University of Bergen, PO Box 7803, Bergen N-5020, Norway
Vivian.Felde@uib.no

[1]David W. Morley
Environmental Change Research Centre, Department of Geography, UCL, London UK, WC1E 6BT.
d.w.morley@gmail.com

[3]Natalia Piotrowska
Department of Radioisotopes, Institute of Physics - CSE, Silesian University of Technology, Konarskiego 22B, 44-100 Gliwice, Poland
Natalia.Piotrowska@polsl.pl

[4]Patrick Rioual
Key Laboratory of Cenozoic Geology and Environment, Institute of Geology & Geophysics, Chinese Academy of Sciences, P.O. box 9825, Beijing 100029, China
prioual@mail.iggcas.ac.cn

[2]Alistair W. R. Seddon
Department of Biological Sciences, and Bjerknes Centre of Climate Research, University of Bergen, PO Box 7803, Bergen N-5020, Norway
alistair.seddon@uib.no

[5]George E. A. Swann
School of Geography, University of Nottingham, University Park, Nottingham, NG7 2RD, UK
George.Swann@nottingham.ac.uk

Correspondence to: Anson W. Mackay (ans.mackay@ucl.ac.uk)

Abstract

Biological diversity is inextricably linked to community stability and ecosystem functioning, but our understanding of these relationships in freshwater ecosystems is largely based on short-term observational, experimental, and modelling approaches. Using a multidecadal diatom record for the past c. 16,000 years from Lake Baikal, we investigate how diversity and palaeoproductivity have responded to climate change during periods of both rapid climate fluctuation, and relative climate stability. We show dynamic changes in diatom communities during the past 16,000 years, with decadal shifts in species dominance punctuating millennial-scale seasonal trends. We describe for the first time in Lake Baikal a gradual shift from spring to autumnal diatom communities that started during the Younger Dryas and peaked during the Late Holocene, and likely represent orbitally-driven ecosystem responses to long-term changes in seasonality. Using a multivariate classification tree, we show that trends in planktonic and tychoplanktonic diatoms broadly reflect both long-term climatic changes associated with the demise of Northern Hemisphere ice sheets, and abrupt climatic changes associated with, for example, the Younger Dryas stadial. Indeed, diatom communities are most different before and after the boundary between the Early and Middle Holocene periods c. 8.2 cal kyr BP, associated with the presence and demise of northern hemisphere ice sheets respectively. Diatom richness and diversity, estimated using Hill's species numbers, are also shown to be very responsive to periods characterised by abrupt climate change, and using knowledge of diatom autecologies in Lake Baikal, diversity trends are interpreted in terms of resource availability. Using diatom biovolume accumulation rates (BVAR; μm^3 cm^{-2} yr^{-1}), we show that spring diatom crops dominate palaeoproductivity for nearly all of our record, apart from a short period during the late Holocene, when autumnal productivity dominated between 1.8–1.4 cal kyr BP. Palaeoproductivity was especially unstable during the Younger Dryas, reaching peak rates of 18.3 x 10^3 μm^3 cm^{-2} yr^{-1} at c. 12.3 cal kyr BP. Generalized additive models (GAM) to explore productivity–diversity relationships (PDR) during pre-defined climate periods, reveal complex relationships. Strongest statistical evidence for GAMs were found during the Younger Dryas, the Early Holocene and the Late Holocene, i.e. periods of rapid climate change. We account for these differences in terms of climate-mediated resource availability, and the ability of endemic diatom species in Lake Baikal to adapt to extreme forms of living in this unique ecosystem. Our analyses offer insight into how productivity–diversity relationships may develop in the future under a warming climate.

Key words: palaeoproductivity, abrupt climate change, palaeolimnology, Holocene, Late glacial, productivity–diversity relationship, generalized additive models, multivariate classification trees

1. Introduction

Understanding the role that biological diversity plays in ecosystem stability and function is an important challenge in ecological research (Tilman et al. 1997; McCann 2000; Loreau et al. 2001; Isbell et al. 2015; Hagen et al. 2021). An ecosystem with higher biodiversity is assumed to be more stable, due to a number of factors, including the presence of species which have considerable plasticity, such that they have wide responses to disturbances (McCann 2000; Luethje and Snyder 2021), and the “insurance effect” (Yachi and Loreau 1999) where species redundancy plays an important stabilizing role. Biodiversity loss can lead to reduced ecosystem functioning (Cardinale et al. 2012), which poses serious threats to ecosystem health in general, and human well-being in particular (e.g. Chivian 2003). While the mechanisms behind how diversity controls functioning are not completely understood, dominant species with distinct functional roles are important (Winfree et al. 2015). For example, primary production, a key ecosystem function which helps regulate the global carbon cycle, is tied to species diversity (Tilman et al. 1997; Cardinale et al. 2009; Tilman et al. 2012). However, our understanding of productivity–diversity relationships (PDR) is largely based on short-term observational (Dodson et al. 2000; Ptacnik et al. 2008; Korhonen et al. 2011), experimental (McGrady-Steed et al. 1997; Interlandi & Kilham 2001; Winfree et al. 2015) and modelling approaches (Aoki 2003), with very few long-term studies undertaken (Rusak et al. 2004). This constitutes an important gap in our knowledge because in terms of climate change, productivity–diversity relationships and resource use efficiency (Gross and Cardinale 2007; Ptacnik et al. 2008) will be fundamentally different over long (e.g. climate and landscape evolution) and short (e.g. pulse disturbances such as climate disturbance events (Kéfi et al. 2019)) timescales.

Palaeoecological approaches provide a potential solution to this challenge, since they can reveal ecological dynamics in response to environmental change which unfold only over very long timescales (National Research Council 2005; Seddon et al. 2014). For example, diatoms are some of the most important primary producers in lake ecosystems, and their sub-fossilised remains provide a record of community variations through time. In addition, because the species composition, biovolume and concentration of diatom valves can be directly measured on sediment sequences, there is a unique opportunity to investigate how community dynamics, diversity and the stability of ecosystem functions such as productivity change over long-timescales. In particular, because the last 16,000 years have been punctuated by a series of large-scale and abrupt climatic shifts, such records open the door for an investigation into the links between biodiversity and the stability of ecosystem functioning associated with climate disturbance events.

Here we investigate the relationship between diatom diversity and ecosystem functioning in Lake Baikal, an ancient lake with a long continuous record with evidence of only very recent human perturbation (Izmest'eva et al. 2016; Roberts et al. 2018) restricted to its coastline (Kravtsova et al. 2014; Timoshkin et al. 2016). We focus on aquatic productivity as a measure of ecosystem function, because of the direct link between diatoms and primary production in the modern lake (Kozhova and Izmest'eva 1998).

As yet we do not assume to know the precise nature of the potential productivity–diversity relationships that may have occurred in Lake Baikal over such long timescales. We do know however, that local diversity will be influenced by a range of chemical, biological and physical factors such as nutrient availability, species interactions, and disturbance events such as rapid climate change. Our approach therefore is to explore productivity– diversity relationships over specific timescales independently determined from palaeoclimate studies. We might hypothesise for example, that productivity and diversity will co-vary linearly during rapid warming because increased energy results in increased metabolic rates in the system, but that this relationship might change during periods of relative climate stability. We investigate the range of possible response functions based on those identified by Smith (2007), whether they be negative or positive, whether they be humped or U-shaped, flat or just random (Smith 2007).

One of the most relevant independent climate studies for this time period is by Tarasov et al. (2009), who modelled pollen-inferred palaeotemperature for neighbouring Lake Kotokel (Fig. 1) for the past 15,000 years. Their reconstructions indicate a period of rapid warming (during the Bølling–Allerød interstadial), rapid cooling (during the Younger Dryas stadial) and relative temperature stability of the Holocene in southern Siberia. However, given that the Holocene has recently been formally subdivided into three ages/subepochs (Walker et al. 2018), it is possible to compare productivity– diversity relationships during the Younger Dyras and the Bølling–Allerød, with the Greenlandian/Early, Northgrippian/Middle, and Meghalayan/Late ages/subepochs of the Holocene (henceforth referred to as Early, Middle, and Late Holocene). Our approach is to coax history to conduct experiments (Deevey 1969) in order to deepen our understanding of (very) long-term biodiversity–ecosystem functioning (Loreau 2001) through the exploration of relationships between diatom diversity and productivity, and to test hypotheses related to how rapid climate change may disrupt these relationships on sub-orbital timescales. We do this by:

- reconstructing trends in diatom communities, diatom diversity and palaeoproductivity in Lake Baikal at a multidecadal resolution for the past c. 16,000 years.
- hypothesizing that relationships between productivity–diversity will differ during periods of rapid climate change and periods of relative climate stability.

2. Methods

Study site

Lake Baikal is situated in southern Siberia at the forest – steppe ecotone (Fig. 1), and is the world's oldest, deepest, and most voluminous lake. The lake is a World Heritage Site, due to its diverse flora and fauna; it contains over 2,500 species of which over 75% are thought to be endemic (Galazii 1989). Its sediments have accumulated for over 25 million years, and decades of research have exploited this sedimentary record to reconstruct environmental change (Williams et al. 2001; Mackay 2007). Sedimentary cores were obtained in 2001 from the research vessel *Vereschagin*, from the Vydrino Shoulder (51.585° N, 104.855° E; water depth 675 m), an underwater high (between 500 – 800 m) off the south-eastern coast of Lake Baikal (Fig. 1). The Vydrino Shoulder was selected because it is an area of stable, fine-grained sedimentation relatively undisturbed by tectonic activity and reworking (Charlet et al. 2005). The cores obtained included a 1.73 m trigger core (CON01–605–3a), a 10.45 m piston core (CON01–605–3), and a 2.50 m box core (CON01–605–5). These records were supplemented with a short gravity core taken from an ice platform in 2001 (CON01–105–6) from the same region.

Dating

Radiocarbon dates for the Vydrino sequence were obtained by accelerated mass spectrometry (AMS) from pollen and spore concentrates (Piotrowska et al. 2004; Demske et al. 2005). The age model is based upon twelve AMS ^{14}C pollen dates from the box core (CON01–605–5) (Piotrowska et al. 2004) and an additional five AMS ^{14}C pollen dates from the piston core

(CON01–605–3) (Demske et al. 2005). Full details are given in Mackay et al. (2011). Radiocarbon dates were calibrated using IntCal20 radiocarbon calibration curve (Reimer *et al.*, 2020), and age-depth modelling was done using ‘Bacon2.2’ (Blaauw & Christen, 2011). No reservoir effect was applied to the calibration because the organic material used for dating, i.e. pollen and spore concentrates, is assumed to be uncontaminated by old carbon.

Diatom analysis

Diatoms amount to between 50-90% of the phytoplankton biomass during spring bloom under ice and after ice break-up (Popovskaya et al. 2015; Panizzo et al. 2017). Spring bloom contributes a significant proportion of overall annual primary productivity (Popovskaya 2000). With the onset of summer warming and surface water stratification, diatoms are succeeded by non-siliceous autotrophic picoplankton and other green algae (Fietz et al. 2005; Belykh et al. 2006). During autumn turnover, a smaller diatom bloom dominates primary production. Nitrogen and phosphorus co-limit photic zone productivity in Lake Baikal (Satoh et al. 2006; O’Donnell et al. 2017), with rates of deep-water nutrient supply increasing markedly since the mid 19th century (Swann et al. 2020).

Diatoms are siliceous, so they generally preserve well in sedimentary environments. We prepared diatom samples for microscopy from sediments sampled every 5mm from the composite sequence derived from the gravity / trigger / piston cores detailed above. Unlike standard diatom preparation analyses (Battarbee et al. 2001), no chemical treatments were needed, although we enabled diatom concentrations to be calculated through the addition of divinylbenzene microspheres (Mackay et al. 1998). Diatom taxa were identified to species level or lower using a range of Russian and other floras, detailed in Mackay et al. (1998). With few exceptions, at least 300 valves from each sample were counted using oil immersion phase-contrast light microscopy at x1000 magnification. Planktonic and tychoplanktonic diatoms account for on average, c. 90 % of all diatoms counted, and here we detail diatom compositional change for planktonic and tychoplanktonic species only, as these were used to determine palaeoproductivity estimates below. The diatom taxonomical nomenclature was updated according to the global online database AlgaeBase https://www.algaebase.org/.

Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used to investigate the total amount of turnover, variation, and compositional changes of the diatom assemblages over time. The analyses were performed on Hellinger transformed data to dampen the effects of highly abundant taxa (Legendre and Gallagher 2001). Multivariate classification tree (MCT) analyses was used to explore how much of the variation in diatom assemblages can be explained by the different climatic periods identified above. MCT is considered a powerful method when there is a non-linear relationship between response and explanatory variables, when there are missing values in the data, or there are higher level interactions between explanatory variables (Borcard et al. 2018). The minimum sized tree was chosen based on the 1se rule, which is the minimum sized tree when the cross-validated relative error (CVRE) is the minimum CVRE value plus 1 standard error (SE) of all the CVRE values (Borcard et al. 2018). The number of multiple cross-validations was set to 100, and the number of *k* groups was set to the number of rows in the dataset. The counts were normalized prior to the analysis and since MCT is in Euclidean space it transforms into the chord distances (sensu the original chord distances proposed by Orloci 1967) between samples. Ordination analyses were done using the R package vegan and results plotted using ggvegan. The MCT was done using the R package mvpart. Stratigraphical profiles were constructed using C2 Data Analysis Version 1.7.7 (Juggins 2014).

