

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

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47

48 **Abstract**

49

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

81 future under a warming climate.

82

83 **Key words:** palaeoproductivity, abrupt climate change, palaeolimnology, Holocene, Late

84 glacial, productivity–diversity relationship, generalized additive models, multivariate

85 classification trees

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90 **1. Introduction**

91

92 Understanding the role that biological diversity plays in ecosystem stability and function is an
93 important challenge in ecological research (Tilman et al. 1997; McCann 2000; Loreau et al.
94 2001; Isbell et al. 2015; Hagen et al. 2021). An ecosystem with higher biodiversity is
95 assumed to be more stable, due to a number of factors, including the presence of species
96 which have considerable plasticity, such that they have wide responses to disturbances
97 (McCann 2000; Luethje and Snyder 2021), and the “insurance effect” (Yachi and Loreau
98 1999) where species redundancy plays an important stabilizing role. Biodiversity loss can
99 lead to reduced ecosystem functioning (Cardinale et al. 2012), which poses serious threats to
100 ecosystem health in general, and human well-being in particular (e.g. Chivian 2003). While
101 the mechanisms behind how diversity controls functioning are not completely understood,
102 dominant species with distinct functional roles are important (Winfree et al. 2015). For
103 example, primary production, a key ecosystem function which helps regulate the global
104 carbon cycle, is tied to species diversity (Tilman et al. 1997; Cardinale et al. 2009; Tilman et
105 al. 2012). However, our understanding of productivity–diversity relationships (PDR) is
106 largely based on short-term observational (Dodson et al. 2000; Ptacnik et al. 2008; Korhonen
107 et al. 2011), experimental (McGrady-Steed et al. 1997; Interlandi & Kilham 2001; Winfree et
108 al. 2015) and modelling approaches (Aoki 2003), with very few long-term studies undertaken
109 (Rusak et al. 2004). This constitutes an important gap in our knowledge because in terms of
110 climate change, productivity–diversity relationships and resource use efficiency (Gross and
111 Cardinale 2007; Ptacnik et al. 2008) will be fundamentally different over long (e.g. climate
112 and landscape evolution) and short (e.g. pulse disturbances such as climate disturbance
113 events (Kéfi et al. 2019)) timescales.

114

115 Palaeoecological approaches provide a potential solution to this challenge, since they can
116 reveal ecological dynamics in response to environmental change which unfold only over very
117 long timescales (National Research Council 2005; Seddon et al. 2014). For example, diatoms
118 are some of the most important primary producers in lake ecosystems, and their sub-
119 fossilised remains provide a record of community variations through time. In addition,
120 because the species composition, biovolume and concentration of diatom valves can be
121 directly measured on sediment sequences, there is a unique opportunity to investigate how
122 community dynamics, diversity and the stability of ecosystem functions such as productivity

123 change over long-timescales. In particular, because the last 16,000 years have been
124 punctuated by a series of large-scale and abrupt climatic shifts, such records open the door
125 for an investigation into the links between biodiversity and the stability of ecosystem
126 functioning associated with climate disturbance events.

127

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

134

135 As yet we do not assume to know the precise nature of the potential productivity–diversity
136 relationships that may have occurred in Lake Baikal over such long timescales. We do know
137 however, that local diversity will be influenced by a range of chemical, biological and
138 physical factors such as nutrient availability, species interactions, and disturbance events such
139 as rapid climate change. Our approach therefore is to explore productivity–diversity
140 relationships over specific timescales independently determined from palaeoclimate studies.
141 We might hypothesise for example, that productivity and diversity will co-vary linearly
142 during rapid warming because increased energy results in increased metabolic rates in the
143 system, but that this relationship might change during periods of relative climate stability. We
144 investigate the range of possible response functions based on those identified by Smith
145 (2007), whether they be negative or positive, whether they be humped or U-shaped, flat or
146 just random (Smith 2007).

147

148 One of the most relevant independent climate studies for this time period is by Tarasov et al.
149 (2009), who modelled pollen-inferred palaeotemperature for neighbouring Lake Kotokel
150 (Fig. 1) for the past 15,000 years. Their reconstructions indicate a period of rapid warming
151 (during the Bølling–Allerød interstadial), rapid cooling (during the Younger Dryas stadial)
152 and relative temperature stability of the Holocene in southern Siberia. However, given that
153 the Holocene has recently been formally subdivided into three ages/subepochs (Walker et al.
154 2018), it is possible to compare productivity–diversity relationships during the Younger
155 Dryas and the Bølling–Allerød, with the Greenlandian/Early, Northgrippian/Middle, and
156 Meghalayan/Late ages/subepochs of the Holocene (henceforth referred to as Early, Middle,

157 and Late Holocene). Our approach is to coax history to conduct experiments (Deevey 1969)
158 in order to deepen our understanding of (very) long-term biodiversity–ecosystem functioning
159 (Loreau 2001) through the exploration of relationships between diatom diversity and
160 productivity, and to test hypotheses related to how rapid climate change may disrupt these
161 relationships on sub-orbital timescales. We do this by:

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

166

167 **2. Methods**

168

169 Study site

170 Lake Baikal is situated in southern Siberia at the forest – steppe ecotone (Fig. 1), and is the
171 world’s oldest, deepest, and most voluminous lake. The lake is a World Heritage Site, due to
172 its diverse flora and fauna; it contains over 2,500 species of which over 75% are thought to
173 be endemic (Galazii 1989). Its sediments have accumulated for over 25 million years, and
174 decades of research have exploited this sedimentary record to reconstruct environmental
175 change (Williams et al. 2001; Mackay 2007). Sedimentary cores were obtained in 2001 from
176 the research vessel *Vereschagin*, from the Vydrino Shoulder (51.585° N, 104.855° E; water
177 depth 675 m), an underwater high (between 500 – 800 m) off the south-eastern coast of Lake
178 Baikal (Fig. 1). The Vydrino Shoulder was selected because it is an area of stable, fine-
179 grained sedimentation relatively undisturbed by tectonic activity and reworking (Charlet et al.
180 2005). The cores obtained included a 1.73 m trigger core (CON01–605–3a), a 10.45 m piston
181 core (CON01–605–3), and a 2.50 m box core (CON01–605–5). These records were
182 supplemented with a short gravity core taken from an ice platform in 2001 (CON01–105–6)
183 from the same region.

184

185 Dating

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

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

195

196 Diatom analysis

197 Diatoms amount to between 50-90% of the phytoplankton biomass during spring bloom
198 under ice and after ice break-up (Popovskaya et al. 2015; Panizzo et al. 2017). Spring bloom
199 contributes a significant proportion of overall annual primary productivity (Popovskaya
200 2000). With the onset of summer warming and surface water stratification, diatoms are
201 succeeded by non-siliceous autotrophic picoplankton and other green algae (Fietz et al. 2005;
202 Belykh et al. 2006). During autumn turnover, a smaller diatom bloom dominates primary
203 production. Nitrogen and phosphorus co-limit photic zone productivity in Lake Baikal (Satoh
204 et al. 2006; O’Donnell et al. 2017), with rates of deep-water nutrient supply increasing
205 markedly since the mid 19th century (Swann et al. 2020).

206

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

220

221 Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA)
222 were used to investigate the total amount of turnover, variation, and compositional changes of
223 the diatom assemblages over time. The analyses were performed on Hellinger transformed

224 data to dampen the effects of highly abundant taxa (Legendre and Gallagher 2001).
225 Multivariate classification tree (MCT) analyses was used to explore how much of the
226 variation the different climatic periods identified above can be explained by the diatom
227 assemblages. MCT is considered a powerful method when there is a non-linear relationship
228 between response and explanatory variables, when there are missing values in the data, or
229 there are higher level interactions between explanatory variables (Borcard et al. 2018). The
230 minimum sized tree was chosen based on the 1se rule, which is the minimum sized tree when
231 the cross-validated relative error (CVRE) is the minimum CVRE value plus 1 standard error
232 (SE) of all the CVRE values (Borcard et al. 2018). The number of multiple cross-validations
233 was set to 100, and the number of k groups was set to the number of rows in the dataset. The
234 counts were normalized prior to the analysis and since MCT is in Euclidean space it
235 transforms into the chord distances (sensu the original chord distances proposed by Orloci
236 1967) between samples. Ordination analyses were done using the R package vegan and
237 results plotted using ggvegan. The MCT was done using the R package mvpart.
238 Stratigraphical profiles were constructed using C2 Data Analysis Version 1.7.7 (Juggins
239 2014).

