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1 **Long term trends in aquatic diversity, productivity and stability: a 15,800**
2 **year multidecadal diatom study from Lake Baikal, southern Siberia**
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48
49 **Abstract**
50

51 Biological diversity is inextricably linked to community stability and ecosystem functioning,

52 but our understanding of these relationships in freshwater ecosystems are largely based on

53 short-term observational, experimental, and modelling approaches. Using a multidecadal

54 diatom record for the past 15,800 years from Lake Baikal, we investigate how three

55 ecosystem components - diversity, productivity, and stability - have responded to climate

56 changes on long-timescales. In addition, we investigate how the relationships between

57 diversity, productivity and stability have changed through time in response to these changes.

58 We show that abrupt changes in diatom stability and diversity during the late glacial and

59 early Holocene are part of a network of responses across southern Siberia as a result of

60 extrinsically-forced climate instability. Productivity - diversity relationships were strongly

61 coupled during the late glacial, which we suggest is linked to resource availability, but

62 showed little relationship during the Holocene, perhaps due to few resources being limiting

63 for extended periods of time. For example, periods of low diatom diversity are associated

64 with peak palaeoproductivity, and coincide with climate disturbance events. Such strong

65 negative relationships may reflect resources becoming limiting during palaeoproductivity,

66 leading to monospecific diatom blooms. While species fluctuations respond rapidly to

67 changing resources during much of the Holocene, the ecosystem function of primary

68 production appears to be relatively resilient. Our study provides important perspectives on

69 lake community stability and ecosystem function in relation to rapid periods of climate

70 change.

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72 **Key words:** diversity, stability, palaeoproductivity, abrupt climate change, extrinsic forcing,

73 palaeolimnology

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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). 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), 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). 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, PDR 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. 2011; 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 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

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110   the last 16000 years have been punctuated by a series of large-scale and abrupt climatic

111   shifts, such records open the door for an investigation into the links between biodiversity and

112   the stability of ecosystem functioning associated with climate disturbance events.

113

114   Here we investigate the relationship between diatom diversity and the stability of ecosystem

115   functioning in Lake Baikal, an ancient lake with a long continuous record which, unlike

116   many other large lakes, only shows limited evidence of human perturbation (Hampton et al.

117   2018; Roberts et al. 2018), restricted to its coastline (Kravtsova et al. 2014; Timoshkin et al.

118   2016). We focus on aquatic productivity as a measure of ecosystem function, because of the

119   direct link between diatoms and primary production in the modern lake (Kozhova and

120   Izmest'eva 1998).

121   • First, we review major climatic changes over the past 15,800 years in order to identify

122   key events of interest relevant to southern Siberia.

123   • Second, we reconstruct trends in diatom communities, diversity and productivity in

124   Lake Baikal through time.

125   • Third, we investigate the relationship between diversity and palaeoproductivity, with

126   particular reference to climate disturbance events.

127

128   We hypothesise for example, that climate disturbance events lead to changes in available

129   resources for different species, which will alter the relationship between productivity and

130   diversity, not experienced during periods when climate is more stable. Our aim is thus to

131   coax history to conduct experiments (Deevey 1969) in order to deepen our understanding of

132   the long-term relationships between aquatic diversity and productivity, and to test hypotheses

133   related to how climate disturbance events, disrupts these relationships on sub-orbital

134   timescales.

135

136   **2. Methods**

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138   <u>Study site</u>

139   Lake Baikal is situated in southern Siberia at the forest – steppe ecotone (Fig. 1), and is the

140   world's oldest, deepest, and most voluminous lake. The lake is a World Heritage Site, due in

141   the main to its diverse flora and fauna; it contains over 2,500 species of which over 75% are

142   thought to be endemic. Its sediments have accumulated for over 20 million years, and

143   decades of research have exploited this sedimentary record to reconstruct environmental

144   change (Williams et al. 2001; Mackay 2007). Sedimentary cores were obtained in 2001 from

145   the research vessel (RV) Vereschagin, from the Vydrino Shoulder (51.585°N, 104.855°E;

146   water depth 675m), an underwater high (between 500 – 800 m) off the south-eastern coast of

147   Lake Baikal (Fig. 1). The Vydrino Shoulder was selected because it's an area of stable, fine-

148   grained sedimentation relatively undisturbed by tectonic activity and reworking (Charlet et al.

149   2005). The cores obtained included a 1.73m trigger core (CON01-605-3a), a 10.45m piston

150   core (CON01-605-3), and a 2.50m box core (CON01-605-5). These records were

151   supplemented with a short gravity core taken from an ice platform in 2001 (CON01-105-6)

152   from the same region.

153

154   **< Fig. 1 here >**
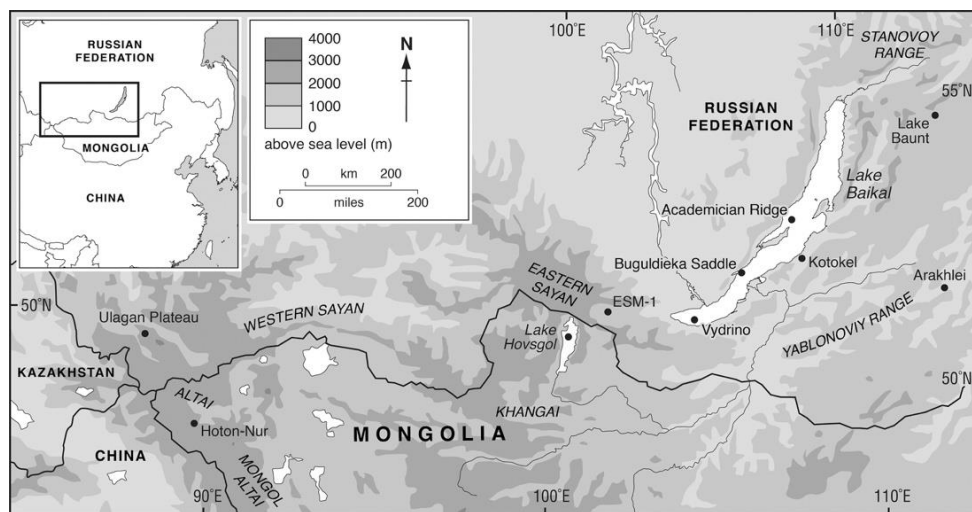
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157   Dating

158   Radiocarbon dates for the Vydrino sequence were obtained by accelerated mass spectrometry

159   (AMS) from pollen and spore concentrates (Piotrowska et al. 2004; Demske et al. 2005). The

160   age model is based upon twelve AMS ^{14}C pollen dates from the box core (CON01-605-5)

161   (Piotrowska et al. 2004) and an additional five AMS ^{14}C pollen dates from the piston core

162   (CON01-605-3) (Demske et al. 2005). Full details are given in Mackay et al. (2011).

163   Radiocarbon dates were calibrated using IntCal13 radiocarbon calibration curve (Reimer *et*

164   *al.*, 2013), and age-depth modelling was done using 'Bacon2.2' (Blaauw & Christen, 2011).

165   No reservoir effect was applied to the calibration due to dating undertaken on pollen and

166   spore concentrates.

167

168   Diatom analysis

169   Diatoms are siliceous, unicellular, algae and are key primary producers in aquatic

170   ecosystems. Because they possess a silica shell, they preserve well in sedimentary

171   environments. We analysed diatom assemblages at 5 mm resolution; samples were prepared

172   from composited gravity / trigger / piston cores detailed above, with no chemical treatments

173   needed (Mackay et al. 1998). Diatom taxa were identified to species level or lower using a

174   range of Russian and other flora, detailed in Mackay et al. (1998). With few exceptions, at

175   least 300 valves from each sample were counted using oil immersion phase-contrast light

176   microscopy at x1000 magnification. Diatom concentrations (valves/g) were calculated by the

177   addition of divinylbenzene (DVB) microspheres (Battarbee et al. 2001). Stratigraphical

178   profiles were constructed using C2 Data Analysis Version 1.7.7 (Juggins 2014).

179

180   Diatom compositional change

181   Principal curve (PrC) analyses was used to investigate compositional changes in the diatom

182   assemblages, using the analogue-package (Simpson and Oksanen 2016) in R version 3.3.1 (R

183   Core Team, 2016). A PrC is a one-dimensional curve that is fitted through data in m

184   dimensions by minimising the square distances from the data points to the curve (De'ath,

185   1999, Simpson and Birks, 2012). A smoothing spline was used and the initial starting point of

186   the PrC was defined by the first component of correspondence analysis (CA). The curve was

187   fitted through several iterations using local averaging to reduce the sum of orthogonal

188   distances between the curve and the data points ((De'ath 1999; Simpson and Birks 2012). The

189   penalty to determine the smoothness of the curve was set to 1.4, and the degree of

190   smoothness was allowed to vary between the different taxa. The diatom counts were

191   transformed into square-root percentages before running the analysis.