Palaeoproductivity

The palaeoecological significance of diatom concentrations can be of limited value unless they can be converted into either diatom flux rates (e.g. Battarbee et al. 2001), or estimates of biovolume (Hillebrand et al., 1999). Diatom flux rates rely on a robust chronology (as determined in this study), while biovolume estimates require representative size measurements for the dominant taxa. We estimate palaeoproductivity through community biomass calculations derived from diatom biovolume accumulation rates (BVAR; μm^3 cm^{-2} yr^{-1}) for all major planktonic and tychoplanktonic species (Interlandi and Kilham 2001). Biovolumes (μm^3) were calculated using the median of measured linear dimensions of 25 valves, and geometric shape guidelines (Hillebrand et al. 1999). Species used for biovolume calculations accounted for on average, over 80 % of total relative abundance, and therefore we assume are a robust estimate of palaeoproductivity.

Diatom richness, diversity and evenness

Richness, diversity and evenness were estimated using Hill's species numbers $N0$, $N1$, and $N2$ using diatom count data of the planktonic and tychoplanktonic flora only. We do not include benthic taxa because they represent a different habitat, far from the core location.

Their persistent presence in the core (average 10 %) is caused by secondary transport processes rather than species competing for the same resources as the planktonic diatoms themselves. Hill's species numbers give easily interpretable numbers by maintaining the doubling effect, and provide information on three levels as to how rare and abundant taxa are weighted in each sample (Hill, 1973; Jost, 2010; Gotelli and Ellison, 2013; Chao et al., 2014). Species richness is estimated using Hill's $N0$, the expected number of taxa where rare and abundant taxa have similar weights. Species diversity is estimated using Hill´s $N1$, which is the expected number of equally common taxa, with less weight on rare taxa, and $N2$, which provides the expected number of equally abundant taxa but puts weight on the numerically dominant taxa. The estimates are represented as the expected number of diatoms based on the smallest sample size (n = 150) to avoid biases related to different sample sizes. To take account of variable sediment accumulation rates (SAR), Hill's measures of richness and diversity were further divided by accumulation rates over time, so these measures become estimated Hill's numbers per cm^2 yr^{-1}. To detect variation in abundance changes over time (evenness) we also include the ratio of $N2/N1$ (Birks et al. 2018), i.e. the proportion of very abundant species to the number of common species identified. When the ratio is 1, it indicates that all taxa were equally abundant. The ratio is calculated based on the Hill's numbers after taking account of SAR.

Palaeoproductivity – Diversity relationships

Relationships between palaeoproductivity and $N2$ diversity were investigated during pre-identified time–intervals (Tarasov et al. 2009; Walker et al. 2018) to test the hypothesis that PDR will differ during periods of rapid climate change and periods of relative climate stability. Defined climate periods are the pre– Bølling–Allerød (15.9–14.7 cal kyr BP), the Bølling–Allerød (14.7–12.9 cal kyr BP), the Younger Dryas (12.9–11.7 cal kyr BP), and the three recently designated sub-epochs of the Holocene (Early (11.7–8.2 cal kyr BP), Middle (8.2–4.2 cal kyr BP) and Late (4.2–0 cal kyr BP). We used generalized additive models (GAM) to explore PDR because we have no prior knowledge of the expected relationships, and the likelihood that the relationships were non-linear or showing different complex patterns within the different time periods. We used $N2$ diversity as the response variable and diatom BVAR as the explanatory variable. $N2$ is a continuous variable so we used a gamma distribution with a log link. Diatom BVAR as a variable was skewed so it was log transformed prior to the analyses, and climatic period was included as a factor variable that allowed for different smooths for each period. The smooths were fitted using thin-plate regression splines, and the model was fitted using the restricted maximum likelihood approach. Prior to analyses, extreme outliers ($\mathrm{BVAR_{log}}$ µ$\mathrm{m^3\ cm^{-2}\ yr^{-1}}$) < 6 were removed to reveal more clearly GAM relationships. This led to only 8 out of 521 samples being removed in total: three, two and one samples removed from the Late, Middle and Early Holocene subepochs respectively, and a further two from the pre–BA period. Models were then refitted.

The model is specified as follows:

$$\log\left([N2_{ij}]\right) = a_1 + f_1\left(Productivity_i,\ Period_j\right) + \varepsilon_i \quad N2_i \sim Gamma$$

where i represents each sample, j is each climate period and a_1 is the intercept term for the periods. Since the data are time ordered, the data points may not be independent and we added a correlation term to the model attempting to reduce effects of potential temporal autocorrelation. However, adding different correlation structures did not improve the model or affect the residual variation, and we therefore removed them to keep the simplest model.

3. Results

Chronology

The calibrated ages for our profile span the last 15.91 cal kyr BP (where kyr = thousands of years, BP = before present, i.e. 1950 CE (common era)) (Figure 2). Sediment accumulation rates ranged between 32–184 yr $\mathrm{cm^{-1}}$ (mean 62 yr $\mathrm{cm^{-1}}$).

Diatoms

The temporal resolution of species compositional change was c. 30 years for the past c. 16,000 years (Fig. 3). DCA axis 1 sample scores show a strong, largely unidirectional trend since the start of the Holocene. Turnover in the planktonic/tychoplanktonic assemblages over the whole time period is 2.71 standard deviation units, reflecting the observation that several species present during the early part of our record are also present during the latter part of our record. The total inertia (variation) measured by CCA is 1.82, and of this the constraining time variable explains 10.6 % of the variation (eigenvalue = 0.193). The ratio of eigenvalues of the constrained axis 1 over the unconstrained axis 2 is 1.29 indicating that the time gradient is explaining an important component of the variation.

During the early stages of the pre– Bølling–Allerød period, *N*0 and *N*2 values were initially relatively high (Fig. 4), before declining as the tychoplanktonic *Aulacoseira skvortzowii* dominated the assemblage (Fig. 3). Dominance by *A. skvortzowii* persists into the Bølling, but is gradually reduced by increasing abundances of the planktonic *Aulacoseira baicalensis* during the later Allerød. DCA axis 1 ordination scores show very little change during the pre– Bølling–Allerød and Bølling–Allerød interstadial, indicative of a rather stable assemblage, with few equally abundant species reflected in low evenness scores (*N*2/*N*1). MCT is not able to discriminate well between diatom assemblages of the pre-Bølling–Allerød and Bølling–Allerød interstadial (Fig. 5).

The Younger Dryas stadial is characterised by major changes in the diatom assemblage – abundances of *Aulacoseira* (especially *A. skvortzowii*) decline, concomitant with a rapid succession of *Ulnaria acus* and *Crateriportula inconspicua*, that bloom in spring and autumn respectively (Fig. 3). These taxa give way to a short-lived peak in *A. baicalensis* dominance, before *A. skvortzowii* once again asserts its dominance by the end of the Younger Dryas, alongside notable increases in *C. inconspicua* and *L. minuta*, resulting in increasing richness (*N*0) and diversity (*N*2) scores (Fig. 4). These changes are reflected in a rapid change in DCA axis 1 scores at the start of the Younger Dryas, with discernible changes in the evenness ratio indicative of increasing importance of different species. The Early Holocene is characterised in the main by declining dominance of *A. skvortzowii* and increasing importance of autumn blooming crops of *C. inconspicua* and *Lindavia minuta*. *U. acus* shows considerable fluctuations, with *Hannaea baicalensis* and *Cyclostephanos dubius* increasing in importance from c. 10 cal kyr BP, driving increases in diatom *N*2 diversity and evenness ratio.

Where the climatic periods are used as a supervised classification technique, MCT analysis reveals the highest variation between the Early and the Middle Holocene subepochs (Fig. 5). This transition also marks the time when the evenness ratio peaks, that then declines to lowest values found in our study during the Middle and Late Holocene (Fig. 4). During the Middle Holocene, several diatom species largely disappear from the stratigraphical record including *Stephanodiscus flabellatus*, *Stephanodiscus skabitchevskii*, *H. baicalensis*, and *C. dubius*, while *C. inconspicua* drops to low values for the remainder of the record (Fig. 3). In their place, *U. acus* and *L. minuta* increase in importance. The loss and gain of species through the Middle Holocene has resulted in a relatively high but stable *N*2 diversity, with peak diversity occurring at the boundary between the Middle and Late Holocene, c. 4.2 cal kyr BP (Fig. 4). Despite relatively high abundances for the first time of *Stephanodiscus parvus* and *Stephanodiscus meyerii*, the Late Holocene sees *L. minuta* increasing to almost complete dominance of the diatom assemblage between 1.8–1.4 cal kyr BP, resulting in some of the lowest diatom diversity values for the study. During the most recent 500 years of our record, the assemblage is characterised by species commonly found in the modern–day lake communities, co-dominated by *A. baicalensis*, *U. acus* and *L. minuta* (Fig. 3).

Palaeoproductivity

Diatom biovolume accumulate rate (BVAR) data show that spring diatom crops have dominated palaeoproductivity for much of the past c. 16,000 years, apart from a short period during the late Holocene, 1.8–1.4 cal kyr BP, when autumnal diatom production increases to more than ten times that of spring production (Fig. 6). BVAR were substantially higher and more unstable during the Younger Dryas stadial than the warm periods before and after it (Fig. 6). Peak palaeoproductivity for the whole study (18.3×10^3 μm^3 cm^{-2} yr^{-1}) was associated with successive peaks in *U. acus* then *A. baicalensis* at c. 12.3 cal kyr BP. BVAR then declined rapidly and remained relatively low for the remainder of the Younger Dryas and the start of the Holocene. Palaeoproductivity increased during the Early and Middle Holocene, before declining to lowest rates during the Late Holocene (mean, 1.3×10^3 μm^3 cm^{-2} yr^{-1}).

The shapes of the productivity–diversity relationships differ among the pre-defined climate periods, with some being negative (e.g. the Younger Dryas and the Middle Holocene periods), positive (e.g. the pre-BA and the Early Holocene periods), and others more complex such as the Late Holocene, dependent on palaeoproductivity rates (Fig. 7). The relationship between palaeoproductivity and diversity during the Bølling–Allerød was flat (Smith 2007). GAMs with very low *p*-values suggest that we have higher confidence that PDR relationships existed during the Younger Dryas, the Early Holocene, and the Late Holocene in comparison to the other time periods (Table 1).

4. Discussion

Over the past 16,000 years diatom trends in Lake Baikal have been dynamic, with decadal shifts in species dominance punctuating millennial-scale trends in seasonal communities. MCT analyses show that the main split in diatom composition occurs between assemblages associated with the Last Glacial – Interglacial Transition (LGIT; 16–8.2 cal kyr BP), and the Middle– Late– Holocene subepochs (8.2 cal kyr–present) (Fig. 5). This suggests that trends in community shifts in diatoms in Lake Baikal broadly reflect climatic changes associated with the demise of Northern Hemisphere ice sheets as the planet transgressed from glacial to interglacial environments (Denton et al. 2010). Here we focus on interpreting trends in diatom communities and diversity through time, before focussing on how productivity–diversity relationships (PDR) vary over long-timescales, including during periods of rapid climate change and periods of relative climate stability.

4.1 Last Glacial – Interglacial Transition

Due to high obliquity (Fig. 8j), the LGIT in the Lake Baikal region was intensely seasonal, resulting in very cold winters but relatively warm, moist summers (Bush, 2005). Cold winters during the late glacial resulted in substantially longer annual ice cover on Lake Baikal of up to 8–9 months, reduced hydrological input by as much as 40 % than the modern day, and restricted inputs of key nutrients such as P, N and Si (Shimaraev & Mizandrontsev 2006). Up to the Bølling–Allerød, diatom assemblages were dominated by spores of the endemic *Aulacoseira skvortzowii* (Fig. 3). *A. skvortzowii* is tychoplanktonic, having evolved a life cycle which utilizes both pelagic and littoral habitats; viable spores remain in coastal sediments down to a water depth of 25 m, where they can be resuspended by strong autumn storms back into the pelagic zone (Jewson et al., 2008) in time to bloom the following spring. *A. skvortzowii* grows best in water temperatures below 5 °C, and to avoid lethal increasing surface water temperatures, spore formation is triggered after ice break-up when phosphate concentrations fall below a threshold level of 15–23 µg L^{-1} (Jewson et al., 2008). Declining phosphate concentrations are caused by P uptake by other algae (e.g. green algae and picoplankton) as surface waters start to stratify. Pigment analyses have shown that green algae were abundant at this time in the south basin of Lake Baikal (Tani et al. 2002; Soma et al. 2007). Relatively low *N*2 plankton diversity and evenness values during much of the late glacial likely reflect P and Si limitation, resulting from overall lower nutrient concentrations due to colder climate (Shimaraev & Mizandrontsev 2006) but possibly also competition from other algae.

The major shift to warmer temperatures during the LGIT occurred with the onset of the Bølling–Allerød interstadial, c. 14.7 cal kyr BP, linked to heat release from warm waters deep in the North Atlantic Ocean (Thiagarajan et al. 2014) which led to the resumption of the Atlantic meridional overturning circulation (AMOC) (McManus et al. 2004) (Fig. 8g). Mean pollen-inferred temperatures of the warmest month from neighbouring Lake Kotokel however (Fig. 8b), reveal a 5 °C increase only during the latter stages of the Bølling–Allerød (Tarasov et al. 2009). At the same time, pollen-inferred mean annual precipitation records show that rainfall increased from c. 300 mm yr^{-1} to c. 460 mm yr^{-1} (Fig. 8c). This warmer, wetter Allerød led to extensive melting of glaciers along the shores of Lake Baikal (Horiuchi et al. 2004; Osipov and Khlystov 2010), major expansion of boreal vegetation (Tarasov et al. 2009; Bezrukova et al. 2010; Reshetova et al. 2013), reduced ice duration on the lake and increased nutrient transport (Shimaraev & Mizandrontsev 2006). The impacts on diatom communities however were subtle, with diatom composition between the pre– Bølling–Allerød and Bølling–Allerød not distinguishable through MCT analyses (Fig. 5). Diversity and evenness show little variability, although relative abundances of a few species show distinct changes. For example, the heavily silicified endemic *Aulacoseira baicalensis* will have benefited from increased availability of dissolved silica (Jewson et al. 2010) while the endemic *Stephanodiscus flabellatus* may have benefited from elevated concentrations of phosphorus (Bradbury et al. 1994). The observed decline in *A. skvortzowii* spore formation may also be attributable to generally increased P availability in the south basin (Jewson et al. 2008).