240

241 Palaeoproductivity

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

253

254 Diatom richness, diversity and evenness

255 Richness, diversity and evenness were estimated using Hill's species numbers N_0 , N_1 , and
256 N_2 using diatom count data of the planktonic and tychoplanktonic flora only. We do not

257 include benthic taxa because they represent a different habitat, far from the core location.
258 Their persistent presence in the core (average 10 %) is caused by secondary transport
259 processes rather than species competing for the same resources as the planktonic diatoms
260 themselves. Hill's species numbers give easily interpretable numbers by maintaining the
261 doubling effect, and provide information on three levels as to how rare and abundant taxa are
262 weighted in each sample (Hill, 1973; Jost, 2010; Gotelli and Ellison, 2013; Chao et al., 2014).
263 Species richness is estimated using Hill's N_0 , the expected number of taxa where rare and
264 abundant taxa have similar weights. Species diversity is estimated using Hill's N_1 , which is
265 the expected number of equally common taxa, with less weight on rare taxa, and N_2 , which
266 provides the expected number of equally abundant taxa but puts weight on the numerically
267 dominant taxa. The estimates are represented as the expected number of diatoms based on the
268 smallest sample size ($n = 150$) to avoid biases related to different sample sizes. To take
269 account of variable sediment accumulation rates (SAR), Hill's measures of richness and
270 diversity were further divided by accumulation rates over time, so these measures become
271 estimated Hill's numbers per $\text{cm}^2 \text{yr}^{-1}$. To detect variation in abundance changes over time
272 (evenness) we also include the ratio of N_2/N_1 (Birks et al. 2018), i.e. the proportion of very
273 abundant species to the number of common species identified. When the ratio is 1, it
274 indicates that all taxa were equally abundant. The ratio is calculated based on the Hill's
275 numbers after taking account of SAR.

276

277 Palaeoproductivity – Diversity relationships

278 Relationships between palaeoproductivity and N_2 diversity were investigated during pre-
279 identified time-intervals (Tarasov et al. 2009; Walker et al. 2018) to test the hypothesis that
280 PDR will differ during periods of rapid climate change and periods of relative climate
281 stability. Defined climate periods are the pre-Bølling-Allerød (15.9–14.7 cal kyr BP), the
282 Bølling-Allerød (14.7–12.9 cal kyr BP), the Younger Dryas (12.9–11.7 cal kyr BP), and the
283 three recently designated sub-epochs of the Holocene (Early (11.7–8.2 cal kyr BP), Middle
284 (8.2–4.2 cal kyr BP) and Late (4.2–0 cal kyr BP). We used generalized additive models
285 (GAM) to explore PDR because we have no prior knowledge of the expected relationships,
286 and the likelihood that the relationships were non-linear or showing different complex
287 patterns within the different time periods. We used N_2 diversity as the response variable and
288 diatom BVAR as the explanatory variable. N_2 is a continuous variable so we used a gamma
289 distribution with a log link. Diatom BVAR as a variable was skewed so it was log
290 transformed prior to the analyses, and climatic period was included as a factor variable that

291 allowed for different smooths for each period. The smooths were fitted using thin-plate
292 regression splines, and the model was fitted using the restricted maximum likelihood
293 approach. Prior to analyses, extreme outliers ($BVAR_{\log \mu m^3 cm^{-2} yr^{-1}} < 6$) were removed to
294 reveal more clearly GAM relationships. This led to only 8 out of 521 samples being removed
295 in total: three, two and one samples removed from the Late, Middle and Early Holocene
296 subepochs respectively, and a further two from the pre-BA period. Models were then refitted.

297

298 The model is specified as follows:

299

$$300 \log ([N2_{ij}]) = a_1 + f_1(Productivity_i, Period_j) + \varepsilon_i \quad N2_i \sim Gamma$$

301

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

307

308 **3. Results**

309

310 Chronology

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

314

315 Diatoms

316 The temporal resolution of species compositional change was c. 30 years for the past c.
317 16,000 years (Fig. 3). DCA axis 1 sample scores show a strong, largely unidirectional trend
318 since the start of the Holocene. Turnover in the planktonic/tychoplanktonic assemblages over
319 the whole time period is 2.71 standard deviation units, reflecting the observation that several
320 species present during the early part of our record are also present during the latter part of our
321 record. The total inertia (variation) measured by CCA is 1.82, and of this the constraining
322 time variable explains 10.6 % of the variation (eigenvalue = 0.193). The ratio of eigenvalues

323 of the constrained axis 1 over the unconstrained axis 2 is 1.29 indicating that the time
324 gradient is explaining an important component of the variation.

325

326 During the early stages of the pre– Bølling–Allerød period, N_0 and N_2 values were initially
327 relatively high (Fig. 4), before declining as the tychoplanktonic *Aulacoseira skvortzowii*
328 dominated the assemblage (Fig. 3). Dominance by *A. skvortzowii* persists into the Bølling,
329 but is gradually reduced by increasing abundances of the planktonic *Aulacoseira baicalensis*
330 during the later Allerød. DCA axis 1 ordination scores show very little change during the
331 pre– Bølling–Allerød and Bølling–Allerød interstadial, indicative of a rather stable
332 assemblage, with few equally abundant species reflected in low evenness scores (N_2/N_1).
333 MCT is not able to discriminate well between diatom assemblages of the pre-Bølling–Allerød
334 and Bølling–Allerød interstadial (Fig. 5).

335

336 The Younger Dryas stadial is characterised by major changes in the diatom assemblage –
337 abundances of *Aulacoseira* (especially *A. skvortzowii*) decline, concomitant with a rapid
338 succession of *Ulnaria acus* and *Crateriportula inconspicua*, that bloom in spring and autumn
339 respectively (Fig. 3). These taxa give way to a short-lived peak in *A. baicalensis* dominance,
340 before *A. skvortzowii* once again asserts its dominance by the end of the Younger Dryas,
341 alongside notable increases in *C. inconspicua* and *L. minuta*, resulting in increasing richness
342 (N_0) and diversity (N_2) scores (Fig. 4). These changes are reflected in a rapid change in DCA
343 axis 1 scores at the start of the Younger Dryas, with discernible changes in the evenness ratio
344 indicative of increasing importance of different species. The Early Holocene is characterised
345 in the main by declining dominance of *A. skvortzowii* and increasing importance of autumn
346 blooming crops of *C. inconspicua* and *Lindavia minuta*. *U. acus* shows considerable
347 fluctuations, with *Hannaea baicalensis* and *Cyclostephanos dubius* increasing in importance
348 from c. 10 cal kyr BP, driving increases in diatom N_2 diversity and evenness ratio.

349

350 Where the climatic periods are used as a supervised classification technique, MCT analysis
351 reveals the highest variation between the Early and the Middle Holocene subepochs (Fig. 5).
352 This transition also marks the time when the evenness ratio peaks, that then declines to
353 lowest values found in our study during the Middle and Late Holocene (Fig. 4). During the
354 Middle Holocene, several diatom species largely disappear from the stratigraphical record
355 including *Stephanodiscus flabellatus*, *Stephanodiscus skabitchevskii*, *H. baicalensis*, and *C.*
356 *dubius*, while *C. inconspicua* drops to low values for the remainder of the record (Fig. 3). In

357 their place, *U. acus* and *L. minuta* increase in importance. The loss and gain of species
358 through the Middle Holocene has resulted in a relatively high but stable N_2 diversity, with
359 peak diversity occurring at the boundary between the Middle and Late Holocene, c. 4.2 cal
360 kyr BP (Fig. 4). Despite relatively high abundances for the first time of *Stephanodiscus*
361 *parvus* and *Stephanodiscus meyerii*, the Late Holocene sees *L. minuta* increasing to almost
362 complete dominance of the diatom assemblage between 1.8–1.4 cal kyr BP, resulting in some
363 of the lowest diatom diversity values for the study. During the most recent 500 years of our
364 record, the assemblage is characterised by species commonly found in the modern-day lake
365 communities, co-dominated by *A. baicalensis*, *U. acus* and *L. minuta* (Fig. 3).