192

193   Diatom richness and diversity

194   Richness and diversity were estimated using Hill's species numbers $N0$, $N1$, and $N2$ using

195   diatom count data. These measures give easily interpretable numbers by maintaining the

196   doubling effect, and provide information on three levels as to how rare and abundant taxa are

197   weighted (Hill, 1973; Jost, 2010; Gotelli and Ellison, 2013; Chao et al., 2014). Species

198   richness is estimated using Hill's $N0$, the expected number of taxa where rare and abundant

199   taxa have similar weights. Species diversity is estimated using Hill´s $N1$, which is the

200   expected number of common taxa and puts more weight on the numerically abundant taxa,

201   and $N2$, which puts weight on the numerically dominant taxa. The estimates are represented

202   as the expected number of diatoms based on the smallest sample size (n = 258) to avoid

203   biases related to different sample sizes. The samples were resampled randomly 1000 times

204   without replacement, and unconditional confidence intervals were estimated using the

205   approached described by Chao et al. (2014). Stability in $N2$ diversity over time was further

206   quantified using its coefficient of variation (CV).

207

208   Palaeoproductivity

209   The palaeoecological significance of diatom concentrations can be of limited value, unless

210   they can be converted into either diatom flux rates (e.g. Battarbee et al. 2001), or estimates of

211   biovolume (Hillebrand et al., 1999). Diatom flux rates rely on a robust chronology (as

212   determined in this study), while biovolume estimates require representative size

213   measurements for the dominant taxa. We estimate palaeoproductivity through community

214   biomass calculations derived from diatom biovolume accumulation rates (BVAR) for all

215   major planktonic species (Interlandi and Kilham 2001). Biovolumes (μm_3) for major

216   planktonic species encountered during the Holocene were calculated using the median of

217   measured linear dimensions of 25 valves, and geometric shape guidelines (Hillebrand et al.

218   1999) (see Table S2). Planktonic species used for biovolume calculations ($\mu m_3/g$) accounted

219   for on average, over 80% of total relative abundance, and therefore we assume are a robust

220   estimate of palaeoproductivity. Stability in palaeoproductivity over time was further

221   quantified using its coefficient of variation (CV), while changes in the relationship between

222   palaeoproductivity and $N2$ diversity (PDR) was investigated using a moving-average

223   correlation analysis, with a window of 1000 years selected to capture millennial-scale

224   variability. Finally, relationships between palaeoproductivity and N2 diversity were further

225   investigated during specific time-intervals, to test the hypothesis that PDR is tightly coupled

226   during periods of rapid climate change, which we suggest is due to changing resource
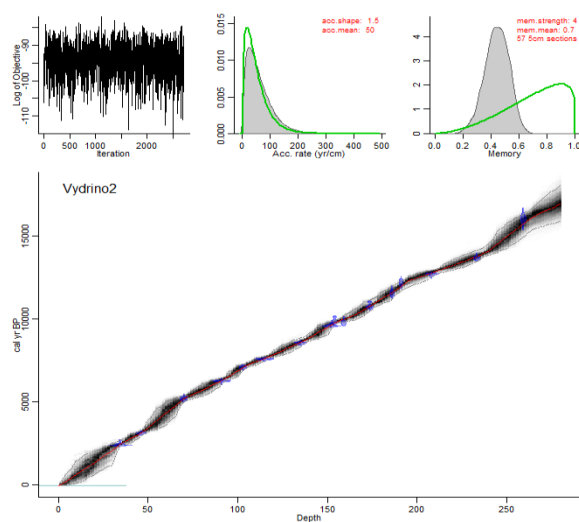
227   availability.

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229   **3. Results**

230

231   Dating

232   The calibrated ages for our profile span the last 15.83 kyr BP (where kyr = thousands of

233   years, BP = before present, i.e. 1950 CE (common era)) (Figure 2). Sediment accumulation

234   rates ranged between 34 - 133 yr/cm (mean 66 yr/cm), with peak accumulation rates

235   occurring at c. 3.9 kyr BP.

236

237   **< Fig. 2 here > Age-Depth model**

238

239

240   Diatom compositional change

241   The temporal resolution of species compositional change was c. 30 years for the past 15.83

242   kyr (Fig. 3). The principal curve (PrC) explained 48.4% of all the variation in the diatom

243   taxa. The taxa which have strongest influence on PrC ($r_2 > 0.3$) include *Aulacoseira*

244   *skvortzowii, Cyclotella minuta, Crateriportula inconspicua, Stephanodiscus meyerii,*

245   *Cyclostephanos dubius,* and *Synedra acus v. radians*. The PrC indicates periods of large

246   fluctuations in species composition (indicative of periods of community instability) between

247   *c.* 12.9-12.4 kyrs BP, 10.4 – 10.1 kyr BP and c. 6.2 – 5.2 kyr BP. Between 1.7 – 1.2 kyr BP,

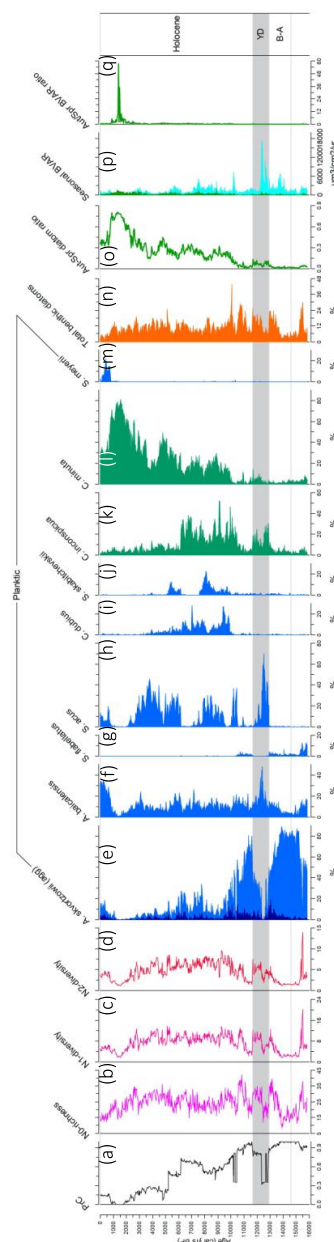248   PrC values are at their lowest.

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250

251   **< Fig. 3 here > Diatom stratigraphy**

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254   Diatom richness and diversity

255   Prior to the Bølling interstadial (c. 15.8 - 14.7 kyr BP), there are abrupt peaks in community

256   metrics of biodiversity, with highest $N1$ and $N2$ diversity values at 15.5 – 15.4 kyr, associated

257   with high abundances of littoral diatoms (Fig. 3). By 15.4 kyr BP, resting spores of *A.*

258   *skvortzowii* dominate, going into the Bølling interstadial (between 14.7 – 14.1 kyr BP),

259   leading to very low Hill's $N0$ richness and $N1$ & $N2$ diversity. Richness and diversity

260   increased during the Allerød (c. 14.1 – 12.9 kyr BP), concomitant with increasing abundances

261   of *Aulacoseira baicalensis*, and littoral species in general. The onset of the Younger Dryas

262   stadial at 12.9 kyr BP is marked by rapid declines in species richness and abundance of

263   common taxa, followed by a decline in Hill's $N2$ several centuries later, associated with peak

264   abundances of *S. acus* v. *radians* (Fig. 3). Richness and diversity measures all rapidly

265   increase again from c. 12.4 kyr BP.

266

267   The start of the Holocene (11.7 kyr BP) is demarcated by a sharp decline in diatom richness

268   and diversity values, before they increase rapidly once more at c. 11.3 kyr BP (Fig 3). $N2$

269   diversity is high (c. 10) between 11.3 - 9.2 kyr BP, with a notable decline between 10.5 –

270   10.2 kyr BP, concurrent with an abrupt decline in diatom richness. Between 9.2 – 5.2 kyr BP,

271   $N2$ diversity fluctuates between 5 and 10, with major declines at c. 6.0 and 5.2 kyr BP. $N2$

272   values remain low for c. 1000 years, before increasing to almost 8, at c. 4.4 kyr BP, after

273   which they decline to their lowest values (just above 1) at between 1.5 – 1.3 kyr BP. When

274   comparing the Holocene with the latter stages of Termination 1 (ie 15.8 – 11.7 kyr BP), there

275   is no significant difference in diatom richness ($N0$) (Table 1), but $N2$ diversity values were

276   substantially higher (MWU test; p=0.000). $N2$ diversity was less stable prior to 10 kyr BP

277   and during the past 2 kyr, as revealed through coefficient of variation (CV) (Fig 4).

278

279   **Table 1:** Median values for diatom fluxes, diatom BVAR, richness ($N0$) and diversity ($N2$),

280   for the Holocene and its preceding Termination period (T1). Differences between medians

281   were assessed using the non-parametric Mann-Whitney U test.