The Younger Dryas stadial (12.9 – 11.7 cal kyr BP) is probably the most studied climate disturbance event of the late Quaternary (Broecker et al. 2010). It was caused by an influx of freshwater from Lake Agassiz into the Arctic Ocean (Tarasov & Peltier 2005; Murton et al. 2010) which led to the decline in AMOC (Fig. 8g) (Bond et al. 2001; McManus et al. 2004), and concomitant cooler temperatures across the Northern Hemisphere (Stuiver et al. 1995) (Fig. 8h). Increased GISP2 K^+ concentrations (Fig. 8f) indicate that the Siberian High intensified at the start of the Younger Dryas (Mayewski et al. 1997), which accounts for both an attenuated Asian summer monsoon (Fig. 8e) (Dykoski et al. 2005) and cooler and more arid climate conditions in the Lake Baikal region (Tarasov et al. 2009) (Fig. 8 b, c). These cooler, more arid conditions led to a decline in hydrological input into Lake Baikal itself Mackay et al. 2011), and a short-lived expansion of the tundra biome (Tarasov et al. 2009; Bezrukova et al. 2010).

Diatom responses to climate change within the Younger Dryas were instantaneous but complex, kick-started by the first appearance and rapid growth of *Ulnaria acus* (Fig. 3) (indicative of higher dissolved silica concentrations in the water column (Bradbury et al. 1994)) and increasing abundance of *C. inconspicua*. However, the decline in *N*2 diversity only from c. 12.6 cal kyr BP (Fig. 4), suggests that resources for diatom growth were not initially limiting. Occupying different seasonal niches, spring blooming *U. acus* and autumnal blooming *C. inconspicua* (Ryves et al. 2003) are unlikely to be directly competing for the same resources, in part because small centric diatoms do not utilise a lot of dissolved silica (Bradbury et al. 1994). Having several co-dominant species is reflected in the relatively high evenness scores for the Younger Dryas (Fig. 4), related to few resources being limiting (Interlandi & Kilham 2001).

The decline in *N*2 diversity is linked to peak values for *A. baicalensis* (Fig. 3), competing directly with *U. acus* for dissolved silica. Diatom population changes in Lake Baikal play an important role in controlling availability of silicic acid for other species (Callender & Granina 1995; Jewson et al., 2010; Shimaraev and Domysheva, 2013; Jewson et al., 2015). In particular, when populations of *A. baicalensis* are very high, the availability of silicic acid uptake for other species declines, leading to a drop in their populations (Jewson et al., 2010; 2015). Being a heavily silicified species, *A. baicalensis* needs a strong period of mixing (Huisman et al. 2004), which suggests that when abundant, turnover is strong, allowing the recycling of nutrients needed for peak palaeoproductivity (Fig. 6). Our diatom records demonstrate that species specially adapted to grow under the ice of Lake Baikal (Bondarenko et al. 2012) have flourished alongside autumnal blooming species during this cold stadial, with, initially at least, few limiting resources.

The latter stages of the Younger Dryas are characterised by a marked increase in diatom richness and diversity associated with both increases in spring and autumn diatoms, and a rapid decline in palaeoproductivity. Given that regional temperatures remain low and unchanged at this time (Demske et al. 2009), internal dynamics in the lake may be driving observed changes in diatom communities, mediating resource availability. Contemporary monitoring studies have shown that populations of *A. baicalensis* can undergo dramatic changes in population size linked to complex interactions including silica availability (Izmest'eva et al. 2006); after populations peak, cells are transported to the bottom sediments, taking with them silica that then becomes unavailable for new diatom growth (Jewson and Granin 2015). But autumnal diatoms are still able to grow, as nutrients become available once more during autumnal turnover.

As detailed above, MCT analyses is unable to distinguish Younger Dryas and Early Holocene diatom communities (Fig. 5), two time periods characterised by significant millennial scale variability (Bond et al., 2001; Fisher *et al.*, 2002; Mayewski et al. 2004; Nesje et al. 2005; Wanner et al. 2014). Overall, the diatom flora is characterised by persistent spring-blooming species that need lots of dissolved silica, but also increasing abundance of autumnal blooming diatoms. A decline in species richness and diversity at the start of the Early Holocene may be indicative of fewer resources (Interlandi & Kilham 2001), coincident at least with the widely expressed cool Preboreal Oscillation (Fisher et al. 2002) and lower river flow into Baikal's south basin (Mackay et al. 2011). After c. 11.3 cal kyr BP diatom diversity and evenness increase for the next few thousand years, indicative of increasingly abundant resources, linked to regional warmer and wetter climates (Tarasov et al. 2009), and generally stronger seasonality. Co–limitation by several nutrients and light allow for greater numbers of planktonic species to co-exist (Burson et al. 2018), leading to highest evenness scores at the Early / Middle Holocene boundary.

4.2 Middle – Late Holocene

Northern Hemisphere cooling, especially from c. 5 cal kyr BP, is linked to declining summer insolation (Marcott et al. 2013) in conjunction with vegetation and snow/ice feedbacks on Earth's surface albedo. This cooling culminated in the neoglacial, which in central Asia resulted in increased aridity (Ganopolski et al. 1998) expressed in the Lake Baikal region as declining mean annual precipitation (Tarasov et al. 2009). The neoglacial also resulted in increased Siberian permafrost formation (Anisimov et al. 2002). Within Lake Baikal, we document a shift from spring to autumnal diatom communities that started during the Early Holocene, concomitant with the first decline in insolation, but then continues to get stronger during the Middle and Late Holocene as both precession and obliquity decline (Fig. 8). The slow unfolding of an increasingly important autumnal diatom community has relatively little impact on palaeoproductivity during much of the Holocene, although autumnal production after 10 cal kyr BP is slightly higher than it was before 10 cal kyr BP, and continues to proportionally increase especially during the Late Holocene. This long-term change in diversity and palaeoproductivity likely represents an orbitally-driven ecosystem response to long-term climate change, possibly linked to changes in seasonality and its impact on, for example, ice cover dynamics and length of summer stratification in the lake.

L. minuta is currently the only pelagic diatom to bloom during the autumn in Lake Baikal in substantial numbers (although it can also grow in smaller numbers during spring turnover). Because *L. minuta* can tolerate surface water temperatures up to 11 °C, cells persist higher in the surface waters for longer during summer stratification, so that when stratification breaks down in the autumn and nutrients are regenerated, cells of *L. minuta* are retrained into the photic zone first, giving them a strong competitive advantage, leading to their dominance during autumn turnover (Jewson et al., 2015). Winter ice cover is a major force driving inter-seasonal connections in lakes that freeze over every year (Sommer et al. 2012; O'Reilly et al. 2015; Hampton et al. 2017), and Lake Baikal is no exception. The gradual decline in proportion of spring diatoms may have resulted in increased resource availability for other diatoms (Interlandi & Kilham 2001; Jewson et al., 2010; 2015). For example, monitoring studies have shown large autumnal populations of *L. minuta* during the 1950s CE when spring populations of *A. baicalensis* were very low (Antipova & Kozhov in Kozhov 1963).

The build-up to peak dominance in *L. minuta* during the Late Holocene is accompanied by the successive decline in spring blooming species, starting with *U. acus*, followed by *A. baicalensis*, species that both rely on availability of dissolved silica (Jewson et al. 2010) and under-ice turbulence to remain in the photic zone (Granin et al. 2000). These shifts are reflected in rapidly declining *N*2 diversity scores since their peak at the Middle / Late Holocene boundary to their lowest values for the Holocene (Fig. 4). This decline is also coincident with a major shift in carbon dynamics in Lake Baikal, linked to increasing regional cooling and aridity (Mackay et al. 2017). The almost monospecific Late Holocene assemblage of *L. minuta* and resultant low *N*2 diatom diversity in the lake are concurrent with the Dark Ages Cold Period (DCAP) (1.8–1.4 cal kyr BP; CE 400–765) (Helama et al. 2017), a climatically cool period, linked to changes in ocean circulation (Bond et al. 2001), and solar and volcanic activity (Helama et al. 2017). The near complete disappearance of *A.*

baicalensis makes this period unique in our Lake Baikal record. However, we are not yet able to say conclusively why growth of *A. baicalensis* was so inhibited during the DCAP, leading to the dominance of *L. minuta* for several centuries. This period almost certainly represents an ecosystem response to abrupt extrinsic change occurring elsewhere in the Northern Hemisphere, super-imposed on longer-term changes in orbital parameters (Williams et al. 2011). It is possible that the smaller biovolume of *L. minuta* in comparison to *A. baicalensis* and *U. acus* may have conferred it a competitive advantage as resources became increasingly limited (Burson et al. 2018). Alternatively, persistent deeper snow cover on the frozen lake could have acted to reduce light penetration through the ice, (i.e. light as a resource is severely limited) resulting in a decline in sub-surface turbulence and loss of spring diatom crops to deeper waters (Granin et al., 2000). It is possible that these responses are linked to orbitally driven seasonal changes such as cooler summers (Fig. 8). It's notable that the ecosystem function of primary production did not decline overall during this period, just the timing of peak production, with autumnal palaeoproductivity far exceeding spring productivity for the only time in our record during the DCAP (Fig. 6).

4.3 Palaeoproductivity–diversity relationships

Productivity–diversity relationships (PDR) in aquatic ecosystems are complex (Aoki 2003; Smith 2007), while also being scale (Chase and Leibold 2002; Korhonen et al. 2011) and time (Rusak et al. 2004) dependent. Our initial hypotheses set out to test if these relationships differ between periods of relative climate stability and periods of rapid climate change. This is borne out, as the shapes of the relationships are very different across the different climate periods (Fig. 7). The strongest evidence for GAMs (with lowest *p* values; (Table 1)) were found during both the Younger Dryas and Early Holocene, periods punctuated by pervasive millennial-scale variability, and the Late Holocene period, characterised by cold events linked to overlapping drivers such as solar minima and volcanic eruptions (Helama et al. 2017), amplified by centennial-scale oceanic variability (Renssen et al. 2006). PDR were different during each of the pre– Bølling–Allerød, the Bølling–Allerød and the Middle Holocene periods, but statistical support for GAMs were much weaker during these periods of relative climate stability (Table 1). During the Bølling–Allerød the PDR is effectively flat (sensu Smith 2007), because $N2$ diversity is restricted to very low values and changes little across the magnitude of the productivity gradient, perhaps due to as yet few available resources for several species to co-exist. During the Middle Holocene, $N2$ diversity values are again more restricted than during either the Early or Late Holocene periods, *N*2 are rarely low (Fig. 7), likely linked to optimal resource availability allowing several species to co–exist (Burson et al. 2018) at similar abundances (Fig. 4) during both spring and autumn (Fig. 3).

The negative PDR during the Younger Dryas likely reflects a complex set of processes linked to both ecosystem responses to abrupt cooling (e.g. increased ice duration but stronger overturn in the lake (Shimaraev & Mizandrontsev 2006), and a reduction in resource heterogeneity due to severe limitation by a few or even single resource (Interlandi & Kilham 2001). Productivity in Lake Baikal is dependent on a sustained supply of nutrients from deeper waters to the photic zone, stimulated by shifting wind dynamics and enhanced deep ventilation (Swann et al. 2020). While increased supply of Si ensured initial resources for *Ulnaria* and *Aulacoseira* growth, Si will ultimately have become unavailable to most other diatoms, due to massive increases in the abundances of *A. baicalensis* (Fig. 3) (Jewson et al., 2010; 2015), leading to declines in diversity while productivity peaked. During the Early Holocene however, there is a positive PDR, especially when palaeoproductivity levels are initially lower. We suggest that rapid melting of glaciers and increased fluvial input (Osipov and Khlystov 2010), and opening up of new habitats as ice-cover duration on the lake declined, contributed to an increased supply of nutrients and habitat availability, such that both diversity and productivity were able to increase from the very low values at the start of the Holocene period. It’s notable that during the Early Holocene the ratio of autumnal to spring species increases markedly, indicative of autumnal overturn niches opening up, allowing increased growth of *C. inconspicua* and *L. minuta* (Fig. 3).

During the Late Holocene however, a negative PDR is apparent only when palaeoproductivity is very low at the transition between the Middle and Late Holocene periods (Fig. 7). Low palaeoproductivity at c. 4.2 cal kyr may be linked to a period of regional cooling and aridity (Mackay et al. 2017) concurrent with weaker Asian summer monsoons (Dixit et al. 2014). It is at this time that new *Stephanodiscus* species become established in the lake (*S. meyeri* and *S. parvus*) alongside existing diatom communities, hence higher *N*2 diversity. *Stephanodiscus* species tend to reflect higher phosphorus than silicon loading rates (Kilham et al. 1986), and may be a community response to cooler, more arid climate (Bradbury et al. 1994) as experienced during the Late Holocene neoglacial. However for the majority of the Late Holocene there is little relationship between palaeoproductivity and diversity, indicative of abundant resources allowing for many planktonic species to co–exist.