366

367 Palaeoproductivity

368 Diatom biovolume accumulate rate (BVAR) data show that spring diatom crops have
369 dominated palaeoproductivity for much of the past c. 16,000 years, apart from a short period
370 during the late Holocene, 1.8–1.4 cal kyr BP, when autumnal diatom production increases to
371 more than ten times that of spring production (Fig. 6). BVAR were substantially higher and
372 more unstable during the Younger Dryas stadial than the warm periods before and after it
373 (Fig. 6). Peak palaeoproductivity for the whole study ($18.3 \times 10^3 \mu\text{m}^3 \text{cm}^{-2} \text{yr}^{-1}$) was
374 associated with successive peaks in *U. acus* then *A. baicalensis* at c. 12.3 cal kyr BP. BVAR
375 then declined rapidly and remained relatively low for the remainder of the Younger Dryas
376 and the start of the Holocene. Palaeoproductivity increased during the Early and Middle
377 Holocene, before declining to lowest rates during the Late Holocene (mean, $1.3 \times 10^3 \mu\text{m}^3$
378 $\text{cm}^{-2} \text{yr}^{-1}$).

379

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

388

389

390 4. Discussion

391

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

403

404 4.1 Last Glacial – Interglacial Transition

405

406 Due to high obliquity (Fig. 8j), the LGIT in the Lake Baikal region was intensely seasonal,
407 resulting in very cold winters but relatively warm, moist summers (Bush, 2005). Cold winters
408 during the late glacial resulted in substantially longer annual ice cover on Lake Baikal of up
409 to 8–9 months, reduced hydrological input by as much as 40 % than the modern day, and
410 restricted inputs of key nutrients such as P, N and Si (Shimaraev & Mizandrontsev 2006). Up
411 to the Bølling–Allerød, diatom assemblages were dominated by spores of the endemic
412 *Aulacoseira skvortzowii* (Fig. 3). *A. skvortzowii* is tychoplanktonic, having evolved a life
413 cycle which utilizes both pelagic and littoral habitats; viable spores remain in littoral
414 sediments down to a depth of 25 m, where they can be resuspended by strong autumn storms
415 back into the pelagic zone (Jewson et al., 2008) in time to bloom the following spring. *A.*
416 *skvortzowii* grows best in water temperatures below 5 °C, and to avoid lethal increasing
417 surface water temperatures, spore formation is triggered after ice break-up when phosphate
418 concentrations fall below a threshold level of 15–23 µg L⁻¹ (Jewson et al., 2008). Declining
419 phosphate concentrations are caused by P uptake by other algae (e.g. green algae and
420 picoplankton) as surface waters start to stratify. Pigment analyses have shown that green
421 algae were abundant at this time in the south basin of Lake Baikal (Tani et al. 2002; Soma et
422 al. 2007). Relatively low *N2* plankton diversity and evenness values during much of the late

423 glacial likely reflect P and Si limitation, resulting from overall lower nutrient concentrations
424 due to colder climate (Shimaraev & Mizandrontsev 2006) but possibly also competition from
425 other algae.

426

427 The major shift to warmer temperatures during the LGIT occurred with the onset of the
428 Bølling–Allerød interstadial, c. 14.7 cal kyr BP, linked to heat release from warm waters
429 deep in the North Atlantic ocean (Thiagarajan et al. 2014) which led to the resumption of the
430 Atlantic meridional overturning circulation (AMOC) (McManus et al. 2004) (Fig. 8g). Mean
431 pollen-inferred temperatures of the warmest month from neighbouring Lake Kotokel
432 however (Fig. 8b), reveal a 5 °C increase only during the latter stages of the Bølling–Allerød
433 (Tarasov et al. 2009). At the same time, pollen-inferred mean annual precipitation records
434 show that rainfall increased from c. 300 mm yr⁻¹ to c. 460 mm yr⁻¹ (Fig. 8c). This warmer,
435 wetter Allerød led to extensive melting of glaciers along the shores of Lake Baikal (Horiuchi
436 et al. 2004; Osipov and Khlystov 2010), major expansion of boreal vegetation (Tarasov et al.
437 2009; Bezrukova et al. 2010; Reshetova et al. 2013), reduced ice duration on the lake and
438 increased nutrient transport (Shimaraev & Mizandrontsev 2006). The impacts on diatom
439 communities however were subtle, with diatom composition between the pre– Bølling–
440 Allerød and Bølling–Allerød not distinguishable through MCT analyses (Fig. 5). Diversity
441 and evenness show little variability, although relative abundances of a few species show
442 distinct changes. For example, the heavily silicified endemic *Aulacoseira baicalensis* will
443 have benefited from increased Si availability (Jewson et al. 2010) while the endemic
444 *Stephanodiscus flabellatus* may have benefited from elevated concentrations of phosphorus
445 (Bradbury et al. 1994). The observed decline in *A. skvortzowii* spore formation may also be
446 attributable to general increased P availability in the south basin (Jewson et al. 2008).

447

448 The Younger Dryas stadial (12.9 – 11.7 cal kyr BP), is probably the most studied climate
449 disturbance event of the late Quaternary (Broecker et al. 2010). It was caused by an influx of
450 freshwater from Lake Agassiz into the Arctic Ocean (Tarasov & Peltier 2005; Murton et al.
451 2010) which led to the decline in AMOC (Fig. 8g) (Bond et al. 2001; McManus et al. 2004),
452 and concomitant cooler temperatures across the Northern Hemisphere (Stuiver et al. 1995)
453 (Fig. 8h). Increased GISP2 K⁺ concentrations (Fig. 8f) indicate that the Siberian High
454 intensified at the start of the Younger Dryas (Mayewski et al. 1997), which accounts for both
455 an attenuated Asian summer monsoon (Fig. 8e) (Dykoski et al. 2005) and cooler and more

456 arid climate conditions in the Lake Baikal region (Tarasov et al. 2009) (Fig. 8 b, c). These
457 cooler, more arid conditions led to a decline in hydrological input into Lake Baikal itself
458 Mackay et al. 2011), and a short-lived expansion of the tundra biome (Tarasov et al. 2009;
459 Bezrukova et al. 2010).

460

461 Diatom responses to climate change within the Younger Dryas were instantaneous but
462 complex, kick-started by the first appearance and rapid growth of *Ulnaria acus* (Fig. 3)
463 (indicative of higher dissolved silica concentrations in the water column (Bradbury et al.
464 1994)), and increasing abundance of *C. inconspicua*. However, the decline in *N2* diversity
465 only from c. 12.6 cal kyr BP (Fig. 4), suggests that resources for diatom growth were not
466 initially limiting. Occupying different seasonal niches, spring blooming *U. acus* and
467 autumnal blooming *C. inconspicua* (Ryves et al. 2003) are unlikely to be directly competing
468 for the same resources, in part because small centric diatoms do not utilise a lot of silica
469 (Bradbury et al. 1994). Having several co-dominant species is reflected in the relatively high
470 evenness scores for the Younger Dryas (Fig. 4), related to few resources being limiting
471 (Interlandi & Kilham 2001).

472

473 The decline in *N2* diversity is linked to peak values for *A. baicalensis* (Fig. 3), competing
474 directly with *U. acus* for dissolved silica. Diatom population changes in Lake Baikal play an
475 important role in controlling availability of silicic acid for other species (Callender & Granina
476 1995; Jewson et al., 2010; Shimaraev and Domysheva, 2013; Jewson et al., 2015). In
477 particular, when populations of *A. baicalensis* are very high, the availability of silicic acid
478 uptake for other species declines, leading to a drop in their populations (Jewson et al., 2010;
479 2015). Being a heavily silicified species, *A. baicalensis* needs a strong period of mixing
480 (Huisman et al. 2004), which suggests that when abundant, turnover is strong, allowing the
481 recycling of nutrients needed for peak palaeoproductivity (Fig. 6). Our diatom records
482 demonstrate that species specially adapted to grow under the ice of Lake Baikal (Bondarenko
483 et al. 2012) have flourished alongside autumnal blooming species during this cold stadial,
484 with, initially at least, few limiting resources.

485

486 The latter stages of the Younger Dryas are characterised by a marked increase in diatom
487 richness and diversity associated with both increases in spring and autumn diatoms, and a
488 rapid decline in palaeoproductivity. Given that regional temperatures remain low and
489 unchanged at this time (Demske et al. 2009), internal dynamics in the lake may be driving

490 observed changes in diatom communities, mediating resource availability. Contemporary
491 monitoring studies have shown that populations of *A. baicalensis* can undergo dramatic
492 changes in population size linked to complex interactions including silica availability
493 (Izmest'eva et al. 2006); after populations peak, cells are transported to the bottom sediments,
494 taking with them silica that then becomes unavailable for new diatom growth (Jewson and
495 Granin 2015). But autumnal diatoms are still able to grow, as nutrients including Si become
496 available once more during autumnal turnover.

