Long term trends in aquatic diversity, productivity and stability: a 15,800 year multidecadal diatom study from Lake Baikal, southern Siberia

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Abstract

Biological diversity is inextricably linked to community stability and ecosystem functioning, but our understanding of these relationships in freshwater ecosystems are largely based on short-term observational, experimental, and modelling approaches. Using a multidecadal diatom record for the past 15,800 years from Lake Baikal, we investigate how three ecosystem components - diversity, productivity, and stability - have responded to climate changes on long-timescales. In addition, we investigate how the relationships between diversity, productivity and stability have changed through time in response to these changes. We show that abrupt changes in diatom stability and diversity during the late glacial and early Holocene are part of a network of responses across southern Siberia as a result of extrinsically-forced climate instability. Productivity - diversity relationships were strongly coupled during the late glacial, which we suggest is linked to resource availability, but showed little relationship during the Holocene, perhaps due to few resources being limiting for extended periods of time. For example, periods of low diatom diversity are associated with peak palaeoproductivity, and coincide with climate disturbance events. Such strong negative relationships may reflect resources becoming limiting during palaeoproductivity, leading to monospecific diatom blooms. While species fluctuations respond rapidly to changing resources during much of the Holocene, the ecosystem function of primary production appears to be relatively resilient. Our study provides important perspectives on lake community stability and ecosystem function in relation to rapid periods of climate change.

Key words: diversity, stability, palaeoproductivity, abrupt climate change, extrinsic forcing, palaeolimnology
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
the last 16,000 years have been punctuated by a series of large-scale and abrupt climatic shifts, such records open the door for an investigation into the links between biodiversity and the stability of ecosystem functioning associated with climate disturbance events.

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

• First, we review major climatic changes over the past 15,800 years in order to identify key events of interest relevant to southern Siberia.
• Second, we reconstruct trends in diatom communities, diversity and productivity in Lake Baikal through time.
• Third, we investigate the relationship between diversity and palaeoproductivity, with particular reference to climate disturbance events.

We hypothesise for example, that climate disturbance events lead to changes in available resources for different species, which will alter the relationship between productivity and diversity, not experienced during periods when climate is more stable. Our aim is thus to coax history to conduct experiments (Deevey 1969) in order to deepen our understanding of the long-term relationships between aquatic diversity and productivity, and to test hypotheses related to how climate disturbance events, disrupts these relationships on sub-orbital timescales.

2. Methods

Study site
Lake Baikal is situated in southern Siberia at the forest – steppe ecotone (Fig. 1), and is the world’s oldest, deepest, and most voluminous lake. The lake is a World Heritage Site, due in the main to its diverse flora and fauna; it contains over 2,500 species of which over 75% are thought to be endemic. Its sediments have accumulated for over 20 million years, and
decades of research have exploited this sedimentary record to reconstruct environmental change (Williams et al. 2001; Mackay 2007). Sedimentary cores were obtained in 2001 from the research vessel (RV) Vereschagin, from the Vydrino Shoulder (51.585°N, 104.855°E; water depth 675m), an underwater high (between 500 – 800 m) off the south-eastern coast of Lake Baikal (Fig. 1). The Vydrino Shoulder was selected because it’s an area of stable, fine-grained sedimentation relatively undisturbed by tectonic activity and reworking (Charlet et al. 2005). The cores obtained included a 1.73m trigger core (CON01-605-3a), a 10.45m piston core (CON01-605-3), and a 2.50m box core (CON01-605-5). These records were supplemented with a short gravity core taken from an ice platform in 2001 (CON01-105-6) from the same region.

Dating

Radiocarbon dates for the Vydrino sequence were obtained by accelerated mass spectrometry (AMS) from pollen and spore concentrates (Piotrowska et al. 2004; Demske et al. 2005). The age model is based upon twelve AMS 14C pollen dates from the box core (CON01-605-5) (Piotrowska et al. 2004) and an additional five AMS 14C pollen dates from the piston core (CON01-605-3) (Demske et al. 2005). Full details are given in Mackay et al. (2011).

Radiocarbon dates were calibrated using IntCal13 radiocarbon calibration curve (Reimer et al., 2013), and age-depth modelling was done using ‘Bacon2.2’ (Blaauw & Christen, 2011).
No reservoir effect was applied to the calibration due to dating undertaken on pollen and spore concentrates.

**Diatom analysis**

Diatoms are siliceous, unicellular, algae and are key primary producers in aquatic ecosystems. Because they possess a silica shell, they preserve well in sedimentary environments. We analysed diatom assemblages at 5 mm resolution; samples were prepared from composited gravity / trigger / piston cores detailed above, with no chemical treatments needed (Mackay et al. 1998). Diatom taxa were identified to species level or lower using a range of Russian and other flora, detailed in Mackay et al. (1998). With few exceptions, at least 300 valves from each sample were counted using oil immersion phase-contrast light microscopy at x1000 magnification. Diatom concentrations (valves/g) were calculated by the addition of divinylbenzene (DVB) microspheres (Battarbee et al. 2001). Stratigraphical profiles were constructed using C2 Data Analysis Version 1.7.7 (Juggins 2014).

**Diatom compositional change**

Principal curve (PrC) analyses was used to investigate compositional changes in the diatom assemblages, using the analogue-package (Simpson and Oksanen 2016) in R version 3.3.1 (R Core Team, 2016). A PrC is a one-dimensional curve that is fitted through data in m dimensions by minimising the square distances from the data points to the curve (De'ath, 1999, Simpson and Birks, 2012). A smoothing spline was used and the initial starting point of the PrC was defined by the first component of correspondence analysis (CA). The curve was fitted through several iterations using local averaging to reduce the sum of orthogonal distances between the curve and the data points ((De'ath 1999; Simpson and Birks 2012). The penalty to determine the smoothness of the curve was set to 1.4, and the degree of smoothness was allowed to vary between the different taxa. The diatom counts were transformed into square-root percentages before running the analysis.