4.4 Comparisons to other studies within Lake Baikal

It has long been recognised that Quaternary biogenic silica and diatom concentrations in Lake Baikal sediments mirror changes in insolation (Khursevich et al. 2001), such that very low concentrations characterise glacial periods, likely due to a number of factors including lower productivity and higher rates of diatom dissolution, as well as dilution due to increased inputs of clastic material (Mackay 2007). The Vydrino LGIT record has an almost identical diatom assemblage to those identified for the same time period in long cores extracted from elsewhere in the lake, including both the Posolskaya Bank (BDP-99) and Academician Ridge (BDP–96–2) (Khursevich et al. 2005) (Fig. 1). In another study of Quaternary Lake Baikal diatoms, this time from the Buguldieka Saddle (Fig. 1), Edlund (2006) found that although earlier glaciations also contained few diatoms, the ‘Sartan glaciation’, i.e. Marine Isotope Stage 2, still contained at least 10 species of planktonic diatoms, and an assemblage again very similar to our Vydrino sequence. Bradbury et al. (1994) produced a similar but much lower resolution record for diatom changes spanning the past 15,000 years from station 305 off the southern margins of the Selenga Delta (Fig. 1), where both the assemblage and sequence of diatoms are similar to Vydrino. However, while observations and conclusions drawn in this study related to PDR are likely applicable to other regions of this vast lake, one of the reasons why Lake Baikal contains a diverse endemic diatom flora is down to its size and heterogeneity of habitats (Jewson et al. 2015). Thus while species declines may be evident in one region, those same species may well persist in other regions of the lake.

Conclusions

This study provides important insights into our understanding of productivity–diversity relationships (PDR) in aquatic ecosystems. We show that diatom communities and palaeoproductivity are sensitive to extrinsic drivers of climate change. These drivers operate at different time scales, from abrupt events during the Younger Dryas resulting in (negative) coupling between palaeoproductivity and diversity, to slower changes in boreal insolation and seasonality, leading to varied PDR relationships. These differences are likely related to resource availability and limitation (or not) of specific nutrients, linked to climate and surface water overturn. We therefore provide important perspective to complement existing short-term observational (Dodson et al. 2000) and experimental (Winfree et al. 2015) approaches. PDR in aquatic systems should not be expected to occur in one direction (Smith 2007), but are very much dependent on other factors such as external disturbances, resource availability, species interactions and abiotic constraints on ecosystem function. Even given the sheer volume of Lake Baikal, diatom responses to abrupt events can be almost instantaneous, showing how tightly coupled ecology and climate have been in the past.

Over sub-orbital timescales, our records suggest that ecosystem function in Lake Baikal is rather resilient to natural disturbance. Following the concept of operation criteria as defined by Jovanovska et al. (2016), after disturbance or “press” events like the Younger Dryas, diatom communities and palaeoproductivity return to pre-disturbance states. Moreover, rather than leading to the demise of certain species, new species are actually ushered into the palaeo record, likely due to increased resources (Fig. 3). And even when a regime shift looks possible with respect to the increasing dominance of an autumnal flora as the Holocene unfolded, in the past 1000 years a spring-dominated flora has returned. These observations may hold insights into observed diversity changes occurring in recent decades, linked to global warming (Roberts et al., 2018). However, what our record cannot provide information on is the resilience of the lake’s flora to multiple stressors such as human driven climate change and anthropogenic nutrient enrichment, which is currently impacting the lake’s littoral communities.

Author Contributions:

Study was conceived by AWM and PR. Diatom counting was undertaken by DWM. Age modelling was done by NP. Data analyses was undertaken by VAF, AWRS and AWM. AWM led the paper writing with significant contributions from AWRS and GEAS. All authors made comments on earlier drafts of the paper.

Acknowledgements:

We wish to acknowledge the various agencies who helped to fund this work, especially the EU FPV programme (EVK2-CT-2000-0057), UK NERC (NE/J010227/1), and the Norwegian Research Council (IGNEX ref: 249894/F20). We thank UCL Geography Cartography Unit who helped prepare the figures. And we especially thank the three reviewers whose observations and comments have helped to improve the focus of the study immensely. AWM would like to say a special thanks to the editorial team of CP guiding the study’s publication over an extended period of time due to illness. The flexibility and understanding shown should be a model for other journals to follow.

References

Anisimov, O. A., Velichko, A. A., Demchenko, P. F., Eliseev, A.V., Mokhov, I. I., Nechaev, V.P.: Effect of climate change on permafrost in the past, present, and future. Izvestiya Atmospheric and Ocean Physics, 38, 25-39, 2002.

Aoki, I.: Diversity–productivity–stability relationship in freshwater ecosystems: Whole-systemic view of all trophic levels, Ecol. Res., 18, 397-404, 2003.

Battarbee, R. W., Jones, V. J., Flower, R. J., Cameron, N.J ., Bennion, H., Carvalho, L., Juggins, S.: Diatoms, in: Tracking environmental change using lake sediments Vol 3, edited by: Smol, J. P., Birks, H. J., and Last, W. M., Dordrecht, Springer, 155-202, 2001.

Belykh, O. I., Ekaterina, G., Sorokovikova, T., SaphonovaI. A., Tikhonova, V: Autotrophic picoplankton of Lake Baikal: Composition, abundance and structure. Hydrobiol., 568, 9-17, 2006.

Berger, A., and Loutre, M. F.: Insolation values for the climate of the past 10 million years, Quat. Sci. Rev., 10, 297–317, 1991

Bezrukova, E. V., Tarasov, P. E., Solovieva, N., Krivonogov, S. K., and Riedel, F.: Last glacial–interglacial vegetation and environmental dynamics in southern Siberia: Chronology, forcing and feedbacks, Palaeogeogr., Palaeoclimatol., Palaeoecol., 296, 185-198, 2010.

Blaauw, M., and Christen, J. A.: Flexible paleoclimate age-depth models using an autoregressive gamma process, Bayesian Analysis, 6, 457-474, 2011.

Bondarenko, N. A,, Belykh, O. I., Golobokova, L. P., Artemyeva, O. V., Logacheva, N. F., Tikhonova, I. V., Lipko, I. A., Kostornova, T. Y., Parfenova, V. V., Khodzher, T. V., Ahn, T. S., Zo, Y. G.: Stratified distribution of nutrients and extremophile biota within freshwater ice covering the surface of Lake Baikal, J. Microbiol., 50, 8-16. 2012.

Bond, G., Kromer, B., Beer, J., Muscheler, R., Evans, M., Showers, W., Hoffmann, S., Lotti-Bond, R., Hajdas, I., and Bonani, G.: Persistent solar influence on North Atlantic climate during the Holocene, Science, 294, 2130-2136, 2001.

Borcard, D., Gillet, F., and Legendre, P.: Numerical ecology with R, 2nd edition. Use R! series, Springer International Publishing AG. Xv + 435 pp 2018.

Bradbury, J. P., Bezrukova, Ye. V., Chernyaeva, G. P., Colman, S. M., Khursevich, G., King, J. W., Likoshway, Ye. V.: A synthesis of post-glacial diatom records from Lake Baikal. J. Paleolim., 10, 213–252, 1994.

Broecker, W. S., Denton, G. H., Edwards, R. L., Cheng, H., Alley, R. B., and Putnam, A. E.: Putting the Younger Dryas cold event into context, Quat. Sci. Rev., 29,1078-1081, 2010.

Burson, A., Stomp, M., Greenwell, E., Grosse, J., and Huisman, J.: Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community, Ecology, 99, 1108-1118, 2018.

Bush, A. B. G.: CO_2/H_2O and orbitally driven climate variability over central Asia through the Holocene. Quat. Int., 136, 15–23, 2005.

Callander, E., and Granina, L.: Biogeochemical silica mass balance in Lake Baikal, Russia, in: Proceedings 8th International Symposium of Water–Rock Interaction, edited by Kharaka, Y. K., Chudaev, O. V., Balkema, Rotterdam, 341–344, 1995.

Cardinale, B. J., Hillebrand, H., Harpole, W. S., Gross, K., and Ptacnik, R.: Separating the influence of resource ‘availability’ from resource ‘imbalance’ on productivity–diversity relationships, Ecol. Lett., 12, 475-487, 2009.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., and Kinzig, A. P.: Biodiversity loss and its impact on humanity, Nature, 486, 59-67, 2012.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., and Ellison, A. M.: Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies, Ecol. Monogr., 84, 45-67, 2014.

Charlet, F., Fagel, N., De Batist, M., Hauregard, F., Minnebo, B., Meischner, D., and SONIC Team.: Sedimentary dynamics on isolated highs in Lake Baikal: evidence from detailed high-resolution geophysical data and sediment cores, Global Planet. Change, 46, 125-144, 2005.

Chase, J., and Leibold, M.: Spatial scale dictates the productivity–biodiversity relationship. Nature, 416, 427–430, 2002.

Chivian, E.: Biodiversity: its importance to human health. Interim Executive Summary. Published by Centre for Global Health and the Environment, Harvard Medical School, Harvard. 2003.

Deevey, E.: Coaxing history to conduct experiments, Bioscience, 19, 40–43, 1969.

Demske, D., Heumann, G., Granoszewski, W., Nita, M., Mamakowa, K., Tarasov, P. E., and Oberhänsli, H.: Late glacial and Holocene vegetation and regional climate variability evidenced in high-resolution pollen records from Lake Baikal, Global Planet. Change, 46, 255-279, 2005.

Denton, G. H., Anderson, R. F., Toggweiler, J. R., Edwards, R. L., Schaefer, J. M., and Putman, A. E.: The Last Glacial Termination. Science, 328, 1652-1656, 2010.

Dixit, Y., Hodell, D.A., and Petrie, C.A.: Abrupt weakening of the summer monsoon in northwest India ~4100 yr ago. Geology, 42, 339–342, 2014.

Dodson, S. I., Arnott, S. E., Cottingham, K. L.: The relationship in lake communities between primary productivity and species richness, Ecology, 81, 2662-2679, 2000.

Dykoski, C. A., Edwards, R. L., Cheng, H., Yuan, D., Cai, Y., Zhang, M., Lin, Y., Qing, J., An, Z., and Revenaugh, J.: A high-resolution, absolute-dated Holocene and deglacial Asian monsoon record from Dongge Cave, China, Earth Planet. Sci. Lett., 233, 71-86, 2005.

Edlund, M. B.: Persistent low diatom plankton diversity within the otherwise highly diverse Lake Baikal ecosystem. Nova Hedwigia 1310, 339–356, 2006.

Fietz, S., Sturm, M., and Nicklisch, A.: Flux of lipophilic photosynthetic pigments to the surface sediments of Lake Baikal. Global Planet. Change, 46, 29-44, 2005.

Fisher, T. G., Smith, D. G., and Andrews, J. T.: Preboreal oscillation caused by a glacial Lake Agassiz flood, Quat. Sci. Rev., 21, 873-878, 2002.

Galazii, G. I.: State of the ecosystem of Lake Baikal and its catchment area: problems of conservation and rational use of resources. In: Conservation and Management of Lakes (Ed. By J.Sal·nki & S. Herodek), (Symp. Biol. Hung.) 38, 349-359, 1989.

Ganopolski, A., Kubatzki, C., Claussen, M., Brovkin, V., and Petoukhov, V.: The influence of vegetation-atmosphere-ocean interaction on climate during the mid-Holocene. Science, 280, 1916-1919, 1998.

Gotelli, N. J., and Ellison, A.: A Primer of Ecological Statistics, Sinauer, Sunderland, 2013.

Granin, N. G., Jewson, D. H., Gnatovsky, R. Yu., Levin, L. A., Zhdanov, A. A., Gorbunova, L. A., Tsekhanovsky, V. V., Doroschenko, L. M., and Mogilev, N. Yu: Turbulent mixing under ice and the growth of diatoms in Lake Baikal. Verh. Internat. Verein. Limnol., 27, 2812-2814, 2000.

Gross, K., and Cardinale, B. J.: Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities, The American Naturalist, 170, 207-220, 2007.

Hagan, J. G., Vanschoenwinkel, B., and Gamfeldt, L.: We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. Ecol. Lett., 00, 1–12. https://doi.org/10.1111/ele.13874 2021.

Hampton, S. E, Galloway, A. W. E., Powers, S. M., Ozersky, T., Woo, K. H., Batt, R. D., Labou, S. G., O'Reilly, C. M., Sharma, S., Lottig, N. R., Stanley, E. H., North, R. L., Stockwell, J. D., Adrian, R., Weyhenmeyer, G. A., Arvola, L., Baulch, H. M., Bertani, I., Bowman, L. L. Jr., Carey, C. C., Catalan, J., Colom-Montero, W., Domine, L. M., Felip, M., Granados, I., Gries, C., Grossart, H.-P., Haberman, J., Haldna, M., Hayden, B., Higgins, S. N., Jolley, J. C., Kahilainen, K. K., Kaup, E., Kehoe, M. J., MacIntyre, S., Mackay, A. W., Mariash, H. L., McKay, R. M., Nixdorf, B,. Nõges, P., Nõges, T., Palmer, M., Pierson, D. C., Post, D. M., Pruett, M. J., Rautio, M., Read, J. S., Roberts, S. L., Rücker, J., Sadro, S., Silow, E. A., Smith, D. E., Sterner, R. W., Swann, G. E. A., Timofeyev, M. A., Toro, M., Twiss, M. R., Vogt, R. J., Watson, S. B., Whiteford, E. J., and Xenopoulos, M. A.: Ecology under lake ice. Ecol. Lett., 20, 98-111, 2017.

Hampton, S. E., McGowan, S., Ozersky, T., Virdis, S. G. P., Vu, T. -T., Spanbauer, T., Kraemer, B., Swann, G., Mackay, A. W., Powers, S., Meyer, M. F., Labou, S. G., O'Reilly, C. M., DiCarlo, M., Galloway, A. W. E., and Fritz, S.: Recent ecological change in ancient lakes, Limnol. Oceanogr., 63, 2277-2304, 2018.

Helama, S., Jones, P. D., and Briffa, K. R.: Dark Ages Cold Period: a literature review and directions for future research, The Holocene, 27, 1600-1606, 2017.

Hill, M. O.: Diversity and evenness: A unifying notation and its consequences, Ecology, 54, 427-432, 1973.

Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, U., and Zohary, T.: Biovolume calculations for pelagic and benthic microalgae, J. Phycol., 35, 403-424, 1999.