497

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

512

513 4.2 Middle – Late Holocene

514

515 Northern Hemisphere cooling, especially from c. 5 cal kyr BP, is linked to declining summer
516 insolation (Marcott et al. 2013) in conjunction with vegetation and snow/ice feedbacks on
517 Earth's surface albedo. This cooling culminated in the neoglacial, which in central Asia
518 resulted in increased aridity (Ganopolski et al. 1998) expressed in the Lake Baikal region as
519 declining mean annual precipitation (Tarasov et al. 2009). The neoglacial also resulted in
520 increased Siberian permafrost formation (Anisimov et al. 2002). Within Lake Baikal, we
521 document a shift from spring to autumnal diatom communities that started during the Early
522 Holocene, concomitant with the first decline in insolation, but then continues to get stronger
523 during the Middle and Late Holocene as both precession and obliquity decline (Fig. 8). The

524 slow unfolding of an increasingly important autumnal diatom community has relatively little
525 impact on palaeoproductivity during much of the Holocene, although autumnal production
526 after 10 cal kyr BP is slightly higher than it was before 10 cal kyr BP, and continues to
527 proportionally increase especially during the Late Holocene. This long-term change in
528 diversity and palaeoproductivity likely represents an orbitally-driven ecosystem response to
529 long-term climate change, possibly linked to changes in seasonality and its impact on, for
530 example, ice cover dynamics and length of summer stratification on the lake.

531

532 *L. minuta* is currently the only pelagic diatom to bloom during the autumn in Lake Baikal in
533 substantial numbers (although it can also grow in smaller numbers during spring turnover).
534 Because *L. minuta* can tolerate surface water temperatures up to 11 °C, cells persist higher in
535 the surface waters for longer during summer stratification, so that when stratification breaks
536 down in the autumn and nutrients are regenerated, cells of *L. minuta* are retrained into the
537 photic zone first, giving them a strong competitive advantage, leading to their dominance
538 during autumn turnover (Jewson et al., 2015). Winter ice cover is a major force driving inter-
539 seasonal connections in lakes that freeze over every year (Sommer et al. 2012; O'Reilly et al.
540 2015; Hampton et al. 2017), and Lake Baikal is no exception. The gradual decline in
541 proportion of spring diatoms may have resulted in increased resource availability for other
542 diatoms (Interlandi & Kilham 2001; Jewson et al., 2010; 2015). For example, monitoring
543 studies have shown large autumnal populations of *L. minuta* during the 1950s CE when
544 spring populations of *A. baicalensis* were very low (Antipova & Kozhov in Kozhov 1963).

545

546 The build-up to peak dominance in *L. minuta* during the Late Holocene is accompanied by
547 the successive decline in spring blooming species, starting with *U. acus* followed by *A.*
548 *baicalensis*, species that both rely on availability of dissolved silica (Jewson et al. 2010) and
549 under-ice turbulence to remain in the photic zone (Granin et al. 2000). These shifts are
550 reflected in rapidly declining *N2* diversity scores since their peak at the Middle / Late
551 Holocene boundary to their lowest values for the Holocene (Fig. 4). This decline is also
552 coincident with a major shift in carbon dynamics in Lake Baikal, linked to increasing
553 regional cooling and aridity (Mackay et al. 2017). The almost monospecific Late Holocene
554 assemblage of *L. minuta* and resultant low *N2* diatom diversity in the lake is concurrent with
555 the Dark Ages Cold Period (DCAP) (1.8–1.4 cal kyr BP; CE 400–765) (Helama et al. 2017),
556 a climatically cool period, linked to changes in ocean circulation (Bond et al. 2001), and solar

557 and volcanic activity (Helama et al. 2017). The near complete disappearance of *A.*
558 *baicalensis* makes this period unique in our Lake Baikal record. However, we are not yet able
559 to say conclusively why growth of *A. baicalensis* was so inhibited during the DCAP, leading
560 to the dominance of *L. minuta* for several centuries. This period almost certainly represents
561 an ecosystem response to abrupt extrinsic change occurring elsewhere in the northern
562 hemisphere, super-imposed on longer-term changes in orbital parameters (Williams et al.
563 2011). It is possible that the smaller biovolume of *L. minuta* in comparison to *A. baicalensis*
564 and *U. acus*, may have conferred it a competitive advantage as resources became increasingly
565 limited (Burson et al. 2018). Alternatively, persistent deeper snow cover on the frozen lake
566 could have acted to reduce light penetration through the ice, (i.e. light as a resource is
567 severely limited) resulting in a decline in sub-surface turbulence and loss of spring diatom
568 crops to deeper waters (Granin et al., 2000). It is possible that these responses are linked to
569 orbitally driven seasonal changes such as cooler summers (Fig. 8). It's notable that the
570 ecosystem function of primary production did not decline overall during this period, just the
571 timing of peak production, with autumnal palaeoproductivity far exceeding spring
572 productivity for the only time in our record during the DCAP (Fig. 6).

573

574 4.3 Palaeoproductivity–diversity relationships

575

576 Productivity–diversity relationships (PDR) in aquatic ecosystems are complex (Aoki 2003;
577 Smith 2007), while also being scale (Chase and Leibold 2002; Korhonen et al. 2011) and
578 time (Rusak et al. 2004) dependent. Our initial hypotheses set out to test if these relationships
579 differ between periods of relative climate stability and periods of rapid climate change. This
580 is borne out, as the shapes of the relationships are very different across the different climate
581 periods (Fig. 7). The strongest evidence for GAMs (with lowest *p* values; (Table 1)) were
582 found during both the Younger Dryas and Early Holocene, periods punctuated by pervasive
583 millennial-scale variability, and the Late Holocene period, characterised by cold events
584 linked to overlapping drivers such as solar minima and volcanic eruptions (Helama et al.
585 2017), amplified by centennial-scale oceanic variability (Renssen et al. 2006). PDR were
586 different during each of the pre–Bølling–Allerød, the Bølling–Allerød and the Middle
587 Holocene periods, but statistical support for GAMs were much weaker during these periods
588 of relative climate stability (Table 1). During the Bølling–Allerød the PDR is effectively flat
589 (*sensu* Smith 2007), because *N*₂ diversity is restricted to very low values and changes little
590 across the magnitude of the productivity gradient, perhaps due to as yet few available

591 resources for several species to co-exist. During the Middle Holocene, N_2 diversity values are
592 again more restricted than during either the Early or Late Holocene periods, N_2 are rarely low
593 (Fig. 7), likely linked to optimal resource availability allowing several species to co-exist
594 (Burson et al. 2018) at similar abundances (Fig. 4) during both spring and autumn (Fig. 3).

595

596 The negative PDR during the Younger Dryas likely reflects a complex set of processes linked
597 to both ecosystem responses to abrupt cooling (e.g. increased ice duration but stronger
598 overturn in the lake (Shimaraev & Mizandrontsev 2006), and a reduction in resource
599 heterogeneity due to severe limitation by a few or even single resource (Interlandi & Kilham
600 2001). Productivity in Lake Baikal is dependent on a sustained supply of nutrients from
601 deeper waters to the photic zone, stimulated by shifting wind dynamics and enhanced deep
602 ventilation (Swann et al. 2020). While increased supply of Si ensured initial resources for
603 *Ulnaria* and *Aulacoseira* growth, Si will ultimately have become unavailable to most other
604 diatoms, due to massive increases in the abundances of *A. baicalensis* (Fig. 3) (Jewson et al.,
605 2010; 2015), leading to declines in diversity while productivity peaked. During the Early
606 Holocene however, there is a positive PDR, especially when palaeoproductivity levels are
607 initially lower. We suggest that rapid melting of glaciers and increased fluvial input (Osipov
608 and Khlystov 2010), and opening up of new habitats as ice-cover duration on the lake
609 declined, contributed to an increased supply of nutrients and habitat availability, such that
610 both diversity and productivity were able to increase from the very low values at the start of
611 the Holocene period. It's notable that during the Early Holocene the ratio of autumnal to
612 spring species increases markedly, indicative of autumnal overturn niches opening up,
613 allowing increased growth of *C. inconspicua* and *L. minuta* (Fig. 3).