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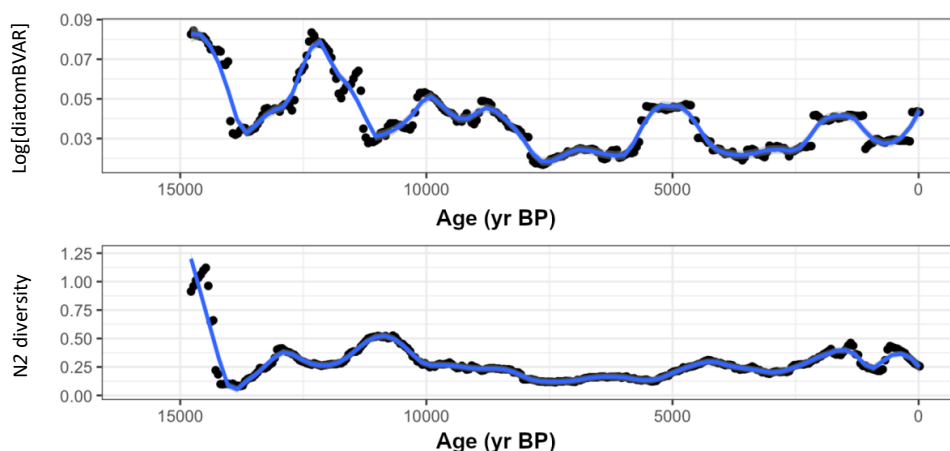|	Diatom valve flux (x 10^6 valves/cm^2/yr)	Palaeoproductivity (BVAR) μm^3/cm^2/yr	N0 richness	N2 diversity
Holocene	0.940	1.46 x10^3	24.1	5.3
T1	1.238	2.16 x10^3	22.7	2.7

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285   **< Fig. 4 here > diversity and productivity CV profiles**

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288
289   Palaeoproductivity

290   Palaeoproductivity was substantially higher and more unstable during the latter stages of

291   Termination 1 than the Holocene (p=0.000; Table 1), with diatom BVAR ($\mu m_3/cm_2/yr$)

292   rapidly increasing at the onset of the Younger Dryas, to reach peak values at c. 12.4 kyr BP

293   (Fig. 3) associated with peaks in *S. acus v. radians* then *A. baicalensis*. Diatom BVAR

294   declined as rapidly, and remained low for the remainder of the Younger Dryas and the start of

295   the Holocene. Palaeoproductivity was generally higher during the early Holocene than the

296   late Holocene, with spring productivity being far more dominant than autumn productivity

297   (Fig 3). After 7 kyr BP, total palaeoproductivity remained relatively low, although the

298   contribution from autumnal blooming diatoms increases (Fig. 3). When we compare the ratio

299   of autumn versus spring productivity, between 1.5 – 1.3 kyr BP autumnal productivity

300   increase to more than ten times that of spring productivity (Fig. 3). CV analyses shows that

301   palaeoproductivity gradually stabilised during the Late Glacial – early Holocene period until

302   c, 7 kyr BP. During the remainder of the Holocene, moderate periods of instability reoccur c.

303   5 kyr BP and between 2 – 1 kyr BP (Fig. 4). A 1000-yr moving window reveals that during

304   Termination 1, correlations flipped from strongly positive to strongly negative with greatest

305   change observed at the start of the Bølling-Allerød (Fig. 5). But over much of the Holocene

306   correlations coefficients are low, until c. 2.0 – 1.0 – kyr BP, when a strong negative

307   correlation develops.

308

309   < Fig. 5 here > 1000 yr moving window correlation analyses

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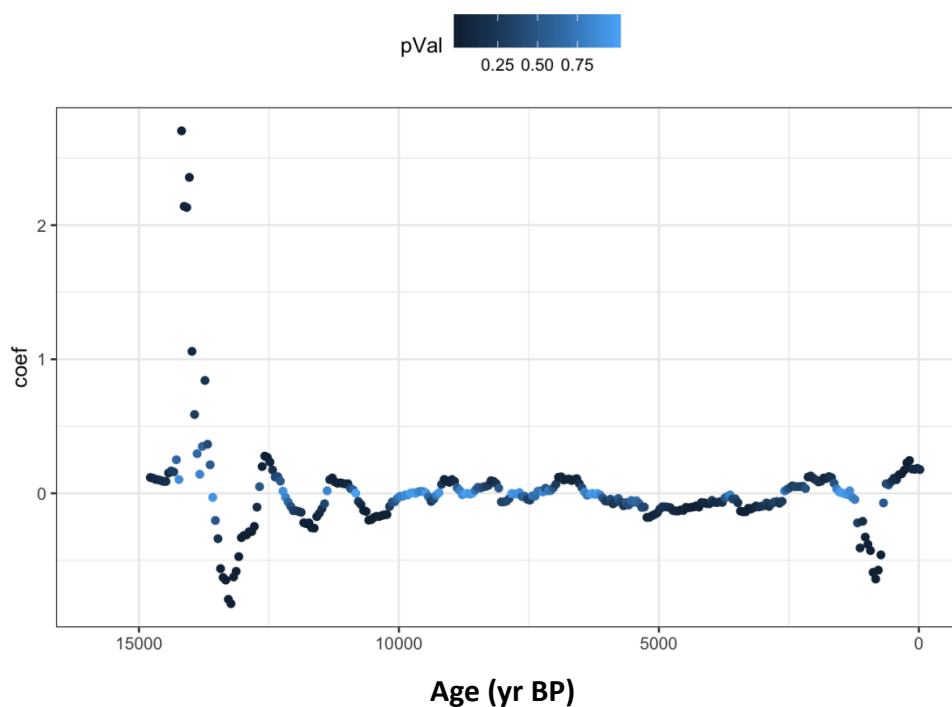
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314   **4. Discussion**

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316   **4.1 The climatic record**

317

318   Our study spans the past 15,800 years, specifically Termination 1 and the Holocene (11.7 kyr

319   – present). Termination periods are defined by the demise of northern hemisphere ice sheets,

320   as the planet transgressed from glacial to interglacial environments (Broecker & Donk 1970).

321   Termination 1, the most recent of these, started in the North Atlantic around 17.5 kyr years

322   ago (Stern & Lisiecki 2014), during which time, temperatures in the northern hemisphere

323   fluctuated by as much as 10 °C in a matter of decades, if not years (Alley 2000). These abrupt

324   temperature changes, linked to iceberg discharge and freshwater surges into the North

325   Atlantic Ocean, caused significant periods of millennial-scale climate variability.

326

327   During Termination 1, the first sign of a shift to warmer temperatures occurred with the onset

328   of the Bølling-Allerød interstadial, c. 14.7 kyr BP. The Bølling-Allerød is linked to warm

329   waters deep in the North Atlantic ocean releasing heat (Thiagarajan et al. 2014) which led to

330   the resumption of the Atlantic meridional overturning circulation (AMOC) (McManus et al.

331   2004) (Fig. 6g), warmer northern hemisphere temperatures (Fig. 6j) (Stuiver et al. 1995) and

332   stronger Asian summer monsoon (Fig. 6f) (Dykoski et al. 2005). Mean pollen-inferred

333   temperatures of the warmest month (July) from neighbouring Lake Kotokel provide an

334   independent climate record for the Lake Baikal region (Fig. 6c), and reveal a 5 °C increase

335   during the Bølling-Allerød (Tarasov et al. 2009). At the same time, pollen-inferred mean

336   annual precipitation records show that rainfall increased from c. 300 mm/yr to c. 460 mm/yr

337   (Fig. 6d). This warmer, wetter climate led to extensive melting of glaciers along the shores of

338   Lake Baikal (Horiuchi et al. 2004), and major expansion of boreal vegetation (Tarasov et al.

339   2009; Bezrukova et al. 2010; Reshetova et al. 2013).