Horiuchi, K., Matsuzaki, H., Osipov, E., Khlystov, O., and Fujii, S.: Cosmogenic ^{10}Be and ^{26}Al dating of erratic boulders in the southern coastal area of Lake Baikal, Siberia, Nucl. Instrum. Methods Phys. Res. Sect., 223, 633-638, 2004.

Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M., Sommeijer, B.: Changes in turbulent mixing shift competition for light between phytoplankton species, Ecology, 85, 2960-2970, 2004.

Interlandi, S. J., and Kilham, S. S.: Limiting resources and the regulation of diversity in phytoplankton communities, Ecology, 82, 1270-1282, 2001.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., De Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S. T., Mori, A. S., Naeem, S., Niklaus, P. A., Polley, W., Reich, P. B., Roscher, C., Seabloom, E. W., Smith, M.D., Thakur, M. P., Tilman, D., Tracy, B. F., van der Putten, W.H ., can Ruijven, J., Weigelt, A., Weisser, W. W., Wilsey, B., and Eisenhauer, N.: Biodiversity increases the resistance of ecosystem productivity to climate extremes, Nature, 526, 574-577, 2015.

Izmest'eva, L. R., Moore, M. V., and Hampton, S.E.: Seasonal dynamics of common phytoplankton in Lake Baikal. Proceedings of Samara RAS (Russian Academy of Sciences) Scientific Centre. 8, 191-196, 2006. (In Russian)

Izmest'eva L. R, Moore, M. V., Hampton, S. E., Ferwerda, C. J., Gray, D. K., Woo, K. H., Pislegina, H. V., Krashchuk, L. S., Shimaraeva, S. V., and Silow, E. A.: Lake-wide physical and biological trends associated with warming in Lake Baikal. Journal of Great Lakes Research, 42, 6-17, 2016.

Jewson, D. H., and Granin, N. G.: Cyclical size change and population dynamics of a planktonic diatom, *Aulacoseira baicalensis,* in Lake Baikal. Eur. J. Phycol., 50, 1-15, 2015.

Jewson, D. H., Granin, N. G., Zhdanov, A. A., Gorbunova, L. A., Bondarenko, N. A., and Gnatovsky, R. Yu.: Resting stages and ecology of the planktonic diatom *Aulacoseira skvortzowii* in Lake Baikal, Limnol. Oceanogr., 53, 1125-1136, 2008.

Jewson, D. H., Granin, N. G., Zhdarnov, A. A., Gorbunova, L. A., and Gnatovsky, R.Y.: Vertical mixing, size change and resting stage formation of the planktonic diatom *Aulacoseira baicalensis*. Eur. J. Phycol., 45, 354-364, 2010.

Jewson, D. H., Granin, N. G., Gnatovsky, R. Y., Lowry, S. F., and Teubner, K., Coexistence of two *Cyclotella* diatom species in the plankton of Lake Baikal, Freshwat. Biol., 60, 2113-2126, 2015.

Jost, L., The relation between evenness and diversity, Diversity, 2, 207-232, 2010.

Jovanovska, E., Cvetkoska, A., Hauffe, T., Levkov, Z., Wagner, B., Sulpizio, R., Francke, A., Albrecht, C., and Wilke, T.: Differential resilience of ancient sister lakes Ohrid and Prespa to environmental disturbances during the Late Pleistocene, Biogeosciences, 13, 1149–1161, https://doi.org/10.5194/bg-13-1149-2016, 2016.

Juggins S. C2 version 1.7.7: Software for ecological and palaeoecological data. University of Newcastle, Newcastle, 2014.

Kéfi, S., Domínguez-Garcia, V., Donohue, I., Fontaine, C., Thébault, E., and Dakos, V.: Advancing out knowledge of ecological stability. Ecol. Lett., 22, 1349-1356, 2019.

Khursevich, G. K., Karabanov, E. B., Prokopenko, A. A., Williams, D. F., Kuzmin, M. I., Fedenya, S. A., Gvozdkov, A. A.: Insolation regime in Siberia as a major factor controlling diatom production in Lake Baikal during the past 800,000 years. Quat. Int. 80–81, 47–58, 2001.

Khursevich, G. K., Prokopenko, A. A., Fedenya, S. A., Tkachenko, L. I., Williams, D. F.: Diatom biostratigraphy of Lake Baikal during the past 1.25 Ma: new results from BDP-96-2 and BDP-99 drill cores. Quat. Int., 136, 95–104, 2005.

Kilham, R., Kilham, S.S., and Hecky, R. E.: Hypothesized resource relationships among African planktonic diatoms. Limnol. Oceanogr. 31, 1169-1181, 1986.

Korhonen, J. J., Wang, J., and Soininen, J.: Productivity–diversity relationships in lake plankton communities, PloS One, 6, p.e22041, 2011.

Kovhova, O. M., and Izmest'eva, L.R.: Lake Baikal: evolution and diversity, Backhuys, Leiden, 1998.

Kozhov, M.: Lake Baikal and its life. W. Junk, The Hague. 344pp, 1963.

Kravtsova, L. S., Izhboldina, L. A., Khanaev, I. V., Pomazkina, G. V., Rodionova, E. V., Domysheva, V. M., Sakirko, M. V., Tomberg, I. V., Kostornova, T. Y., Kravchenko, O. S., and Kupchinsky, A. B.: Nearshore benthic blooms of filamentous green algae in Lake Baikal, J. Great Lakes Res., 40, 441-448, 2014.

Legendre P, and Gallagher E. D.: Ecologically meaningful transformations for ordination of species data. Oecologia, 129, 271–280, 2001.

Luethje, M., and Snyder, J.: Climate-related morphological changes in *Pantocsekiella* (Mediophyceae) spanning 0-1.2 Ma in the Lake El'gygytgyn, northeastern Russia including *Pantocsekiella elgygytgynensis* sp. nov. Phytotaxa, 478, 67-91, 2021.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., and Tilman, D.: Biodiversity and ecosystem functioning: current knowledge and future challenges, Science, 294, 804-808, 2001.

Mackay, A. W.: The paleoclimatology of Lake Baikal: a diatom synthesis and prospectus, Earth Sci. Rev., 82, 181-215, 2007.

Mackay, A. W., Flower, R. J., Kuzmina, A. E., Granina, L. Z., Rose, N. L., Appleby, P. G., Boyle, J. F., and Battarbee, R. W.: Diatom succession trends in recent sediments from Lake Baikal and their relation to atmospheric pollution and to climate change, Philos. T. R. Soc. B: Biol. Sci., 353, 1011-1055, 1998.

Mackay, A. W., Swann, G. E. A., Brewer, T. S., Leng, M. J., Morley, D. W., Piotrowska, N., Rioual, P., and White, D.: A reassessment of late glacial - Holocene diatom oxygen isotope record from Lake Baikal using a geochemical mass-balance approach, J. Quat. Sci., 26, 627-634, 2011.

Mackay, A. W., Seddon, A. W. R., Leng, M. J., Heumann, G., Morley, D. W., Piotrowska, N., Rioual, P., Roberts, S., and Swann, G.E.A.: Holocene carbon dynamics at the forest-steppe ecotone of southern Siberia, Global Change Biol., 23, 1942-1960, 2017.

Marcott, S. A., Shakun, J. D., Clark, P.U., and Mix, A.C.: A reconstruction of regional and global temperature for the past 11,300 years. Science, 339, 1198-1201, 2013.

Mayewski, P. A., Meeker, L. D., Twickler, M. S., Whitlow, S., Yang, Q., and Prentice, M.: Major features and forcing of high latitude Northern Hemisphere atmospheric circulation using a 110,000 year long glaciochemical series, J. Geophys. Res., 102, 26345-26366, 1997.

Mayewski, P. A., Rohling, E. E., Stager, J. C., Karlén, W., Maasch, K. A., Meeker, L. D., Meyerson, E. A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R. R., and Steig, E. J.: Holocene climate variability, Quat. Res., 62, 243-255, 2004.

McCann, K.S.: The diversity-stability debate, Nature 405, 228-233, 2000.

McGrady-Steed, J., Harris, P. M., and Morin, P. J.: Biodiversity regulates ecosystem predictability, Nature, 390, 162–165, 1997.

McManus, J. F., Francois, R., Gherardi, J.-M., Keigwin, L. D. and Brown-Leger, S.: Collapse and rapid resumption of Atlantic meridional circulation linked to deglacial climate changes. Nature, 428, 834-837, 2004.

Murton, J. B., Bateman, M. D., Dallimore, S. R., Teller, J. T., and Yang, Z.: Identification of Younger Dryas outburst flood path from Lake Agassiz to the Arctic Ocean, Nature, 464, 740-743, 2010.

National Research Council.: The geological record of ecological dynamics: understanding the biotic effects of future environmental change, The National Academies Press, Washington DC, USA 2005.

Nesje, A., Jansen, E., Birks, H. J .B., Bjune, A. E., Bakke, J., Andersson, C., Dahl, S. O., Kristensen, D. K., Lauritzen, S., Lie, O., and Risebrobakken, B.: Holocene climate variability in the northern North Atlantic region: a review of terrestrial and marine evidence, Geophysical Monograph-American Geophysical Union, 158, 289-322, 2005.

O'Donnell, D. R., Wilburn, P., Silow, E. A., Yampolsky, L. Y., Litchman, E: Nitrogen and phosphorus colimitation of phytoplankton in Lake Baikal: insights from a spatial survey and nutrient enrichment experiments. Limnol. Oceanogr. 62, 1383-1392, 2017.

O’Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., et al.: Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters, 42, 10773-10781, 2015.

Orlóci. L.: An agglomerative method for classification of plant communities. J. Ecol., 55, 193–205, 1967.

Osipov, E. Y., and Khlystov, O. M.: Glaciers and meltwater flux to Lake Baikal during the Last Glacial Maximum, Palaeogeogr., Palaeoclimatol., Palaeoecol., 294, 4-15, 2010.

Panizzo, V. N., Swann, G. E. A., Mackay, A. W., Vologina, E., Alleman, L., Andre, L., Pashley, V. H., Horstwood, M. S. A: Constraining modern day silicon cycling in Lake Baikal. Global. Biogeochem. Cy. 31, 556-574, 2017.

Piotrowska, N., Bluszcz, A., Demske, D., Granoszewski, W., and Heumann, G.: Extraction and AMS radiocarbon dating of pollen from Lake Baikal sediments, Radiocarbon, 46, 181-187, 2004.

Popovskaya, G. I.: Ecological monitoring of phytoplankton in Lake Baikal. Aquat. Ecosyst. Health. 3, 215-225. 2000.

Popovskaya, G. I. Usol'tseva, M. V. Domysheva, V. M. Sakirko, M. V. Blinov, V. V. Khodzher, T. V: The spring phytoplankton in the pelagic zone of Lake Baikal during 2007- 2011. Geogr. Nat. Resour. 36, 253-262, 2015.

Ptacnik, R., Solimini, A. G., Andersen, T., Tamminen, T., Brettum, P., Lepistö, L., Willén, E., and Rekolainen, S.: Diversity predicts stability and resource use efficiency in natural phytoplankton communities, Proc. Natl. Acad. Sci., 105, 5134-5138, 2008.

R Core Team.: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, 2016.

Rasmussen, D. O., Andersen, K. K., Svensson, A. M., Steffensen, J. P., Vinther, B. M., Clausen, H. B., Siggaard-Andersen, M. -L., Johnsen, S. J., Larsen, L. B., Dahl-Jensen, D., Bigler, M., Rothlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., and Ruth, U.: A new Greenland ice core chronology for the last glacial termination. J. Geophys. Res, 111, D06102, 2006.

Reimer, P. J., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A.G., Hughen, K. A., Kromer, B., Manning, S. W., Muscheler, R., Palmer, J. G., Pearson, C., van der Plicht, J., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Turney, C. S. M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S. M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S.: The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon, 62, 725–757, 2020.

Renssen, H., Goosse, H., and Muscheler, R.: Coupled climate model simulation of Holocene cooling events: oceanic feedback amplifies solar forcing. Clim. Past, 2, 79–90, 2006.

Reshetova, S. A., Bezrukova, E. V., Panizzo, V., Henderson, A., Ptitsyn, A. B., Daryin, A. V., and Kalugin, I. A.: Vegetation of Central Transbaikalia in the Late Glacial Period and Holocene, Geography and Natural Resources, 34,172-178, 2013.

Roberts, S., Swann, G. E. A., McGowan, S., Panizzo, V., Vologina, E., Sturm, M., Mackay, A. W.: Evidence of 20th Century ecosystem change in Lake Baikal, Siberia, PLoS One, 13, e0208765. 2018.

Rusak, J. A., Leavitt, P. R., McGowan, S., Chen, G., Olson, O., Wunsam, S., and Cumming, B.F.: Millennial-scale relationships of diatom species richness and production in two prairie lakes, Limnol. Oceanogr., 49, 1290-1299, 2004.

Ryves, D. B., Jewson, D. H., Sturm, M., Battarbee, R. W., Flower, R. J., Mackay, A. W., Granin, N. G.: Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia. Limnol. Oceanogr., 48, 1183-1192, 2003.

Satoh, Y. Katano, T. Satoh, T, Mitamura, O. Anbutsu, K. Nakano, S. Ueno, H. Kihira, M. Drucker, V. Tanaka, Y. Mimura, T. Watanabe, Y. Sugiyama, M.: Nutrient limitation of the primary production of phytoplankton in Lake Baikal. Limnology 7, 225-229, 2006.

Seddon, A. W., Mackay, A. W., Baker, A. G., Birks, H. J. B., Breman, E., Buck, C. E., Ellis, E. C., Froyd, C. A., Gill, J. L., Gillson, L., and Johnson, E.A.: Looking forward through the past: identification of 50 priority research questions in palaeoecology, J. Ecol., 102, 256-267, 2014.