614

615 During the Late Holocene however, a negative PDR is apparent only when
616 palaeoproductivity is very low at the transition between the Middle and Late Holocene
617 periods (Fig. 7). Low palaeoproductivity at c. 4.2 cal kyr may be linked to a period of
618 regional cooling and aridity (Mackay et al. 2017) concurrent with weaker Asian summer
619 monsoons (Dixit et al. 2014). It is at this time that new *Stephanodiscus* species become
620 established in the lake (*S. meyeri* and *S. parvus*) alongside existing diatom communities,
621 hence higher N_2 diversity. *Stephanodiscus* species tend to reflect higher phosphorus than
622 silicon loading rates (Kilham et al. 1986), and may be a community response to cooler, more
623 arid climate (Bradbury et al. 1994) as experienced during the Late Holocene neoglacial.
624 However for the majority of the Late Holocene there is little relationship between

625 palaeoproductivity and diversity, indicative of abundant resources allowing for many
626 planktonic species to co-exist.

627

628 4.4 Comparisons to other studies within Lake Baikal

629

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

649

650 Conclusions

651

652 This study provides important insights into our understanding of productivity–diversity
653 relationships (PDR) in aquatic ecosystems. We show that diatom communities and
654 palaeoproductivity are sensitive to extrinsic drivers of climate change. These drivers operate
655 at different time scales, from abrupt events during the Younger Dryas resulting in (negative)
656 coupling between palaeoproductivity and diversity, to slower changes in boreal insolation
657 and seasonality, leading to varied PDR relationships. These differences are likely related to
658 resource availability and limitation (or not) of specific nutrients, linked to climate and surface

659 water overturn. We therefore provide important perspective to complement existing short-
660 term observational (Dodson et al. 2000) and experimental (Winfree et al. 2015) approaches.
661 PDR in aquatic systems should not be expected to occur in one direction (Smith 2007), but
662 are very much dependent on other factors such as external disturbances, resource availability,
663 species interactions and abiotic constraints on ecosystem function. Even given the sheer
664 volume of Lake Baikal, diatom responses to abrupt events can be almost instantaneous,
665 showing how tightly coupled ecology and climate have been in the past.

666

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

680

681 **Author Contributions:**

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

686

687

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697

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1151

1152 Table 1: GAMs to investigate PDR trends during pre-defined climate periods. edf = effective
 1153 degrees of freedom, and ref.df = reference degrees of freedom. The goodness-of-fit statistics
 1154 show the adjusted $r^2= 0.462$ and the deviance explained is 53.2 %.

1155

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 *

1156 Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

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1160 **Figure Legends:**

1161

1162 Fig. 1: Map of Lake Baikal and its catchment, with locations of the different cores used or mentioned
1163 in this paper, including the coring location on the Vydrino Shoulder, where our study was undertaken.
1164 Also shown is Lake Kotokel that has provided independent climate reconstructions used in this study
1165 (Tarasov et al. 2009).

1166

1167 Fig. 2: ‘Bacon’ Age-depth model (Blaauw & Christen, 2011) for Vydrino box (CON01–605–05) and
1168 piston cores (CON01–605–03) of radiocarbon AMS dates calibrated using IntCal20 radiocarbon
1169 calibration curve (Reimer et al., 2020).

1170

1171 Fig. 3: Relative abundances of sub-fossil planktonic and tychoplanktonic diatoms spanning the past c.
1172 16,000 years from Vydrino Shoulder. Diatoms which grow mainly before summer stratification are
1173 shown in blue, while those that mainly grow after summer stratification are shown in green. DCA axis
1174 1 sample scores summarize the major trend in species turnover.

1175

1176 Fig. 4: Comparison of Hill’s richness (N_0), diversity (N_1 and N_2) and evenness (N_2/N_1 ratio) trends
1177 over the past c. 16,000 years. Richness and diversity values were further divided by sediment
1178 accumulation rates over time, so these measures become estimated Hill’s numbers per $\text{cm}^{-2} \text{yr}^{-1}$

1179

1180 Fig. 5: Multivariate classification tree (MCT) for Lake Baikal planktonic and tychoplanktonic diatoms
1181 over the past c. 16,000 years. Time periods used in multivariate classification tree analyses are: the
1182 pre Bølling–Allerød (pre–BA), the Bølling–Allerød (B–A) interstadial, the Younger Dryas stadial and
1183 the three recently ratified Early, Middle and Late Holocene subepochs (Walker et al. 2018). The
1184 histograms show the transformed abundances of the discriminating taxa within each leaf. These are
1185 listed in decreasing order. The numbers under the histograms represent the relative error within each
1186 leaf, and $n =$ the total number of samples. At the bottom is the summary of the residual error (RE),
1187 cross-validated error (CVRE), and standard error (SE). The r^2 will be 1-RE.

1188

1189 Fig. 6: Stratigraphical profile showing trends in palaeoproductivity over the past c. 16,000 years: the
1190 proportion of diatoms that bloom in the autumn versus those that bloom in the spring; estimates of
1191 palaeoproductivity derived from spring (orange) and autumn (dark brown) diatom biovolume
1192 accumulate rates (BVAR $\mu\text{m}^3 \text{cm}^{-2} \text{yr}^{-1}$); and log-transformed ratio of autumnal / spring
1193 palaeoproductivity.

1194

1195 Fig. 7: Palaeoproductivity–diversity relationships explored using generalized additive models
1196 (GAMs) that allow different smooths for the pre–defined climatic periods: pre Bølling–Allerød,
1197 (Bølling–Allerød), Younger Dryas, Early Holocene, Middle Holocene, and Late Holocene. The dots
1198 represent the data points, the thick line is the fitted GAM response for each period, and the shaded
1199 areas represent the 95 % confidence intervals around the mean fitted response.

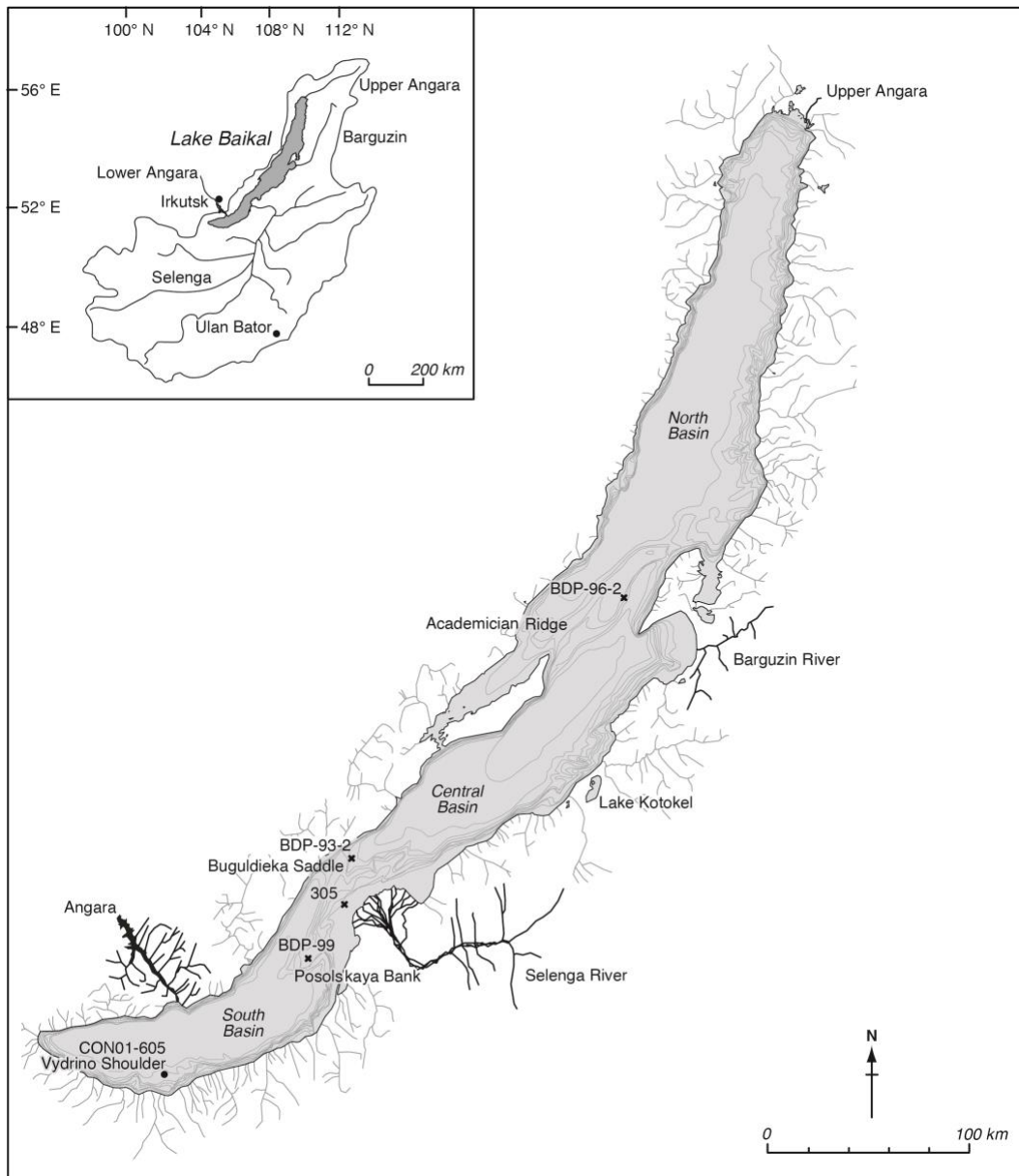
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1201 Fig. 8: Multi-archive data plotted alongside (a) DCA axis 1 sample scores of Lake Baikal diatoms, as
1202 a measure of turnover over the past c. 16,000 years; (b) mean pollen–inferred annual precipitation
1203 from Lake Kotokel, with smooth line representing the mean 3–point moving average (Tarasov et al.
1204 2009); (c) mean pollen–inferred temperature of the warmest month from Lake Kotokel, with smooth
1205 line representing the mean 3–point moving average (Tarasov et al. 2009); (d) mean Northern
1206 Hemisphere temperature stack records for 60° latitude bands (30° N – 90° N; Marcott et al. 2013); (e)
1207 $\delta^{18}\text{O}$ values of Dongge Cave stalagmite D4 (Dykoski et al. 2005); (f) K^+ ion concentrations (ppb)
1208 from GISP2 D core (Mayewski et al. 1997); (g) North Atlantic core GGC5 $^{231}\text{Pa}/^{230}\text{Th}$ meridional
1209 circulation data; (h) $\delta^{18}\text{O}$ values of NGRIP ice core (Rasmussen et al. 2006); (i) June insolation 60° N
1210 (W m^{-2} ; Berger & Loutre, 1991); (j) obliquity (ϵ).