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341   **< Fig. 6 here > external forcings**

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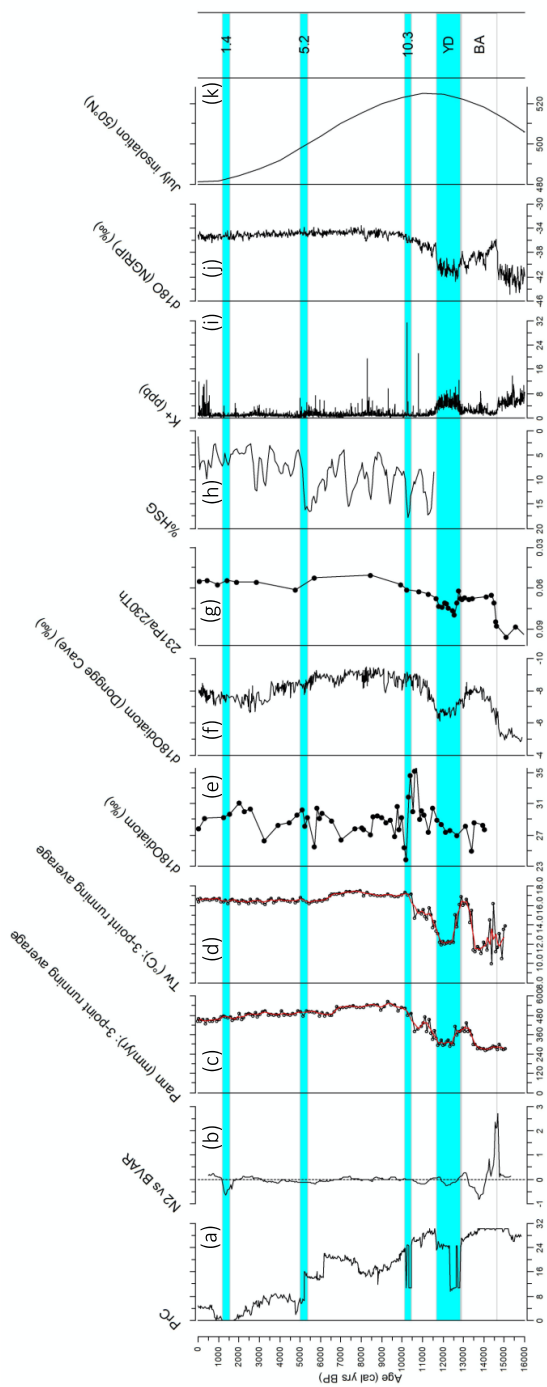
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347   The Younger Dryas stadial (12.9 – 11.7 kyr BP), is probably the most studied climate
348   disturbance event of the late Quaternary (Broecker et al. 2010). It was caused by an influx of
349   freshwater from Lake Agassiz into the Arctic Ocean (Tarasov & Peltier 2005; Murton et al.
350   2010) which led to the decline in AMOC (Fig. 6g) (Bond et al. 2001; McManus et al. 2004),
351   and concomitant cooler temperatures across the northern hemisphere (Stuiver et al. 1995)
352   (Fig 7j), and an attenuated Asian summer monsoon (Fig. 6f) (Dykoski et al. 2005). Increased
353   GISP2 K_+ concentrations (Fig.7i) indicate that the Siberian High intensified at the start of the
354   Younger Dryas (Mayewski et al. 1997), which accounts for cooler and more arid climate
355   conditions inferred from Lake Kotokel (Tarasov et al. 2009) (Fig. 7 c,d). These cooler, more
356   arid conditions led to a decline in hydrological input into Lake Baikal itself (Fig. 6e; Mackay
357   et al. 2011), and a short-lived expansion of the tundra biome (Tarasov et al. 2009; Bezrukova
358   et al. 2010).
359
360   Finally, although millennial scale variability is a feature of Holocene records (e.g. Bond *et*
361   *al.*, 1997, 2001; Fisher *et al.*, 2002; Mayewski et al. 2004; Nesje et al. 2005; Wanner *et al.*,
362   2008; Wanner & Bütikofer, 2008), the causes of this variability differs among the early, mid
363   and late Holocene periods (Wanner et al. 2014). During the early Holocene, climate
364   disturbance events are generally associated with pulses of freshwater discharge from northern
365   hemisphere ice sheets, which forced AMOC to decline, resulting in atmospheric cooling
366   (Rasmussen *et al.*, 2006). We use the stacked record of relative abundance of haematite
367   stained grains (%HSG) as tracers of Holocene drift ice in the North Atlantic (Bond et al.
368   2001), as a proxy for this variability (Fig. 6h). The causes of climate disturbance events
369   associated with millennial-scale variability during the mid- to late- Holocene are less certain,
370   but involve solar and volcanic forcing, often amplified by complex interactions between
371   ocean and the atmosphere (PAGES 2k Consortium 2013; Wanner et al. 2014). Moreover,
372   environmental impacts of mid- late- Holocene events are often not characterised by regional
373   cooling, but by hydrological variability instead. In Lake Baikal, the impact of early-, mid-
374   and late- Holocene climate disturbance events are implicated in understanding Holocene
375   variability in hydrological variability (Mackay et al. 2011) and carbon dynamics in the lake
376   (Mackay et al. 2017). Here we focus on climate disturbance events from the Younger Dryas,
377   and each of the early (10.3 kyr), mid (5.2 kyr) and late (1.4 kyr) periods, as these are
378   concurrent with major shifts in diatom community stability (Fig. 3a).

379

4.2 Temporal trends in diatom communities, diversity and palaeoproductivity

381

382 Although community turnover, as indicated by the principal curve (Fig 3a), was rather stable

383 during the latter stages of Termination 1 (Fig 3a), diatom communities were already species-

384 rich (Table 1), indicative that Lake Baikal species were able to tolerate and survive preceding

385 very cold glacial conditions, challenging the notion of an ecological collapse in Lake Baikal

386 during the Last Glacial Maximum (Karabanov et al. 2004). *A. skvortzowii* thrives in cold

387 water temperatures below 5°C (Jewson et al., 2008), and dominates the cool period prior to

388 the Bølling-Allerød interstadial. To avoid higher surface-water temperatures, it produces a

389 resting stage, or spore. The trigger for the production of spores is phosphate utilisation by

390 other algae (e.g. picoplankton) (Jewson et al., 2008). For *A. skvortzowii* spores to dominate,

391 phosphate concentrations must have fallen below a threshold level of 15-23 µg/L (Jewson et

392 al., 2008). Prior to the Bølling-Allerød, pigment analyses of Baikal sediments highlight

393 increased productivity from many algal groups (Tani et al. 2002; Soma et al. 2007) which

394 likely caused intensive competition for P during the short, ice-free summer. Nutrient,

395 especially P, limitation may be why we also observe low $N2$ diatom diversity during

396 Termination 1 (Fig. 3d), i.e. resources available were strongly limited (Interlandi & Kilhman

397 2001) at this time.

398

399 During the early stages of the Bølling, pre- Bølling diatom flora persists, with concomitant

400 low richness and diversity (Fig. 3b,d). Increasing diatom richness ($N0$) during the Allerød is

401 associated with the presence of littoral diatoms on the Vydrino Shoulder (Fig. 3n), cells of

402 which have to be transported from near-shore environments to the site of the core location.

403 Transport would have been greatly facilitated by increased fluvial input into the south basin,

404 linked to rapidly melting glaciers at the start of the Allerød at c. 14.1 kyr BP (Osipov and

405 Khlystov 2010). Increasing $N2$ diversity in Lake Baikal during the Allerød suggests an

406 increase in available resources (Interlandi & Kilham 2001), such as Si and P; co-limitation by

407 several nutrients and light allows more planktonic species to co-exist (Burson et al. 2018),

408 which in Lake Baikal at this time includes the heavily silicified endemic *A. baicalensis*,

409 which needs relatively high concentrations of Si to grow, and a high degree of turbulence to

410 remain in the photic zone (Jewson et al. 2010).

411

412   Simultaneous with the onset of the Younger Dryas, principal curve (PrC), and community

413   metrics of species richness and diversity show evidence of an abrupt ecological shift in Lake

414   Baikal (Fig. 3). While changes in stability and richness were almost instantaneous, $N2$ diversity

415   declined only about 200 years later (Fig. 3d). The decline in $N0$ in the Younger Dryas is mainly

416   driven by a decline in littoral taxa, which could be related to increased ice cover on the lake

417   and lower littoral productivity. Alternatively, lower $N0$ may be linked to the decline in fluvial

418   input into the south basin (Fig. 6e) reducing transport of littoral diatoms off-shore. The lag in

419    $N2$ diversity decline suggests that available resources for diatom growth were not initially

420   limiting; species composition at this time is dominated by the spring blooming *S. acus* v.

421   *radians* and the autumnal blooming *C. inconspicua* (Fig. 3h,k), and therefore these species may

422   not be directly competing for the same resources (Interlandi & Kilham 2001). The eventual

423   decline in $N2$ diversity is linked to peak values for *A. baicalensis* for the whole record at c.

424   12.4 kyr BP (Fig. 3f), which likely caused the decline in *S. acus* v. *radians*. Silicic acid

425   availability in Lake Baikal is strongly controlled by diatom population changes (Callender &

426   Granina 1995; Jewson et al., 2010; Shimaraev and Domysheva, 2013; Jewson et al., 2015). In

427   particular, when populations of *A. baicalensis* are very high, the availability of silicic acid

428   uptake by other species declines, leading to a drop in their populations, (Jewson et al., 2010;

429   2015). Being a heavily silicified species, *A. baicalensis* needs a strong period of mixing, which

430   suggests that when abundant, turnover is strong, allowing the recycling of nutrients needed for

431   peak palaeoproductivity. Changes in climate and resource availability together (e.g. Huisman

432   et al. 2004) therefore explain the rapid successional changes in planktonic diatoms during the

433   early stages of the Younger Dryas, and concomitant decline in $N2$ diversity. During the latter

434   stages of the Younger Dryas, increasing $N2$ diversity reflects an increase in the abundance of

435   *A. skvortzowii* spores, along with autumnal blooming species *C. inconspicua* and *Cyclotella*

436   *minuta* (Fig. 3).