Shimaraev, M. N., and Mizandrontsev, I. B.: Changes in the Lake Baikal ecosystem during the Late Pleistocene and Holocene. Hydrobio., 568, 259-263, 2006.

Shimaraev, M. N., and Domysheva, V. M.: Trends in hydrological and hydrochemical processes in Lake Baikal under conditions of modern climate change, in: Climatic Change and Global Warming of Inland Waters, edited by: Colman, C. R., Kumagai, M., and Robarts, R. D., John Wiley & Sons Ltd, Chichester, UK, 43-66., 2013.

Simpson, G., and Birks, H. J.: Statistical Learning In Palaeolimnology, in: Tracking Environmental Change Using Lake Sediments, edited by: Birks, H. J. B., Lotter, A. F., Juggins, S., and Smol, J. P., Dordrecht, Springer, 249-327, 2012.

Simpson, G. L., and Oksanen, J.: analogue: Analogue matching and Modern Analogue Technique transfer function models, R package version 0.17-1, https://cran.r-project.org/package=analogue, 2016.

Smith, V. H.: Microbial diversity-productivity relationships in aquatic ecosystems, FEMS Microbiol. Ecol., 62, 181-186, 2007.

Soma, Y., Tani, Y., Soma, M., Mitake, H., Kurihara, R., Hashomoto, S., Watanabe, T., and Nakamura, T.: Sedimentary steryl chlorin esters (SCEs) and other photosynthetic pigments as indicators of palaeolimnological change over the last 28,000 years from the Buguldeika Saddle of Lake Baikal, J. Paleolim., 37, 163-175, 2007.

Sommer, U., Adrian, R., Domis, L. D. S., Elser, J. J., Gaedke, U., Ibelings, B. et al: Beyond the plankton ecology group (PEG) model: mechanisms driving plankton succession. Annu. Rev. Ecol. Evol. Syst., 43, 429–448, 2012.

Stuiver, M., Grootes, P. M., and Braziunas, T. F.: The GISP2 δ^{18}O climatic record of the past 16,500 years and the role of the sun, ocean, and volcanoes, Quat. Res., 44, 341-354, 1995.

Swann, G. E. A, Panizzo, V. N., Piccolroaz, S., Pashley, V., Horstwood, M. S. A., Roberts, S., Vologina, E., Piotrowska, N., Sturm, M., Zhdanoc, A., Granin, N., Normal, C., McGowan, S., Mackay, A. W: Changing nutrient cycling in Lake Baikal: the world's oldest lake. Proc. Nat. Acad. Sci., 117, 27211-27217, 2020.

Tani, Y., Kurihara, K., Nara, F., Itoh, N., Soma, M., Soma, Y., Tanaka, A., Yoneda, M., Hirota, M., and Shibata, Y.: Temporal changes in the phytoplankton community of the southern basin of Lake Baikal over the last 24,000 years recorded by photosynthetic pigments in a sediment core, Org. Geochem., 33, 1621-1634, 2002.

Tarasov, L., and Peltier W. R.: Arctic freshwater forcing of the Younger Dryas cold reversal. Nature, 435, 662-665, 2005.

Tarasov, P. E., Bezrukova, E. V., Krivonogov, S. K.: Late Glacial and Holocene changes in vegetation cover and climate in southern Siberia derived from a 15 kyr long pollen record from Lake Kotokel, Clim. Past, 5, 285-295, 2009.

Thiagarajan, N., Subhas, A. V., Southon, J. R., Eiler, J. M., and Adkins, J. F.: Abrupt pre-Bølling–Allerød warming and circulation changes in the deep ocean, Nature, 511, 75-78, 2014.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E.: The influence of functional diversity and composition on ecosystem processes, Science, 277, 1300-1302, 1997.

Tilman, D., Reich, P. B., and Isbell, F.: Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc. N. Acad. Sci., 109, 10394–10397, 2012.

Timoshkin, O A., Samsonov, D. P., Yamamuro, M., Moore, M. V., Belykh, O. I., Malnik, V. V., Sakirko, M. V., Shirokaya, A. A., Bondarenko, N. A., Domysheva, V. M., Fedorova, G. A., Kochetkov, A. I., Kuzmin, A. V., Lukhnev, A. G., Medvezhonkova, O. V., Nepokrytykh, A. V., Pasynkova, E. M., Poberezhnaya, A. E., Potapskaya, N. V., Rozhkova, N. A., Sheveleva, N. G., Tikhonova, I. V., Timoshkina, E. M., Tomberg, I.V ., Volkova, E. A., Zaitseva, E. P., Zvereva, Y. M., Kupchinsky, A. B., and Bukshuk, N. A.: Rapid ecological change in the coastal zone of Lake Baikal

(East Siberia): Is the site of the world's greatest freshwater biodiversity in danger?, J. Great Lakes Res., 42, 487-497, 2016.

Walker, M., Head, M. J., Berkelhammer, M., Björck, S., Cheng, H., Cwynar, L., Fisher, D., Gkinis, V., Long, A., Lowe, J. and Newnham, R.: Formal ratification of the subdivision of the Holocene Series/Epoch (Quaternary System/Period): two new Global Boundary Stratotype Sections and Points (GSSPs) and three new stages/subseries. Episodes, 41, 213-223, 2018.

Wanner, H., Mercolli, L., Grosjean, M., and Ritz, S. P.: Holocene climate variability and change: a database review, J. Geol. Soc. Lond., 172, 254-263, 2014.

Williams, D. F., Kuzmin, M. I., Prokopenko, A. A., Karabanov, E. B., Khursevich, G. K., and Bezrukova, E.V.: The Lake Baikal drilling project in the context of a global lake drilling initiative, Quat. Int., 80, 3-18, 2001.

Williams, J. W., Blois, J. L., and Shuman, B. N.: Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary, J. Ecol., 99, 664-677, 2011.

Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R. and Cariveau, D. P.: Abundance of common species, not species richness, drives delivery of a real-world ecosystem service, Ecol. Lett., 18, 626-635, 2015.

Yachi, S., and Loreau, M.: Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis, Proc. Natl. Acad. Sci., 96, 1463-1468, 1999.

Table 1: GAMs to investigate PDR trends during pre-defined climate periods. edf = effective degrees of freedom, and ref.df = reference degrees of freedom. The goodness-of-fit statistics show the adjusted $r^2 = 0.462$ and the deviance explained is 53.2 %.

Climate period	**edf**	**ref.df**	**F**	***p*–value**
Late Holocene	3.719	4.481	5.242	0.0002 ***
Middle Holocene	1.001	1.002	6.672	0.0100 *
Early Holocene	2.291	2.916	7.183	0.0001 ***
Younger Dryas	1.001	1.001	20.168	9.18e-06 ***
Bølling–Allerød	1.105	1.203	0.652	0.4030
pre-BA	2.562	3.167	2.760	0.0443 *

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Figure Legends:

Fig. 1: Map of Lake Baikal and its catchment, with locations of the different cores used or mentioned in this paper, including the coring location on the Vydrino Shoulder, where our study was undertaken. Also shown is Lake Kotokel that has provided independent climate reconstructions used in this study (Tarasov et al. 2009).

Fig. 2: 'Bacon' Age-depth model (Blaauw & Christen, 2011) for Vydrino box (CON01–605–05) and piston cores (CON01–605–03) of radiocarbon AMS dates calibrated using IntCal20 radiocarbon calibration curve (Reimer et al., 2020).

Fig. 3: Relative abundances of sub-fossil planktonic and tychoplanktonic diatoms spanning the past c. 16,000 years from Vydrino Shoulder. Diatoms which grow mainly before summer stratification are shown in blue, while those that mainly grow after summer stratification are shown in green. DCA axis 1 sample scores summarize the major trend in species turnover.

Fig. 4: Comparison of Hill's richness ($N0$), diversity ($N1$ and $N2$) and evenness ($N2/N1$ ratio) trends over the past c. 16,000 years. Richness and diversity values were further divided by sediment accumulation rates over time, so these measures become estimated Hill's numbers per cm^{-2} yr^{-1}

Fig. 5: Multivariate classification tree (MCT) for Lake Baikal planktonic and tychoplanktonic diatoms over the past c. 16,000 years. Time periods used in multivariate classification tree analyses are: the pre Bølling–Allerød (pre–BA), the Bølling–Allerød (B–A) interstadial, the Younger Dryas stadial and the three recently ratified Early, Middle and Late Holocene subepochs (Walker et al. 2018). The histograms show the transformed abundances of the discriminating taxa within each leaf. These are listed in decreasing order. The numbers under the histograms represent the relative error within each leaf, and $n =$ the total number of samples. At the bottom is the summary of the residual error (RE), cross-validated error (CVRE), and standard error (SE). The r^2 will be 1-RE.

Fig. 6: Stratigraphical profile showing trends in palaeoproductivity over the past c. 16,000 years: the proportion of diatoms that bloom in the autumn versus those that bloom in the spring; estimates of palaeoproductivity derived from spring (orange) and autumn (dark brown) diatom biovolume accumulate rates (BVAR μm^3 cm^{-2} yr^{-1}); and log-transformed ratio of autumnal / spring palaeoproductivity.

Fig. 7: Palaeoproductivity–diversity relationships explored using generalized additive models (GAMs) that allow different smooths for the pre–defined climatic periods: pre Bølling–Allerød, (Bølling–Allerød), Younger Dryas, Early Holocene, Middle Holocene, and Late Holocene. The dots represent the data points, the thick line is the fitted GAM response for each period, and the shaded areas represent the 95 % confidence intervals around the mean fitted response.

Fig. 8: Multi-archive data plotted alongside (a) DCA axis 1 sample scores of Lake Baikal diatoms, as a measure of turnover over the past c. 16,000 years; (b) mean pollen–inferred annual precipitation from Lake Kotokel, with smooth line representing the mean 3–point moving average (Tarasov et al. 2009); (c) mean pollen–inferred temperature of the warmest month from Lake Kotokel, with smooth line representing the mean 3–point moving average (Tarasov et al. 2009); (d) mean Northern Hemisphere temperature stack records for 60° latitude bands (30° N – 90° N; Marcott et al. 2013); (e) $\delta^{18}O$ values of Dongge Cave stalagmite D4 (Dykoski et al. 2005); (f) K^+ ion concentrations (ppb) from GISP2 D core (Mayewski et al. 1997); (g) North Atlantic core GGC5 $^{231}Pa/^{230}Th$ meridional circulation data; (h) $\delta^{18}O$ values of NGRIP ice core (Rasmussen et al. 2006); (i) June insolation 60° N (W m^{-2}; Berger & Loutre, 1991); (j) obliquity (ε).

Fig. 1

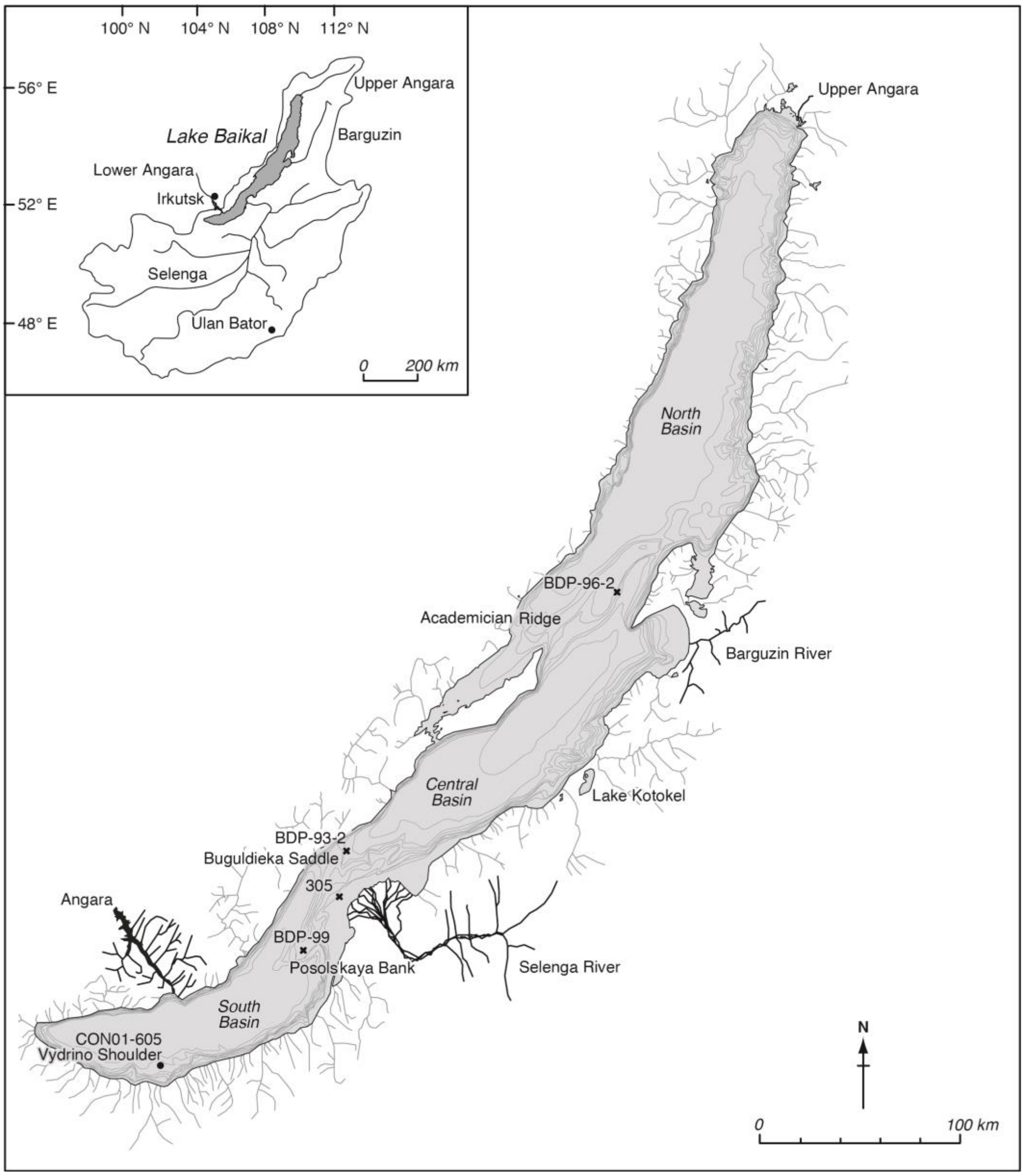

100° N
104° N
108° N
112° N
56° E
52° E
48° E
Upper Angara
Lake Baikal
Barguzin
Lower Angara
Irkutsk
Selenga
Ulan Bator
0
200 km
Upper Angara
North Basin
BDP-96-2
Academician Ridge
Barguzin River
Central Basin
Lake Kotokel
BDP-93-2
Buguldieka Saddle
305
Angara
BDP-99
Posolskaya Bank
Selenga River
South Basin
CON01-605
Vydrino Shoulder
N
0
100 km