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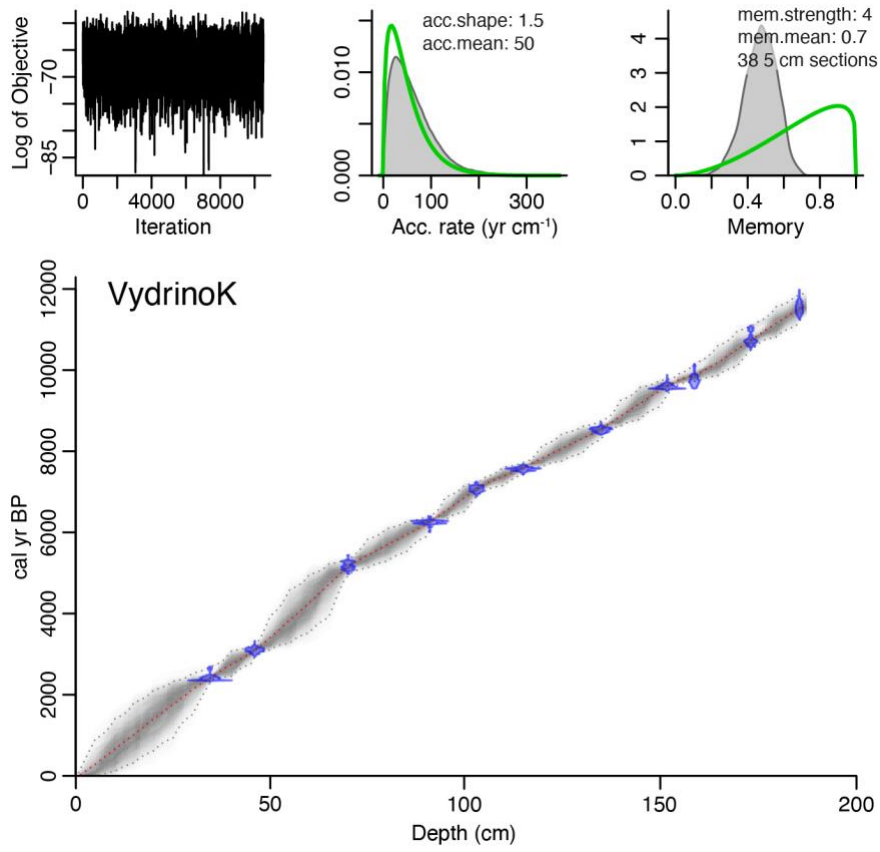
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1213 Fig. 1
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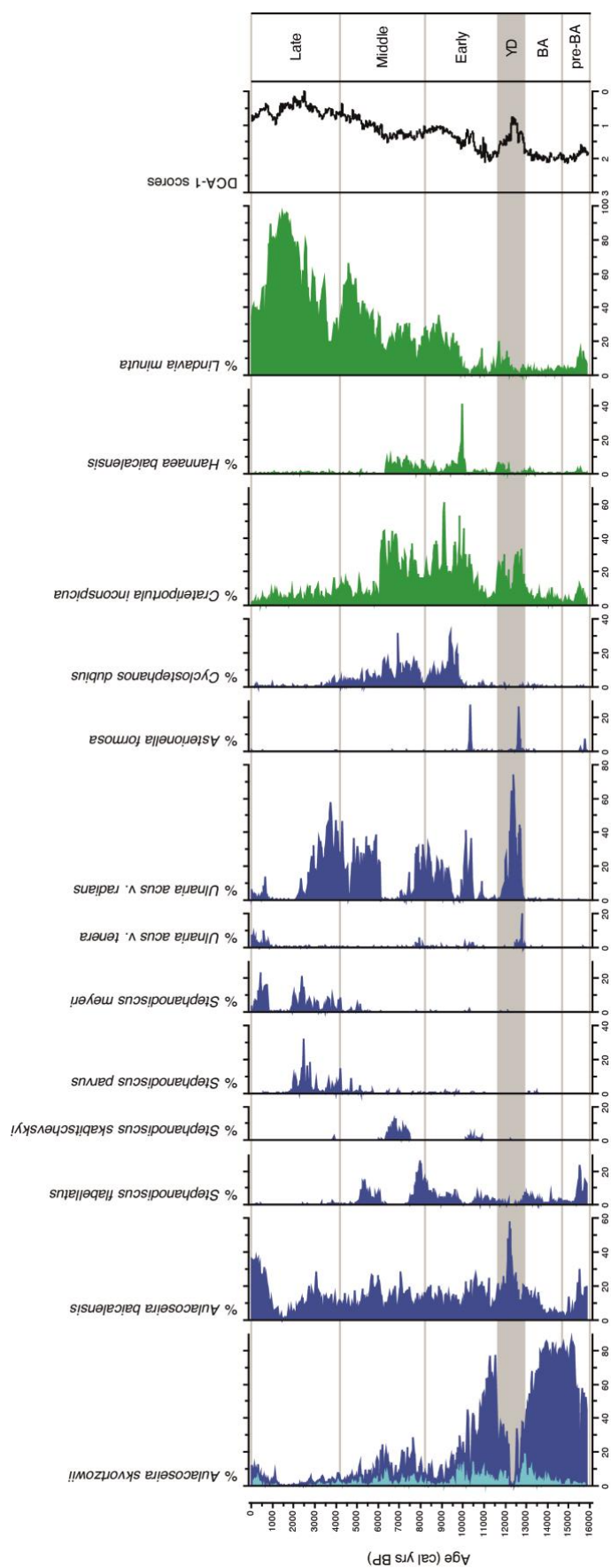
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1220 Fig. 2
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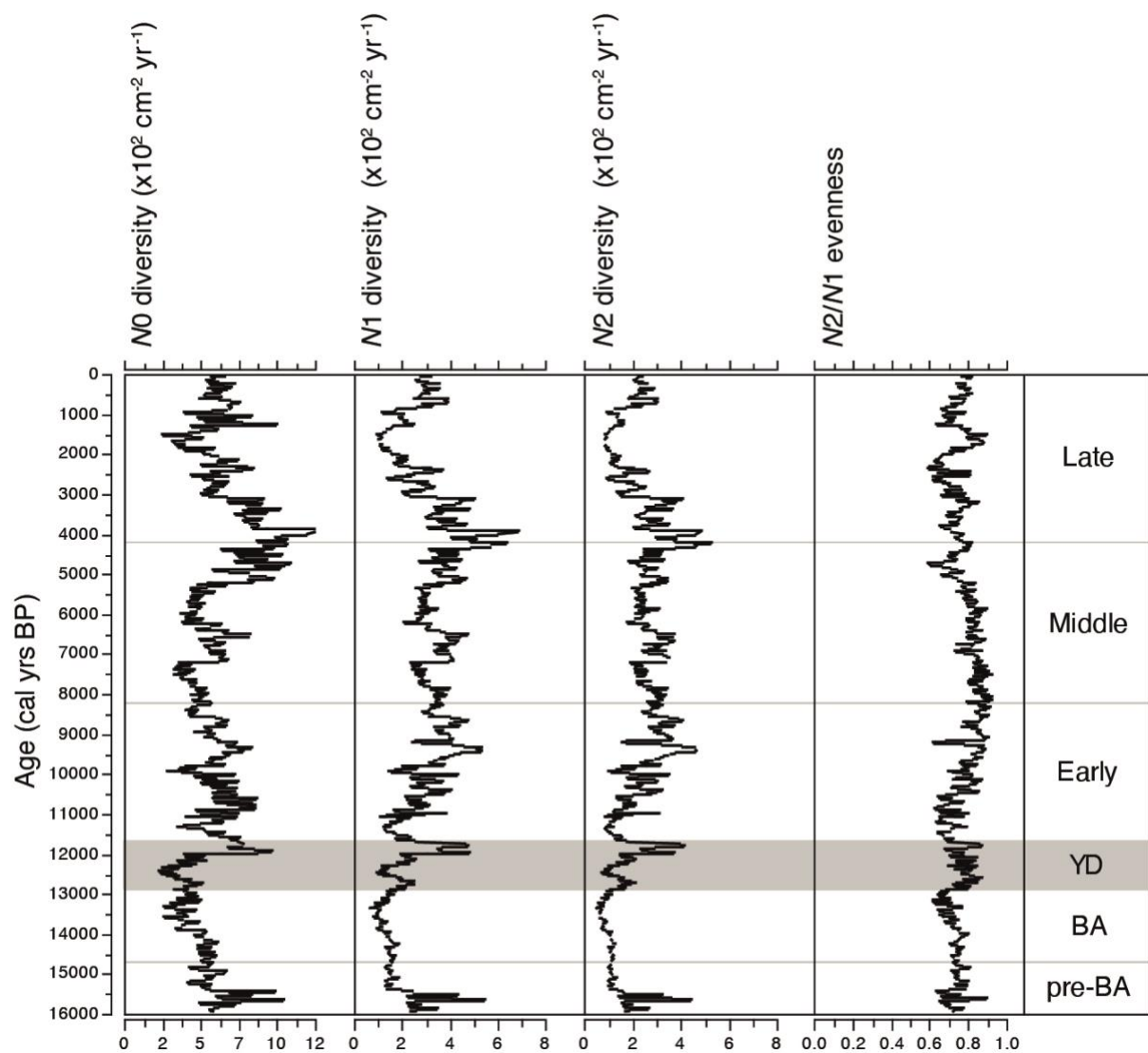