437

438   Although our data highlight a rapid decline in diatom richness and diversity from the start of

439   the Holocene to 11.3 kyr BP (Fig. 3b,d), coincident with tracers of increased drift ice in the

440   North Atlantic (stacked record of haematite-stained grains; Fig. 6h) (Bond et al. 1997; 2001)

441   here we focus on the period of abrupt ecological change that occurred between 10.5 – 10.2

442   kyr BP, (Fig. 3a). Just before this period, it is useful to note that peak June isolation (Fig. 6k)

443   resulted in increasing mean annual precipitation in the region (Fig. 6d) (Tarasov et al. 2009),

444   which, alongside glacier melt, will have contributed to peak Holocene hydrological input into

445   Lake Baikal (Fig. 6e) (Mackay et al. 2011). Then at c. 10.5 kyr BP, we have this record of

446   rapid diatom successional changes, with distinct multidecadal variability (Fig. 3). The decline

447   in community metrics for richness and diversity (Fig. 3,d) are concurrent with a slow-down

448   in AMOC (Bond et al. 2007; IRD7) (Fig. 6h) concurrent with a very intense Siberian High

449   (Fig. 6i) (Mayewski et al. 1997). Together, these resulted in regional aridity and cooler

450   temperatures, which led to the decline in river flow into the south basin of Lake Baikal (Fig.

451   6e) (Mackay et al. 2011). Diatom community instability (Fig. 3a) reflects rapid switches in

452   dominance between spring blooming *S. acus* and *A. skvortzowii*, alongside increasing autumn

453   blooming *C. inconspicua*. *S. acus* has one of the highest cell division rates of all the Lake

454   Baikal phytoplankton (Jewson et al. 2015), which allows it to respond rapidly to changes in

455   resource availability. Large blooms of *S. acus* will have utilised resources, including P, which

456   then would have stimulated *A. skvortozowii* to produce resting cells (Jewson et al. 2008). The

457   increase in *C. inconspicua* is indicative of a shift in balance towards autumnal production,

458   perhaps due to sustained ice cover during this cool event leading to a decline in spring

459   diatoms.

460

461   Another notable period of community instability occurs between 6 – 5 kyr BP, with a major

462   decline in community turnover occurring at 5.2 kyr BP (Fig. 3a). Globally, this period marks

463   the transition from Holocene Thermal Maximum to the Neoglacial, as northern hemisphere

464   summer insolation levels declined (Steig 1999; Wanner et al. 2008). Again, increased diatom

465   instability is concurrent with a major slow-down in AMOC, as reflected in the large increase

466   in haematite stained grains (Fig. 6h) (IRD 4; Bond et al. 2001) and the end of a period of

467   more intense Siberian High (Mayewski et al. 1997). In general, regions around the world

468   became cooler (see Magny et al. 2006 for a review), but some also became wetter (e.g.

469   Ireland; Roland et al. 2015) while in central and southern Asia they became more arid (see

470   Magny et al. 2006). Terrestrial ecosystem changes in northeast China have also been

471   attributed to the weakening of the East Asian winter monsoon (Wu et al. 2019). In Lake

472   Baikal, there is little overall change in diatom richness at this time (Fig. 3b), although *N*2

473   diversity declines, reflecting a shift from spring to autumn diatom communities (Fig. 3d).

474   Tentatively, we conclude that this period of ecological change was likely extrinsically forced

475   (Williams et al. 2011; biome reconstruction in the Easter Sayan Mountains show an increase

476   in steppe grasslands from c. 6.0 kyr BP, indicative of more arid conditions (Mackay et al.

477   2012), while maximum taiga biome reconstructions occurred at c. 5.0 kyr BP, after which

478   they declined, again indicative of cooler, more arid climate in the Lake Baikal region

479   (Bezrukova et al. 2005; Prokopenko et al. 2007). Further afield in the Altai Mountains, there

480   is also strong evidence for a marked increase in aridity after 6.0 kyr BP (Blyakharchuk et al.

481   2007; Rudaya et al. 2009) (Fig. 1), while glaciers advanced across Europe, North America

482   and mountain regions of central Asia (reviewed in Mayewski et al. (2004).

483

484   During the late Holocene, diatom communities were increasingly dominated by the autumnal

485   blooming *Cyclotella minuta* (Fig. 3l), leading to increasing ratio of autumn versus spring

486   diatom communities (Fig. 3o). This increasing ratio is concurrent with declining June

487   insolation (Fig. 6k) which may be an wide-scale ecosystem response to long-term orbital

488   forcing. The final peak in *C. minuta* comes first of all at the expense of the cosmopolitan *S.*

489   *acus*, then by the endemic *A. baicalensis*. Between c. 1.7 – 1.2 kyr BP, the pelagic

490   community consists almost of only *C. minuta* to such an extent that N2 diversity reaches

491   some of their lowest values (Fig. 3d), comparable to diversity during the Bølling-Allerød.

492   Even more striking is the development of autumnal productivity between 1.48 – 1.32 kyr BP,

493   which is unique for the 15,800 year record, and reaches almost 60 times that of spring

494   productivity at c. 1.40 kyr BP (Fig. 3q). This dominance of autumnal productivity is

495   concurrent with the Dark Ages Cold Period (DCAP) (CE 400 – 765) (Helama et al. 2017), a

496   climatically cool period, linked to changes in ocean circulation (IRD1; Bond et al. 2001), and

497   solar & volcanic activity (Helama et al. 2017). *C. minuta* is currently the only pelagic diatom

498   to bloom during the autumn in Lake Baikal in substantial numbers. Because this species can

499   tolerate surface water temperatures up to 11 °C, cells can persist in the surface waters for

500   longer during summer stratification, so that when stratification breaks down in the autumn

501   and nutrients are regenerated, cells of *C. minuta* are retrained into the photic first, giving

502   them a strong competitive advantage (Jewson et al., 2015). From the available evidence, it is

503   still not clear why *C. minuta* should dominate over all other species at this time. It may be

504   that cold conditions associated with the DCAP led to extended ice cover such that growth of

505   spring blooming species was inhibited, allowing *C. minuta* to exploit available resources. For

506   the past 1000 years, spring blooming diatoms once more dominate communities.

507

508   To further investigate Lake Baikal's resilience, we specifically tested whether total, spring

509   and autumn productivity, and N2 diversity, were different for the three centuries immediately

510   before and after the three Holocene climate disturbance events using the non-parametric

511   Kruskal-Wallis one-way analysis of variance (Table 2).

512

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513   Table 2: Kruskal-Wallis one-way analysis of variance for measures of palaeoproductivity and

514   N2 diversity

	TotValve BVAR	Spring BVAR	Autumn BVAR	N2
10.3 kyr BP Chi-Square	5.343	6.150	.130	5.343
Asymp. Sig.	.021	.013	.718	.021
5.2 kyr BP Chi-Square	1.058	.659	.949	2.550
Asymp. Sig.	.304	.417	.330	.110
1.4 kyr BP Chi-Square	3.552	1.464	12.052	19.221
Asymp. Sig.	.059	.226	.001	.000

515

516   Productivity and diversity show only minor or no lasting difference during the early- and

517   mid- Holocene climate disturbance events. Only during the late Holocene climate event at 1.4

518   kyr BP are autumnal productivity and N2 diversity very different (higher and lower

519   respectively), suggesting perhaps of lowered ecosystem resilience at this time.

520

521   Overall, community metrics for richness and biodiversity suggest that over much of the

522   record, the ecosystem of Lake Baikal has also shown considerable ecological resilience

523   (Holling 1973). Despite repeated impacts on diatom communities from disruptive climate

524   events, diversity recovers to higher $N2$ values than reached previously (Fig. 3d), at least until

525   the start of the Neoglacial. The impact-recovery response occurs in a saw-tooth pattern,

526   similar to the trapezoidal model of Dansgaard-Oeschger (D-O) cycles (Schulz 2002), where

527   recovery takes hundreds of years (Pimm 1984). Our palaeoecological analyses highlight that

528   succession of planktonic flora in Lake Baikal has always been very dynamic, such that

529   shifting patterns of dominance indicate low stability, but strong resilience. Our analyses also

530   highlight that despite successive abrupt ecological responses to rapid climate change, Lake

531   Baikal planktonic diatoms contain considerable plasticity that has allowed them to tolerate

532   major changes to their aquatic environment for the majority of the Holocene (Hof et al.

533   2011).

534

535   **4.3 Relationship between diversity and stability of ecosystem functioning**

536

537   N2 diatom diversity is highest (Fig. 3d) when there is both strong spring and autumnal

538   productivity during the middle Holocene (Fig. 3p), indicative of optimal growing conditions

539   throughout the year. When growing conditions are optimal, productivity and diversity are not

540   strongly coupled during much of the Holocene (10 – 2.5 kyr BP (Fig 5), indicating that while

541   species fluctuations respond rapidly to changing resources (Fig. 3, the ecosystem function of

542   primary production is relatively resilient. This is likely because of the "insurance effect"

543   described by (Yachi and Loreau 1999), with different plankton playing similar functional

544   roles in pelagic Lake Baikal.