Fig. 2

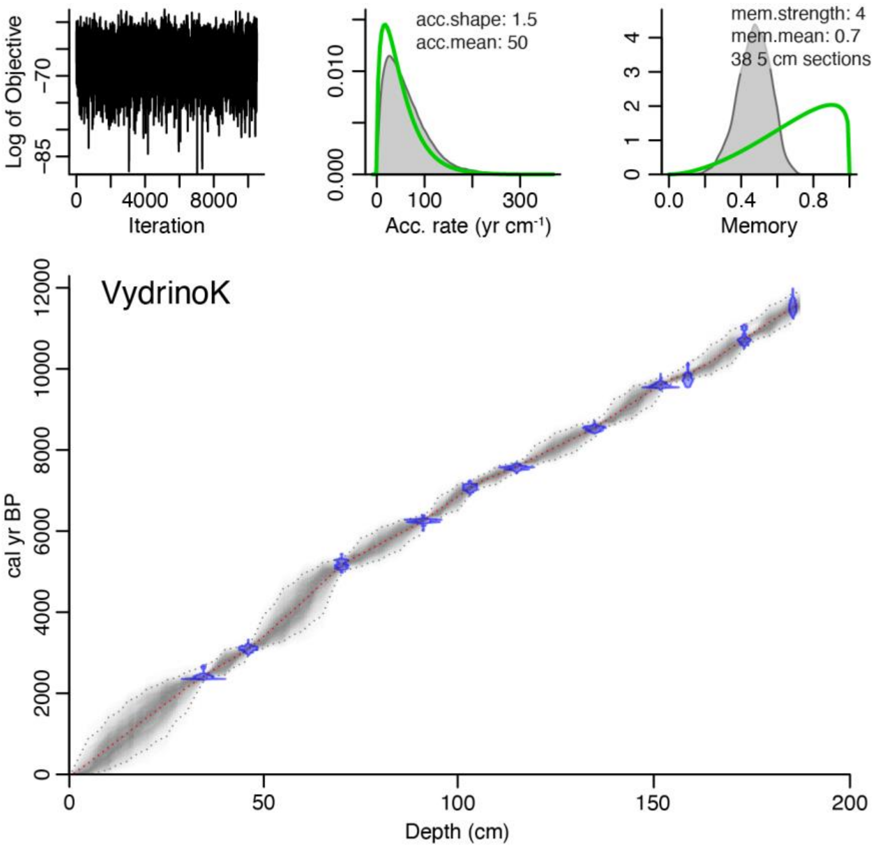

Log of Objective
−70
−85
0
4000
8000
Iteration
acc.shape: 1.5
acc.mean: 50
0.000
0.010
0
100
300
Acc. rate (yr cm^{-1})
mem.strength: 4
mem.mean: 0.7
38 5 cm sections
0
1
2
3
4
0.0
0.4
0.8
Memory
VydrinoK
cal yr BP
0
2000
4000
6000
8000
10000
12000
0
50
100
150
200
Depth (cm)

Fig. 3

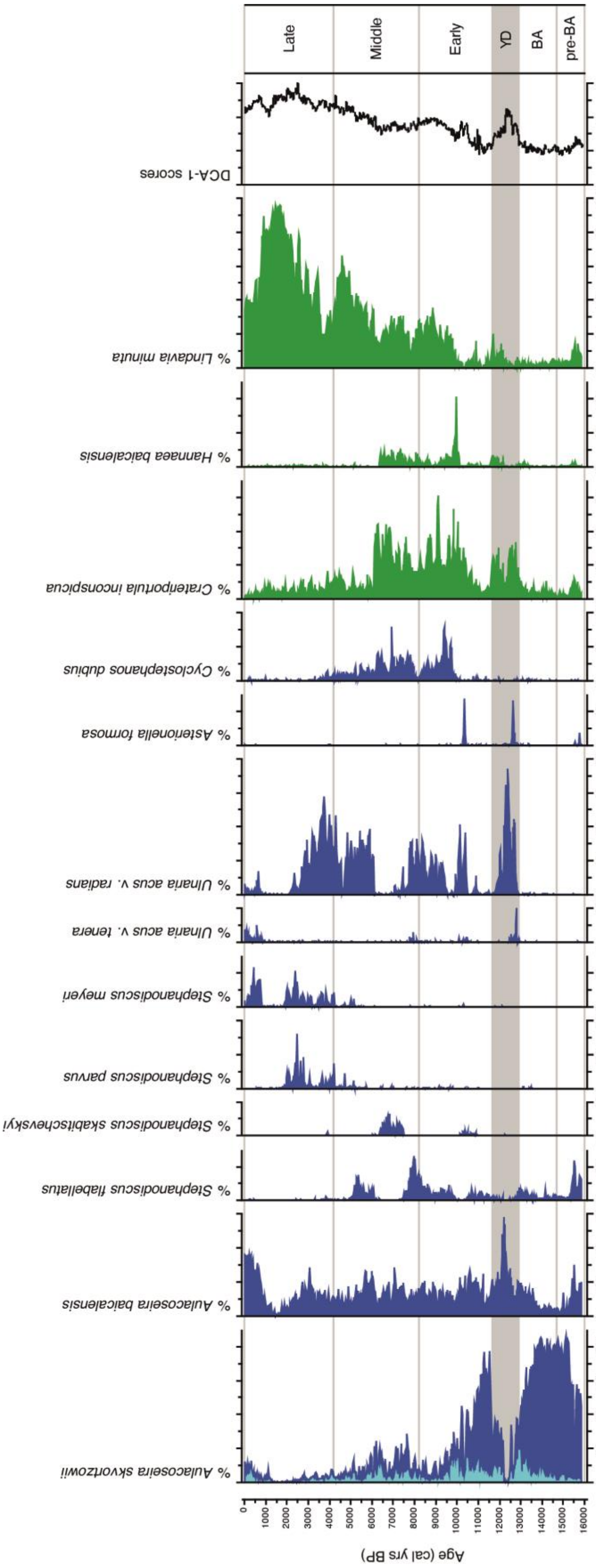

Late
Middle
Early
YD
BA
pre-BA
DCA-1 scores
% Lindavia minuta
% Hannaea baicalensis
% Crateripontula inconspicua
% Cyclostephanos dubius
% Asterionella formosa
% Ulnaria acus v. radians
% Ulnaria acus v. tenera
% Stephanodiscus meyeri
% Stephanodiscus parvus
% Stephanodiscus skabitschevskyi
% Stephanodiscus flabellatus
% Aulacoseira baicalensis
% Aulacoseira skvortzowii
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000
Age (cal yrs BP)

Fig. 4

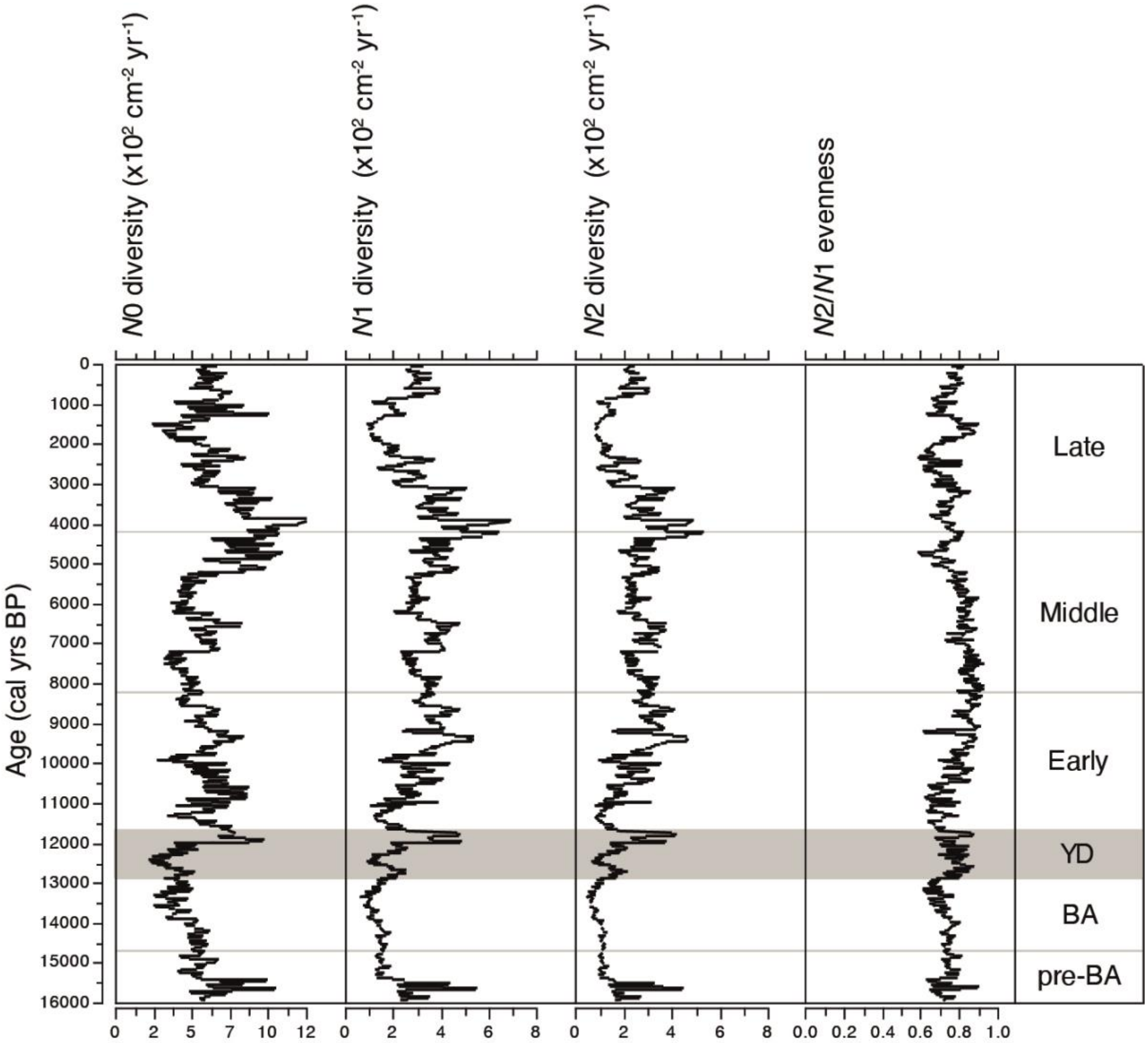

N0 diversity (x10² cm⁻² yr⁻¹)
N1 diversity (x10² cm⁻² yr⁻¹)
N2 diversity (x10² cm⁻² yr⁻¹)
N2/N1 evenness
Age (cal yrs BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000
0 2 5 7 10 12
0 2 4 6 8
0 2 4 6 8
0.0 0.2 0.4 0.6 0.8 1.0
Late
Middle
Early
YD
BA
pre-BA

Fig. 5

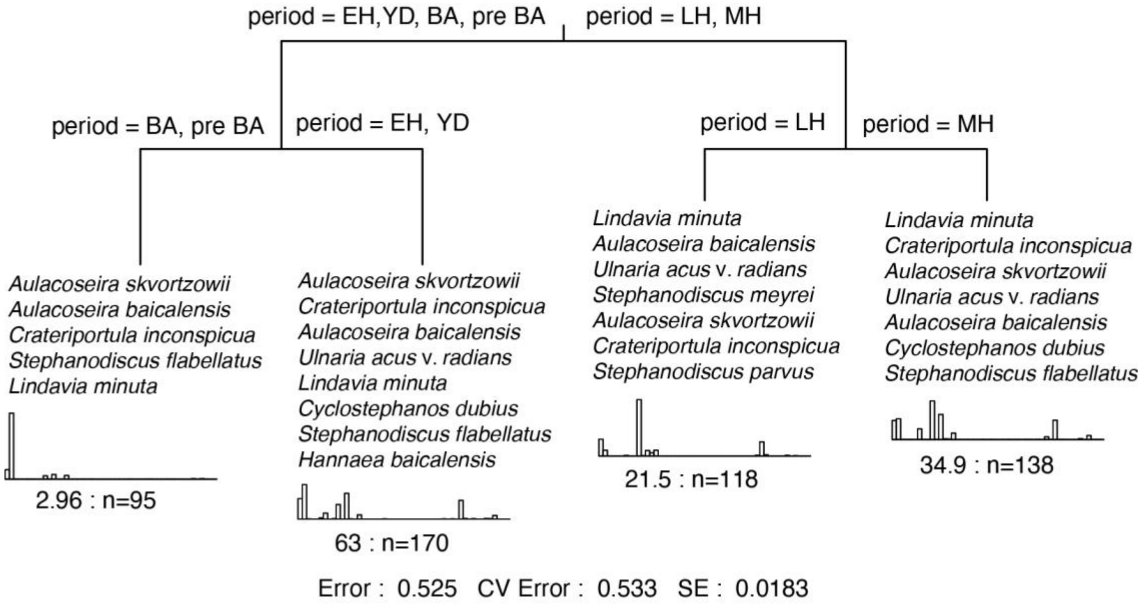

period = EH,YD, BA, pre BA
period = LH, MH
period = BA, pre BA
period = EH, YD
period = LH
period = MH
Aulacoseira skvortzowii
Aulacoseira baicalensis
Crateriportula inconspicua
Stephanodiscus flabellatus
Lindavia minuta
2.96 : n=95
Aulacoseira skvortzowii
Crateriportula inconspicua
Aulacoseira baicalensis
Ulnaria acus v. *radians*
Lindavia minuta
Cyclostephanos dubius
Stephanodiscus flabellatus
Hannaea baicalensis
63 : n=170
Lindavia minuta
Aulacoseira baicalensis
Ulnaria acus v. *radians*
Stephanodiscus meyrei
Aulacoseira skvortzowii
Crateriportula inconspicua
Stephanodiscus parvus
21.5 : n=118
Lindavia minuta
Crateriportula inconspicua
Aulacoseira skvortzowii
Ulnaria acus v. *radians*
Aulacoseira baicalensis
Cyclostephanos dubius
Stephanodiscus flabellatus
34.9 : n=138
Error : 0.525 CV Error : 0.533 SE : 0.0183