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1227 Fig. 3
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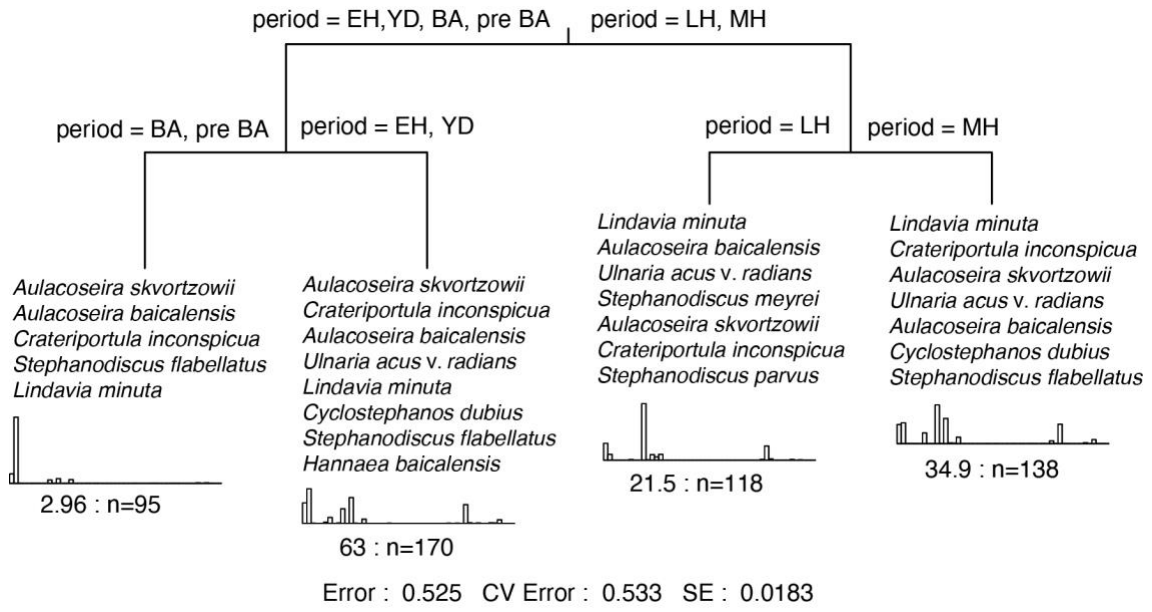
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1231 Fig. 4
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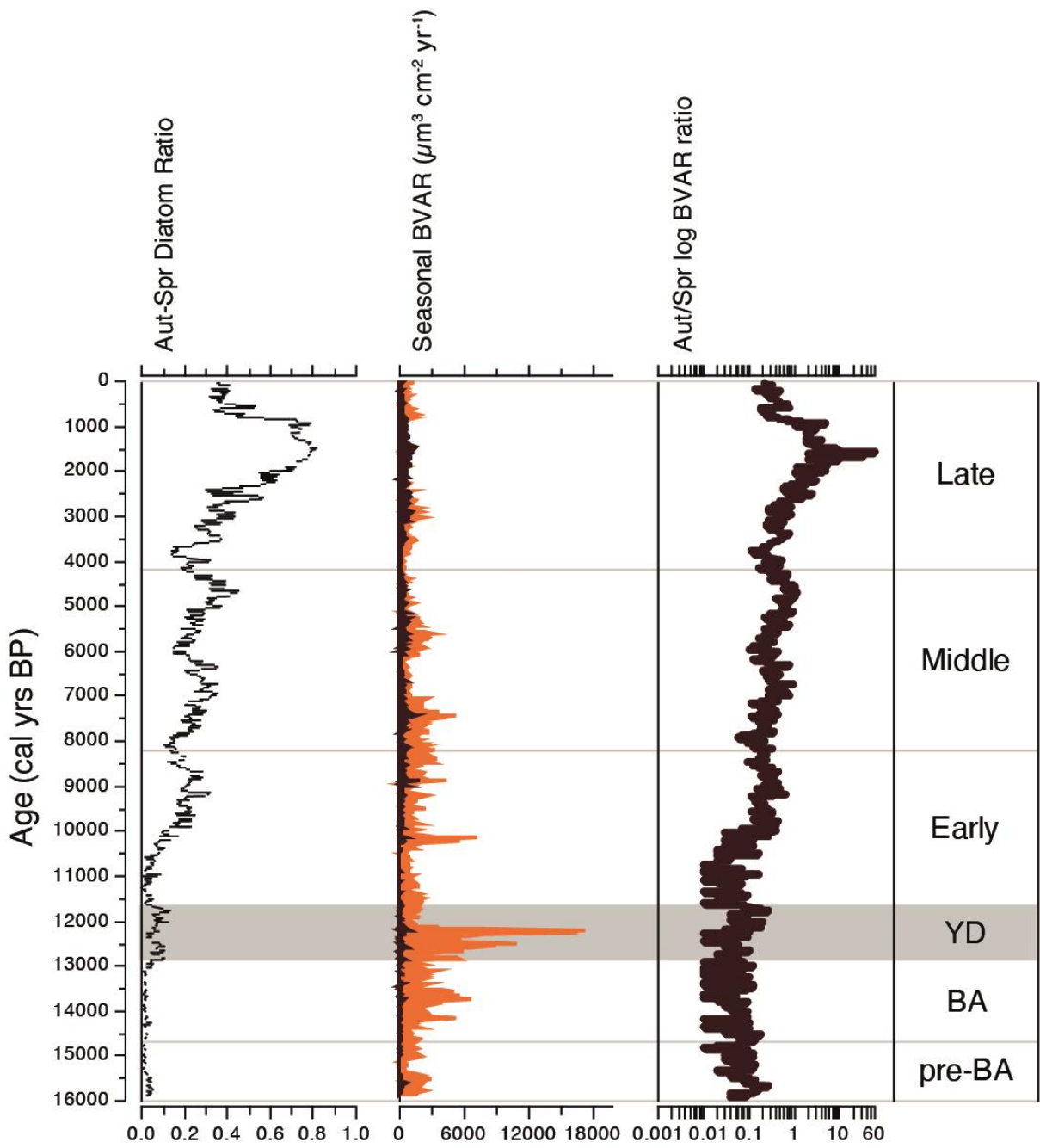
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1237 Fig. 5