545

546   During periods when diversity was less stable (e.g. during the period before 10 kyr BP),

547   productivity is also unstable, for example, prior to 10 kyr BP, and again during 1-2 kyr BP

548   (Fig. 5). The tightly coupled productivity – diversity relationship (PDR) during Termination

549   1 is likely down to climate disturbance events having direct impact on resource availability.

550   For example, as the regional climate warmed up, new resources become available, and

551   nutrients could be transported to the lake through increased river flow from melting glaciers

552   (Osipov and Khlystov 2010). Shorter ice duration on the lake will also have led to an increase

553   in productivity due to a lengthening of the growing season. The switch to a strong negative

554   relationship between 2 – 1.2 kyr BP, likely reflects a complex set of processes linked to both

555   extreme ecosystem disturbance (eg increased ice cover and duration), and a reduction in

556   resource heterogeneity (Interlandi & Kilham 2001) due to severe limitation by a single

557   resource, indicative of a disturbed system (Interlandi & Kilham 2001). For example, silicon is

558   likely limiting during the Younger Dryas due to massive increases in the abundances of *A.*

559   *baicalensis* (Fig. 3) (Jewson et al., 2010; 2015). During 1.6 – 1.2 kyr BP, autumnal diatoms

560   are in greater proportion than spring diatoms, concurrent with a strong negative correlation

561   between palaeoproductivity and N2 diversity. This is also indicative of a reduction in

562   resource heterogeneity (Interlandi & Kilham 2001), with silicon availability again being a

563   likely contender.

564

565

566   **Conclusions**

567

568   This study provides many new insights into the development of primary producer

569   communities in Lake Baikal. That diatom communities are very dynamic, they respond

570   quickly to disturbance, but they also recover. These observations may hold insights into the

571   unfolding changes occurring in recent decades; for example the decline in heavily silicified

572   endemic taxa and the growth of the cosmopolitan *S. acus* (Roberts et al., 2018). That this

573 change has occurred earlier in the Holocene suggests that the lake is very resilient, and such

574 changes may be, in the context of long timescales, temporary. However, what our record

575 cannot provide information on is the resilience of the lake's flora to multiple stressors such as

576 human driven climate change and anthropogenic nutrient enrichment, which is currently

577 impacting the lake's littoral communities.

578

579 In relation to the wider ecological picture, our study has provided important insights into our

580 understanding of productivity-diversity relationships (PDR). We show that diatoms

581 communities and palaeoproductivity are sensitive to extrinsic drivers of climate change.

582 These drivers operate at different time scales, from abrupt events during the Termination1,

583 resulting in a tight coupling between palaeoproductivity and diversity, to slower changes in

584 boreal insolation linked to orbital forcing, leading to gradual changes in seasonal productivity

585 as the Holocene unfolds. We therefore provide important perspective to complement existing

586 short-term observational (Dodson et al. 2000) and experimental (Winfree et al. 2015)

587 approaches. Diatom responses (i.e. stability and diversity) to abrupt events are instantaneous,

588 and although recovery occurs at a slower rate (which may be because resources take time to

589 be replenished, or that disrupted food webs take longer to re-establish), N2 diversity tends to

590 be higher than before the disturbance, indicative of strong resilience (McCann 2000), at least

591 in freshwater ecosystems not damaged by environmental pollution.

592

593

594 **Author Contributions:**

595 Study was conceived by AWM and PR. Diatom counting was undertaken by DM. Age

596 modelling was done by NP. Data analyses was undertaken by AWM, VF and AS. AWM led

597 the paper writing with significant contributions from AS and GEAS. All authors made

598 comments on earlier drafts of the paper.

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607   **References**

608

609   Alley, R. B.: The Younger Dryas cold interval as viewed from central Greenland, Quat. Sci. Rev., 19,
610   213-226, 2000.

611

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

614

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

618

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

621

622   Bezrukova, E. V., Abzaeva, A. A., Letunova, P. P., Kulagina, N. V., Vershin, K. E., Belov, A. V.,
623   Orlova, L. A., Danko, L. V., and Krapivina, S. M.: Post-glacial history of Siberian sprice (*Picea*
624   *obovata*) in the Lake Baikal area and the significance of this species as a paleo-environmental indicator,
625   Quat. Int., 136, 47-57, 2005.

626

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

630

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

633

634   Blyakharchuk, T. A., Wright, H. E., Borodavko, P. S., van der Knaap, W. O., and Ammann, B.: Late
635   glacial and Holocene vegetational history of the Altai mountains (southwestern Tuva Republic,
636   Siberia), Palaeogeogr., Palaeoclimatol., Palaeoecol., 245, 518-534, 2007.

637

638   Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal,, P., Priore, P., Cullen, H.,
639   Hajdas, I., and Bonani, G.: A pervasive millennial scale cycle in North Atlantic Holocene and glacial
640   climates, Science, 278, 1257-1256, 1997.

641

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

645

646   Broecker, W. S., and Donk, J.: Insolation changes, ice volumes, and the O18 record in deep-sea
647   cores, Rev. Geophys., 8, 169-198, 1970

648

649   Broecker, W. S., Denton, G. H., Edwards, R. L., Cheng, H., Alley, R. B., and Putnam, A. E.: Putting
650   the Younger Dryas cold event into context, Quat. Sci. Rev., 29,1078-1081, 1970.

651

652   Burson, A., Stomp, M., Greenwell, E., Grosse, J., and Huisman, J.: Competition for nutrients and
653   light: testing advances in resource competition with a natural phytoplankton community, Ecology, 99,
654   1108-1118, 2018.

655

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

659

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

663

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

667

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

671

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

675

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

678

679   De'ath, G.: Principal Curves: A New Technique for Indirect and Direct Gradient Analysis, Ecology 80,
680   2237-2253, 1999.

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

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

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

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

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

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

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

704   Hampton, S. E., McGowan, S., Ozersky, T., Virdis, S. G. P., Vu, T. -T., Spanbauer, T., Kraemer, B.,
705   Swann, G., Mackay, A. W., Powers, S., Meyer, M. F., Labou, S. G., O'Reilly, C. M., DiCarlo, M.,
706   Galloway, A. W. E., and Fritz, S.: Recent ecological change in ancient lakes, Limnol. Oceanogr., 63,
707   2277-2304, 2018.

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

712   Hill, M. O.: Diversity and evenness: A unifying notation and its consequences, Ecology, 54, 427-432,
713   1973.

714

715   Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, U., and Zohary, T.: Biovolume calculations

716   for pelagic and benthic microalgae, J. Phycol., 35, 403-424, 1999.

717

718   Hof, C., Levinsky, I., Araújo, M. B., and Rahbek, C.: Rethinking species' ability to cope with rapid

719   climate change, Global Change Biol., 17, 2987-2990, 2011.

720

721   Holling, C. S.: Resilience and stability of ecological systems, Annu. Rev. Ecol. Syst., 4 ,1-23, 1973.

722

723   Horiuchi, K., Matsuzaki, H., Osipov, E., Khlystov, O., and Fujii, S.: Cosmogenic ^{10}Be and ^{26}Al dating

724   of erratic boulders in the southern coastal area of Lake Baikal, Siberia, Nucl. Instrum. Methods Phys.

725   Res. Sect., 223, 633-638, 2004.

726

727   Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M.,

728   Sommeijer, B.: Changes in turbulent mixing shift competition for light between phytoplankton species,

729   Ecology, 85, 2960-2970, 2004.

730

731   Interlandi, S. J., and Kilham, S. S.: Limiting resources and the regulation of diversity in phytoplankton

732   communities, Ecology, 82, 1270-1282, 2001.

733

734   Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin,

735   C., Bruelheide, H., De Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch,

736   A., Kreyling, J., Lanta, V., Manning, P., Meyer, S. T., Mori, A. S., Naeem, S., Niklaus, P. A., Polley,

737   W., Reich, P. B., Roscher, C., Seabloom, E. W., Smith, M.D., Thakur, M. P., Tilman, D., Tracy, B. F.,

738   van der Putten, W.H ., can Ruijven, J., Weigelt, A., Weisser, W. W., Wilsey, B., and Eisenhauer, N.:

739   Biodiversity increases the resistance of ecosystem productivity to climate extremes, Nature, 526, 574-

740   577, 2015.

741

742   Jewson, D. H., Granin, N. G., Zhdanov, A. A., Gorbunova, L. A., Bondarenko, N. A., and Gnatovsky,

743   R. Yu.: Resting stages and ecology of the planktonic diatom *Aulacoseira skvortzowii* in Lake Baikal,

744   Limnol. Oceanogr., 53, 1125-1136, 2008.

745

746   Jewson, D. H., Granin, N. G., Zhdarnov, A. A., Gorbunova, L. A., and Gnatovsky, R.Y.: Vertical

747   mixing, size change and resting stage formation of the planktonic diatom Aulacoseira baicalensis. Eur.