Fig. 6

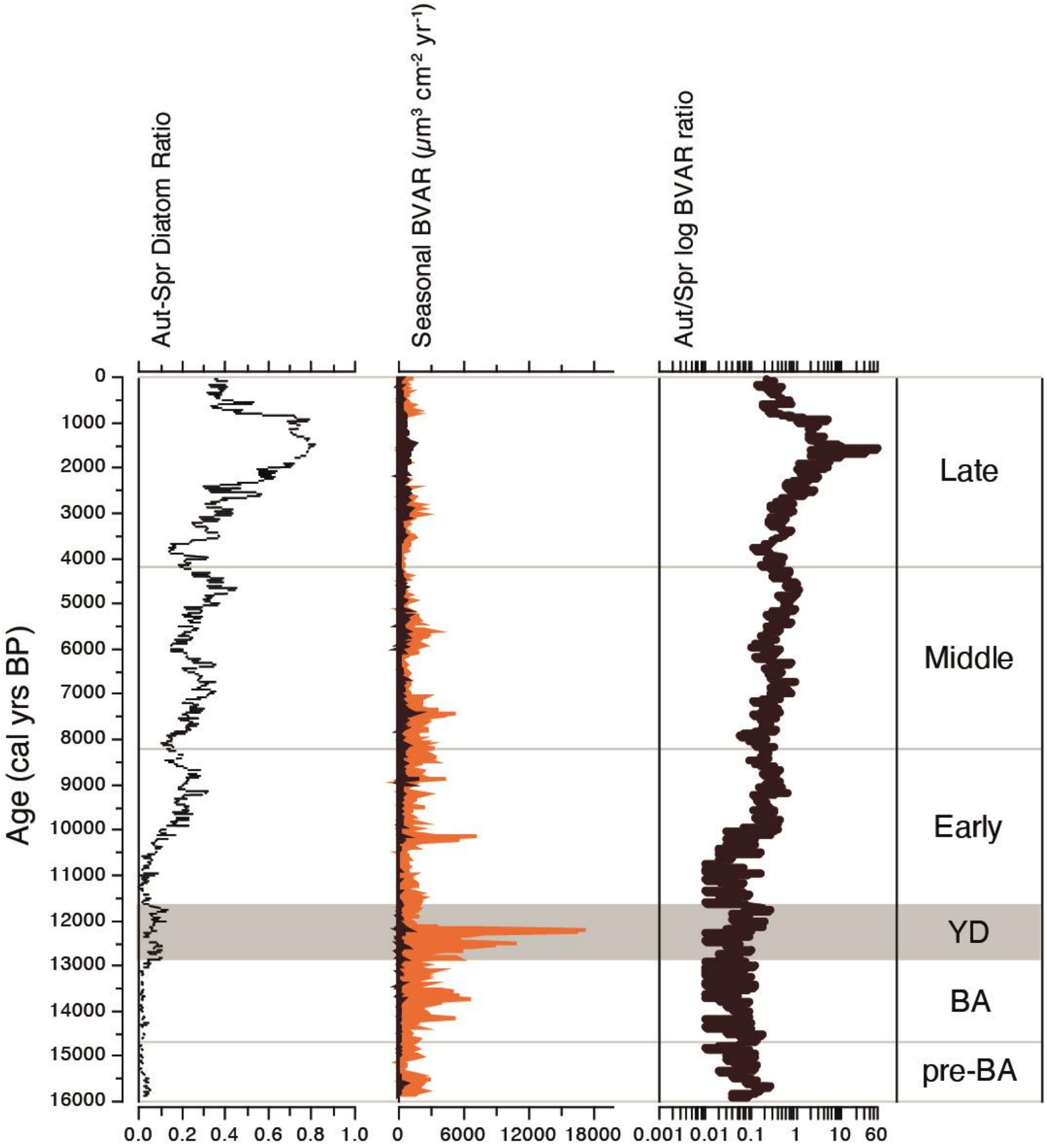
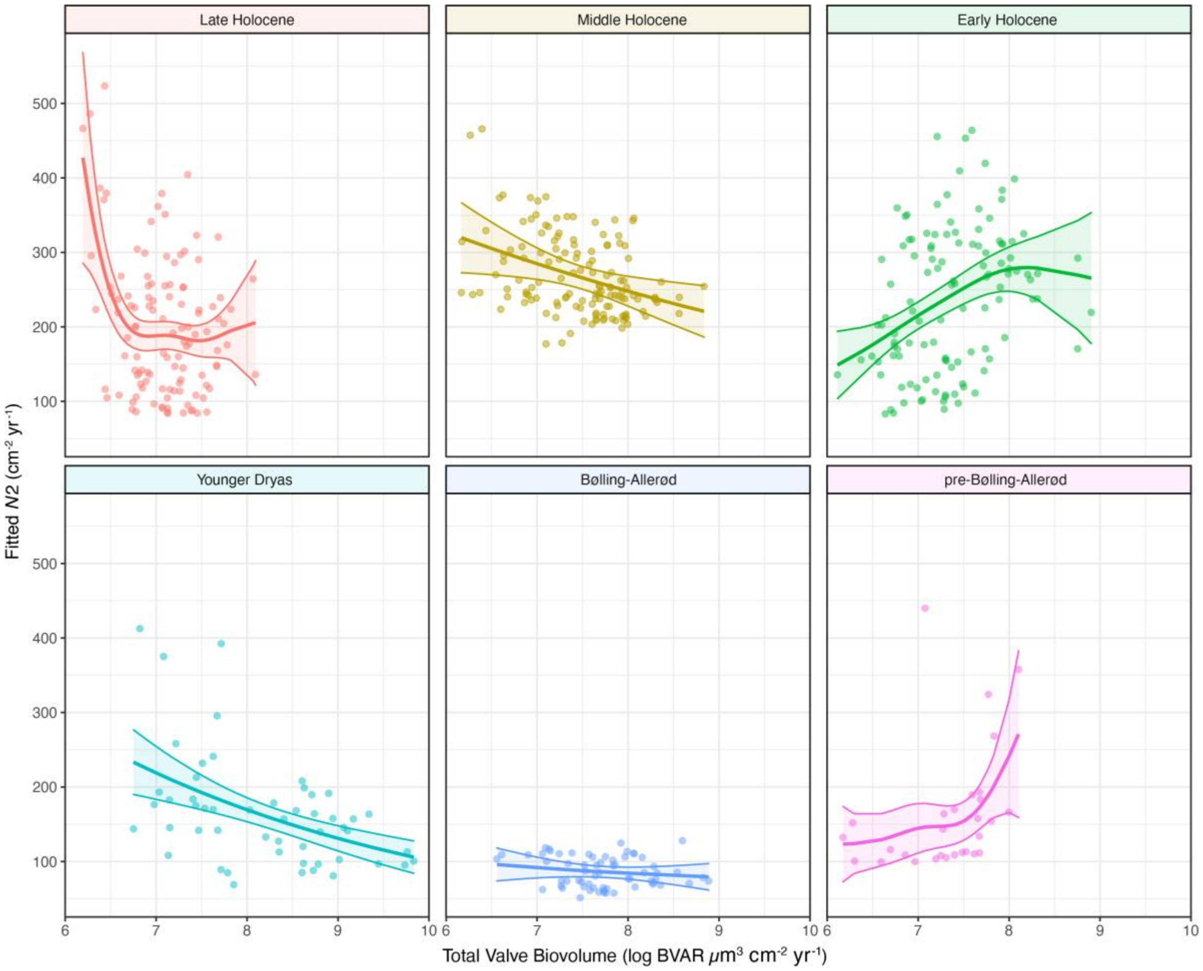
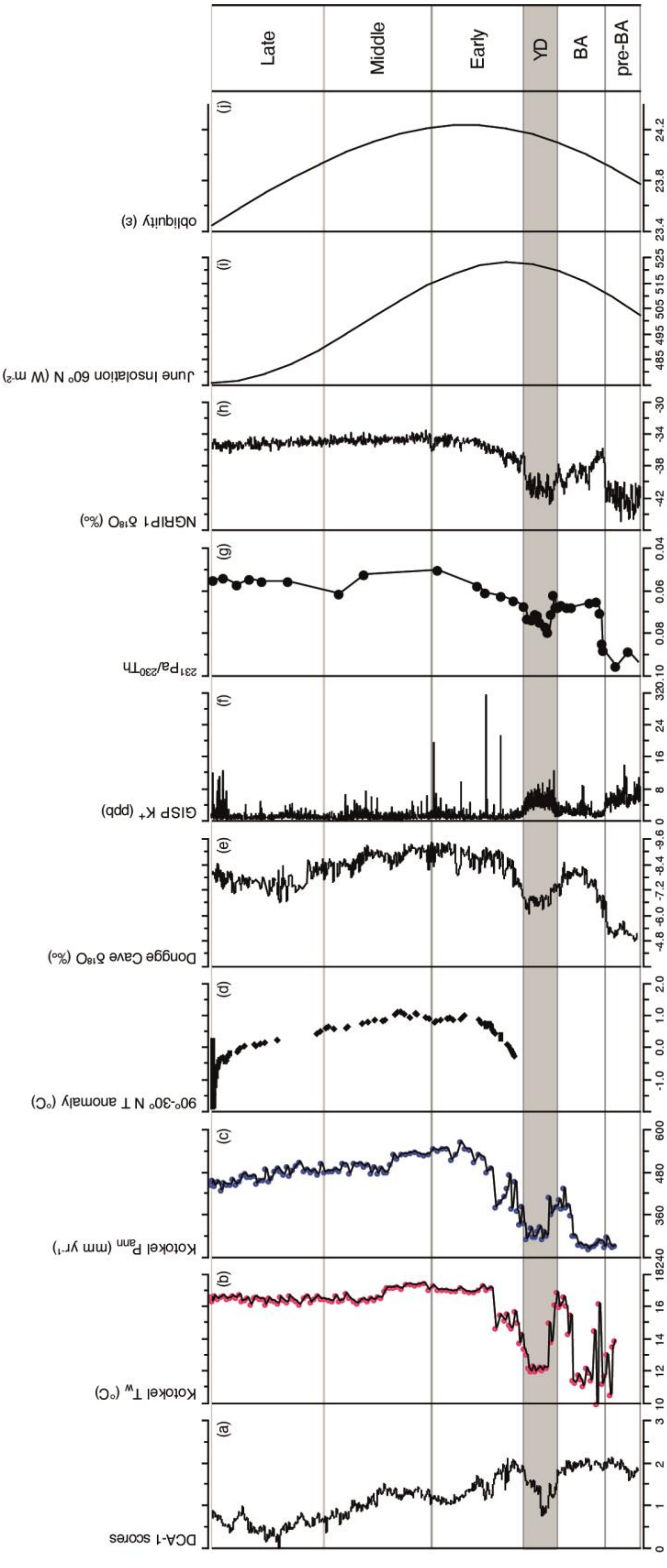

Aut-Spr Diatom Ratio
Seasonal BVAR ($\mu m^3\ cm^{-2}\ yr^{-1}$)
Aut/Spr log BVAR ratio
Age (cal yrs BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000
0.0
0.2
0.4
0.6
0.8
1.0
0
6000
12000
18000
0.001
0.01
0.1
1
10
60
Late
Middle
Early
YD
BA
pre-BA

Fig. 7



Late Holocene
Middle Holocene
Early Holocene
Younger Dryas
Bølling-Allerød
pre-Bølling-Allerød
Fitted $N2$ (cm^{-2} yr^{-1})
500
400
300
200
100
6
7
8
9
10
Total Valve Biovolume (log BVAR μm^3 cm^{-2} yr^{-1})

Fig. 8



Late
Middle
Early
YD
BA
pre-BA
(j)
obliquity (ε)
23.4
23.8
24.2
(i)
June Insolation 60° N (W m-2)
485
495
505
515
525
(h)
NGRIP1 δ18O (‰)
-42
-38
-34
-30
(g)
231Pa/230Th
0.10
0.08
0.06
0.04
(f)
GISP K+ (ppb)
0
8
16
24
32
(e)
Dongge Cave δ18O (‰)
-4.8
-6.0
-7.2
-8.4
-9.6
(d)
90°-30° N T anomaly (°C)
-1.0
0.0
1.0
2.0
(c)
Kotokel Pann (mm yr-1)
240
360
480
600
(b)
Kotokel Tw (°C)
10
12
14
16
18
(a)
DCA-1 scores
0
1
2
3
Age (cal yrs BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000