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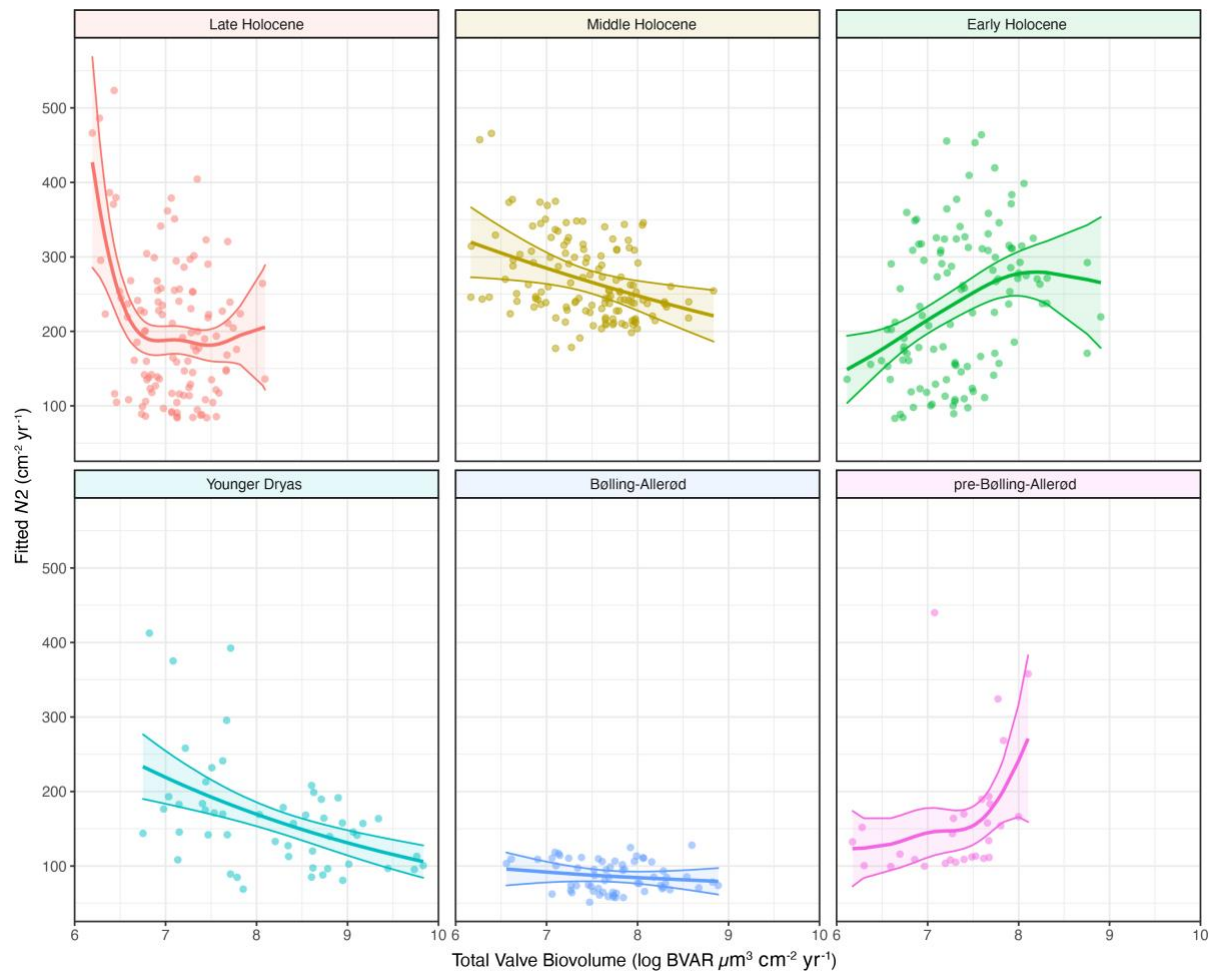
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1243 Fig. 6
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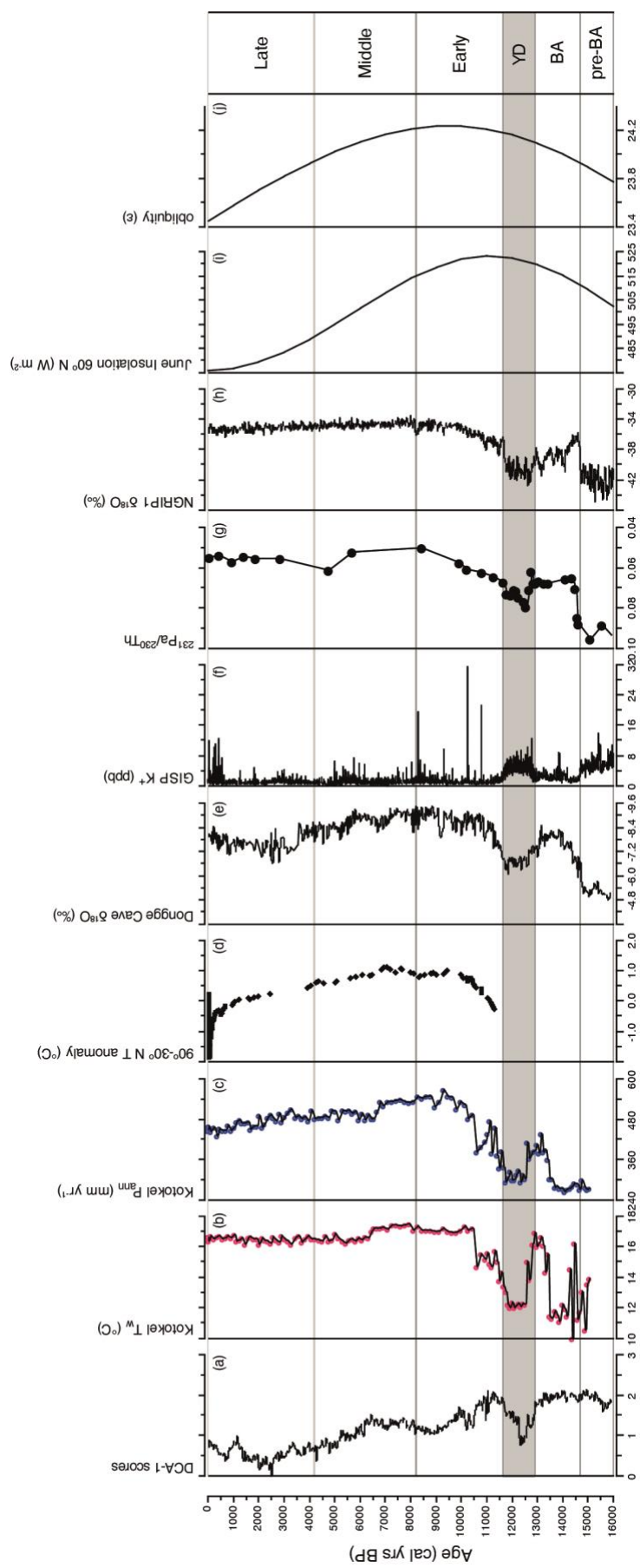
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1249 Fig. 7
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1254 Fig. 8
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