748   J. Phycol., 45, 354-364, 2010

749

750   Jewson, D. H., Granin, N. G., Gnatovsky, R. Y., Lowry, S. F., and Teubner, K., Coexistence of two

751   Cyclotella diatom species in the plankton of Lake Baikal, Freshwat. Biol., 60, 2113-2126, 2015.

752

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

754

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

757

758   Karabanov, E., Williams, D., Kuzmin, M., Sideleva, V., Khursevich, G., Prokopenko, A., Solotchina,
759   E., Tkachenko, L., Fedenya, S., Kerber, E., and Gvozdkov, A.: Ecological collapse of Lake Baikal and
760   Lake Hovsgol ecosystems during the Last Glacial and consequences for aquatic species diversity,
761   Palaeogeogr., Palaeoclimatol., Palaeoecol., 209, 227-243, 2004.

762

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

765

766

767   Korhonen, J. J., Wang, J., and Soininen, J.; Productivity-diversity relationships in lake plankton
768   communities, PLoS One, 6, p.e22041, 2011.

769

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

771

772   Kravtsova, L. S., Izhboldina, L. A., Khanaev, I. V., Pomazkina, G. V., Rodionova, E. V., Domysheva,
773   V. M., Sakirko, M. V., Tomberg, I. V., Kostornova, T. Y., Kravchenko, O. S., and Kupchinsky, A. B.:
774   Nearshore benthic blooms of filamentous green algae in Lake Baikal, J. Great Lakes Res., 40, 441-
775   448, 2014.

776

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

780

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

783

784   Mackay, A. W., Flower, R. J., Kuzmina, A. E., Granina, L. Z., Rose, N. L., Appleby, P. G., Boyle, J.
785   F., and Battarbee, R. W.: Diatom succession trends in recent sediments from Lake Baikal and their
786   relation to atmospheric pollution and to climate change, Philos. T. R. Soc. B: Biol. Sci., 353, 1011-
787   1055, 1998.

788

789   Mackay, A. W., Swann, G. E. A., Brewer, T. S., Leng, M. J., Morley, D. W., Piotrowska, N., Rioual,
790   P., and White, D.: A reassessment of late glacial - Holocene diatom oxygen isotope record from Lake
791   Baikal using a geochemical mass-balance approach, J. Quat. Sci., 26, 627-634, 2011.
792
793   Mackay, A. W., Bezrukova, E. V., Leng, M. J., Meaney, M., Nunes, A., Piotrowska, N., Self, A.,
794   Shchetnikov, A., Shilland, E., Tarasov, P., Wang, L., and White, D.: Aquatic ecosystem responses to
795   Holocene climate change and biome development in boreal, central Asia, Quat. Sci. Rev., 41, 119-131,
796   2012.
797
798   Mackay, A. W., Seddon, A. W. R., Leng, M. J., Heumann, G., Morley, D. W., Piotrowska, N., Rioual,
799   P., Roberts, S., and Swann, G.E.A.: Holocene carbon dynamics at the forest-steppe ecotone of southern
800   Siberia, Global Change Biol., 23, 1942-1960, 2017.
801
802   Magny, M., Leuzinger, U. R. S., Bortenschlager, S., and Haas, J. N.: Tripartite climate reversal in
803   Central Europe 5600–5300 years ago, Quat. Res., 65, 3-19, 2006.
804
805   Mayewski, P. A., Meeker, L. D., Twickler, M. S., Whitlow, S., Yang, Q., and Prentice, M.: Major
806   features and forcing of high latitude Northern Hemisphere atmospheric circulation using a 110,000 year
807   long glaciochemical series, J. Geophys. Res., 102, 26345-26366, 1997.
808
809   Mayewski, P. A., Rohling, E. E., Stager, J. C., Karlén, W., Maasch, K. A., Meeker, L. D., Meyerson,
810   E. A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser,
811   M., Schneider, R. R., and Steig, E. J.: Holocene climate variability, Quat. Res., 62, 243-255, 2004.
812
813   McCann, K.S.: The diversity-stability debate, Nature 405, 228-233, 2000.
814
815   McGrady-Steed, J., Harris, P. M., and Morin, P. J.: Biodiversity regulates ecosystem predictability,
816   Nature, 390, 162–165, 1997.
817
818   Murton, J. B., Bateman, M. D., Dallimore, S. R., Teller, J. T., and Yang, Z.: Identification of Younger
819   Dryas outburst flood path from Lake Agassiz to the Arctic Ocean, Nature, 464, 740-743, 2010.
820
821   National Research Council.: The geological record of ecological dynamics: understanding the biotic
822   effects of future environmental change, The National Academies Press, Washington DC, USA 2005.
823
824   Nesje, A., Jansen, E., Birks, H. J .B., Bjune, A. E., Bakke, J., Andersson, C., Dahl, S. O., Kristensen,
825   D. K., Lauritzen, S., Lie, O., and Risebrobakken, B.: Holocene climate variability in the northern North

826   Atlantic region: a review of terrestrial and marine evidence, Geophysical Monograph-American
827   Geophysical Union, 158, 289-322, 2005.

828

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

831

832   PAGES 2k Consortium.: Continental-scale temperature variability during the past two millennia, Nat.
833   Geosci., 6, 339-346, 2013.

834

835   Pimm, S.L.: The complexity and stability of ecosystems, Nature, 307, 321, 1984

836

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

839

840   Prokopenko, A. A., Khursevich, G. K., Bezrukova, E. V., Kuzmin, M. I., Boes, X., Williams, D. F.,
841   Fedenya, S. A., Kulagina, N. V., Letunova, P. P., and Abzaeva, A. A.: Paleoenvironmental proxy
842   records from Lake Hovsgol, Mongolia, and a synthesis of Holocene climate change in the Lake Baikal
843   watershed, Quat. Res., 68, 2-17, 2007.

844

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

848

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

851

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

856

857   Reimer, P., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Bronk Ramsey, C., Buck, C. E., Cheng,
858   H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Haflidason, H., Hajdas, I., Hatté,
859   C., Heaton, T. J., Hoffmann, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning,
860   S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S.
861   M., and van der Plicht, J.: IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years
862   cal BP, Radiocarbon, 55, 1869–1887, 2013.

863

864   Reshetova, S. A., Bezrukova, E. V., Panizzo, V., Henderson, A., Ptitsyn, A. B., Daryin, A. V., and

865   Kalugin, I. A.: Vegetation of Central Transbaikalia in the Late Glacial Period and Holocene, Geography

866   and Natural Resources, 34,172-178, 2013.

867

868   Roberts, S., Swann, G. E. A., McGowan, S., Panizzo, V., Vologina, E., Sturm, M., Mackay, A. W.:

869   Evidence of 20th Century ecosystem change in Lake Baikal, Siberia, PLoS One, 13, e0208765. 2018.

870

871   Roland, T. P., Daley, T. J., Caseldine, C. J., Charman, D. J., Turney, C. S. M., Amesbury, M. J.,

872   Thompson, G. J., and Woodley, E. J.: The 5.2 ka climate event: Evidence from stable isotope and multi-

873   proxy palaeoecological peatland records in Ireland, Quat. Sci. Rev., 124, 209-223, 2015.

874

875   Rudaya, N., Tarasov, P., Dorofeyuk, N., Solovieva, N., Kalugin, I., Andreev, A., Daryin, A., Diekmann,

876   B., Riedel, F., Tserendash, N., and Wagner, M.: Holocene environments and climate in the Mongolian

877   Altai reconstructed from the Hoton-Nur pollen and diatom records: a step towards better understanding

878   climate dynamics in Central Asia, Quat. Sci. Rev., 28, 540-554, 2009.

879

880   Rusak, J. A., Leavitt, P. R., McGowan, S., Chen, G., Olson, O., Wunsam, S., and Cumming, B.F.:

881   Millennial-scale relationships of diatom species richness and production in two prairie lakes, Limnol.

882   Oceanogr., 49, 1290-1299, 2004

883

884   Schulz, M.: On the 1470-year pacing of Dansgaard-Oeschger warm events. Paleoceanography, 17, 4-

885   9, 2002.

886

887   Seddon, A. W., Froyd, C. A., Leng, M. J., Milne, G. A. and Willis, K. J.: Ecosystem resilience and

888   threshold response in the Galápagos coastal zone, PloS One, 6, e22376, 2011.

889

890   Seddon, A. W., Mackay, A. W., Baker, A. G., Birks, H. J. B., Breman, E., Buck, C. E., Ellis, E. C.,

891   Froyd, C. A., Gill, J. L., Gillson, L., and Johnson, E.A.: Looking forward through the past: identification

892   of 50 priority research questions in palaeoecology, J. Ecol., 102, 256-267, 2014.

893

894   Shimaraev, M. N., and Domysheva, V. M.: Trends in hydrological and hydrochemical processes in

895   Lake Baikal under conditions of modern climate change, in: Climatic Change and Global Warming of

896   Inland Waters, edited by: Colman, C. R., Kumagai, M., and Robarts, R. D., John Wiley & Sons Ltd,

897   Chichester, UK, 43-66., 2013

898

Climate
of the Past
Discussions

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

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

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

911 Steig, E .J.: Mid-Holocene climate change, Science, 286, 1485-1487, 1999.

913 Stern, J. V., and Lisiecki, L. E: Termination 1 timing in radiocarbon dated regional benthic δ_{18}O
914 stacks, Paleoceanography, 29, 1127-1142, 2014.

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

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

924 Tarasov, L., and Peltier W.R.: Arctic freshwater forcing of the Younger Dryas cold reversal. Nature,
925 435, 662-665, 2005.

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

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

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

936

937 Timoshkin, O A., Samsonov, D. P., Yamamuro, M., Moore, M. V., Belykh, O. I., Malnik, V. V.,

938 Sakirko, M. V., Shirokaya, A. A., Bondarenko, N. A., Domysheva, V. M., Fedorova, G. A.,

939 Kochetkov, A. I., Kuzmin, A. V., Lukhnev, A. G., Medvezhonkova, O. V., Nepokrytykh, A. V.,

940 Pasynkova, E. M., Poberezhnaya, A. E., Potapskaya, N. V., Rozhkova, N. A., Sheveleva, N. G.,

941 Tikhonova, I. V., Timoshkina, E. M., Tomberg, I.V ., Volkova, E. A., Zaitseva, E. P., Zvereva, Y. M.,

942 Kupchinsky, A. B., and Bukshuk, N. A.: Rapid ecological change in the coastal zone of Lake Baikal

943 (East Siberia): Is the site of the world's greatest freshwater biodiversity in danger?, J. Great Lakes

944 Res., 42, 487-497, 2016.

945

946 Wanner, H., and Bütikofer, J.: Holocene Bond cycles: real or imaginary, Geografie-Sborník České

947 Geografické Společnosti, 113, 338-350, 2008

948

949 Wanner, H., Beer, J., Bütikofer, J., Crowley, T. J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean,

950 M., Joos, F., Kaplan, J. O., Küttel, M., Müller, S. A., Prentice, C., Solomina, O., Stocker, T. F., Tarasov,

951 P., Wagner, M., and Widmann, M.: Mid- to Late Holocene climate change: an overview, Quat. Sci.

952 Rev., 27, 1791-1828, 2008.

953

954 Wanner, H., Mercolli, L., Grosjean, M., and Ritz, S. P.: Holocene climate variability and change: a

955 database review, J. Geol. Soc. Lond., 172, 254-263, 2014.

956

957 Watanabe, T., Nakamura, T., Watanabe Nara, F., Kakegawa, T., Nishimura, M., Shimokawara, M.,

958 Matsunaka, T., Senda, R., and Kawai, T.: A new age model for the sediment cores from Academician

959 ridge (Lake Baikal) based on high-time-resolution AMS ^{14}C data sets over the last 30 kyr: paleoclimatic

960 and environmental implications, Earth Planet. Sci. Lett., 286, 347-354, 2009.

961

962 Williams, D. F., Kuzmin, M. I., Prokopenko, A. A., Karabanov, E. B., Khursevich, G. K., and

963 Bezrukova, E.V.: The Lake Baikal drilling project in the context of a global lake drilling

964 initiative, Quat. Int., 80, 3-18, 2001.

965

966 Williams, J. W., Blois, J. L., and Shuman, B. N.: Extrinsic and intrinsic forcing of abrupt ecological

967 change: case studies from the late Quaternary, J. Ecol., 99, 664-677, 2011.

968

969 Williamson, C. E., Saros, J. E., Vincent, W. F., and Smol, J.P.: Lakes and reservoirs as sentinels,

970 integrators, and regulators of climate change, Limnol. Oceanogr., 54,2273-2282, 2009

971

Climate
of the Past
Discussions

972   Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R. and Cariveau, D. P.: Abundance of common

973   species, not species richness, drives delivery of a real-world ecosystem service, Ecol. Lett., 18, 626-

974   635, 2015

975

976   Wu, J., Liu, Q., Cui, Q.Y., Xu, D.K., Wang, L., Shen, C.M., Chu, G.Q., and Liu, J.Q.: Shrinkage of

977   East Asia winter monsoon associated with increased ENSO events since the mid-Holocene, J.

978   Geophys. Res. D: Atmos., 124. 3839-3848, 2019.

979

980   Yachi, S., and Loreau, M.: Biodiversity and ecosystem productivity in a fluctuating environment: the

981   insurance hypothesis, Proc. Natl. Acad. Sci., 96, 1463-1468, 1999.

982

Climate
of the Past
Discussions

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983

984   **Figure Legends:**

985

986   Fig. 1: Map showing location of the Lake Baikal (inset), together with the coring location on the

987   Vydrino Shoulder, where the main sediment core analysed in this study was taken from. Also shown

988   are selected sites which have been impacted by rapid climate change events during the past 15.8 kyr.

989   These include a suite of cores taken from other locations in Lake Baikal, including the Academician

990   Ridge (Watanabe et al. 2009), and from the Buguldieka Saddle, opposite the shallow waters of the

991   Selenga Delta which separates the south and central basins (Prokopenko et al. 2007). Also shown are

992   sites analysed east of Lake Baikal, including lakes Kotokel and Arakhlei, and to the west of the lake,

993   including Lake ESM-1, Lake Hosvgol and Hoton-Nur in Mongolia, and lakes in the Ulagan Plateau in

994   the Western Sayan Mountains.

995

996   Fig. 2: 'Bacon' Age-depth model (Blaauw & Christen, 2011) for Vydrino box (CON01-605-05) and

997   piston cores (CON01-605-03) of radiocarbon AMS dates calibrated using IntCal13 radiocarbon

998   calibration curve (Reimer et al., 2013).

999

1000   Fig. 3: Diatom data determined for sediments spanning the past 15.8 kyr BP from Vydrino Shoulder,

1001   Lake Baikal. (a): principal curve component 1; (b-d) Hill's N0, N1 and N2 indices; (e) – (m) major

1002   planktonic species; (n) all littoral diatoms grouped into the 'benthic' habitat guild. Planktonic diatoms

1003   which grow mainly before summer stratification are coloured blue, while those that grow after

1004   summer stratification are coloured green. Planktonic diatoms have been ordered according to their

1005   ordination score for axis 1. (o): The proportion of diatoms that bloom in the autumn versus those that

1006   bloom in the spring; (p): estimates of palaeoproductivity derived from spring (light blue) and autumn

1007   (black line) diatom biovolume accumulate rates (BVAR um3/cm2/yr); (q): the ratio of autumnal /

1008   spring palaeoproductivity. Three major time periods have been highlighted: the Bølling-Allerød (B-A)

1009   interstadial, the Younger Dryas stadial and the Holocene Epoch.

1010

1011   Fig. 4: Coefficient of Variation (CV) plots against time (cal yrs BP) for N2 diversity (lower chart) and

1012   log diatom BVAR as a proxy for palaeoproductivity (upper chart).

1013

1014   Fig. 5: Changes in the relationship (correlation coefficient) between diversity (N2) and

1015   palaeoproductivity over time as assessed though a 1000-year moving window

1016

1017   Fig. 6: Multiarchive data plotted alongside original (a) principal curve, and (b) coef N2 versus

1018   palaeoproductivity with a 1000-year moving window analyses; (c) mean pollen-inferred annual

1019   precipitation from Lake Kotokel, with smooth line representing the mean 3-point moving average

1020   (Tarasov et al. 2009); (d) mean pollen-inferred temperature of the warmest month from Lake Kotokel,

1021   with smooth line representing the mean 3-point moving average (Tarasov et al. 2009); (e) $\delta_{18}O_{diatom}$

1022   record from Vydrino Shoulder piston-core CON01-605-05 (Mackay et al., 2011); (f) $\delta_{18}O$ values of

1023   Dongge Cave stalagmite D4 (Dykoski et al. 2005); (g) North Atlantic core GGC5 231Pa/230Th

1024   meridional circulation data; (h) four stacked records of relative abundance of haematite- stained

1025   grains (%HSG) in North Atlantic sediments (Bond et al., 2001); (i) K+ ion concentrations (ppb) from

1026   GISP2 D core (Mayewski et al., 1997); (j) $\delta_{18}O$ values of NGRIP ice core (Rasmussen et al. 2006);

1027   (k) July insolation 50° N (W/m2; Berger & Loutre, 1991). Light blue zones denote climate

1028   disturbance events at the Younger Dryas, and at c. 10.3, 5.2, and 1.4 kyr BP.

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