**Diatom richness and diversity**

Richness and diversity were estimated using Hill’s species numbers N0, N1, and N2 using diatom count data. These measures give easily interpretable numbers by maintaining the doubling effect, and provide information on three levels as to how rare and abundant taxa are weighted (Hill, 1973; Jost, 2010; Gotelli and Ellison, 2013; Chao et al., 2014). Species richness is estimated using Hill’s N0, the expected number of taxa where rare and abundant
taxa have similar weights. Species diversity is estimated using Hill’s $N_1$, which is the 
expected number of common taxa and puts more weight on the numerically abundant taxa, 
and $N_2$, which puts weight on the numerically dominant taxa. The estimates are represented 
as the expected number of diatoms based on the smallest sample size ($n = 258$) to avoid 
biases related to different sample sizes. The samples were resampled randomly 1000 times 
without replacement, and unconditional confidence intervals were estimated using the 
approached described by Chao et al. (2014). Stability in $N_2$ diversity over time was further 
quantified using its coefficient of variation (CV).

**Palaeoproductivity**

The palaeoecological significance of diatom concentrations can be of limited value, unless 
they can be converted into either diatom flux rates (e.g. Battarbee et al. 2001), or estimates of 
biovolume (Hillebrand et al., 1999). Diatom flux rates rely on a robust chronology (as 
determined in this study), while biovolume estimates require representative size 
measurements for the dominant taxa. We estimate palaeoproductivity through community 
biomass calculations derived from diatom biovolume accumulation rates (BVAR) for all 
major planktonic species (Interlandi and Kilham 2001). Biovolumes ($\mu$m$^3$) for major 
planktonic species encountered during the Holocene were calculated using the median of 
measured linear dimensions of 25 valves, and geometric shape guidelines (Hillebrand et al. 
1999) (see Table S2). Planktonic species used for biovolume calculations ($\mu$m$^3$/g) accounted 
for on average, over 80% of total relative abundance, and therefore we assume are a robust 
estimate of palaeoproductivity. Stability in palaeoproductivity over time was further 
quantified using its coefficient of variation (CV), while changes in the relationship between 
palaeoproductivity and $N_2$ diversity (PDR) was investigated using a moving-average 
correlation analysis, with a window of 1000 years selected to capture millennial-scale 
variability. Finally, relationships between palaeoproductivity and $N_2$ diversity were further 
investigated during specific time-intervals, to test the hypothesis that PDR is tightly coupled 
during periods of rapid climate change, which we suggest is due to changing resource 
availability.

3. Results

**Dating**
The calibrated ages for our profile span the last 15.83 kyr BP (where kyr = thousands of years, BP = before present, i.e. 1950 CE (common era)) (Figure 2). Sediment accumulation rates ranged between 34 - 133 yr/cm (mean 66 yr/cm), with peak accumulation rates occurring at c. 3.9 kyr BP.

< Fig. 2 here > Age-Depth model

Diatom compositional change

The temporal resolution of species compositional change was c. 30 years for the past 15.83 kyr (Fig. 3). The principal curve (PrC) explained 48.4% of all the variation in the diatom taxa. The taxa which have strongest influence on PrC ($r^2 > 0.3$) include *Aulacoseira skvortzowii*, *Cyclotella minuta*, *Crateriportula inconspicua*, *Stephanodiscus meyerii*, *Cyclostephanos dubius*, and *Synedra acus v. radians*. The PrC indicates periods of large fluctuations in species composition (indicative of periods of community instability) between c. 12.9-12.4 kyr BP, 10.4 – 10.1 kyr BP and c. 6.2 – 5.2 kyr BP. Between 1.7 – 1.2 kyr BP, PrC values are at their lowest.
< Fig. 3 here > Diatom stratigraphy
Diatom richness and diversity

Prior to the Bølling interstadial (c. 15.8 - 14.7 kyr BP), there are abrupt peaks in community metrics of biodiversity, with highest N1 and N2 diversity values at 15.5 – 15.4 kyr, associated with high abundances of littoral diatoms (Fig. 3). By 15.4 kyr BP, resting spores of A. skvortzowii dominate, going into the Bølling interstadial (between 14.7 – 14.1 kyr BP), leading to very low Hill’s N0 richness and N1 & N2 diversity. Richness and diversity increased during the Allerød (c. 14.1 – 12.9 kyr BP), concomitant with increasing abundances of Aulacoseira baicalensis, and littoral species in general. The onset of the Younger Dryas stadial at 12.9 kyr BP is marked by rapid declines in species richness and abundance of common taxa, followed by a decline in Hill’s N2 several centuries later, associated with peak abundances of S. acus v. radians (Fig. 3). Richness and diversity measures all rapidly increase again from c. 12.4 kyr BP.

The start of the Holocene (11.7 kyr BP) is demarcated by a sharp decline in diatom richness and diversity values, before they increase rapidly once more at c. 11.3 kyr BP (Fig 3). N2 diversity is high (c. 10) between 11.3 - 9.2 kyr BP, with a notable decline between 10.5 – 10.2 kyr BP, concurrent with an abrupt decline in diatom richness. Between 9.2 – 5.2 kyr BP, N2 diversity fluctuates between 5 and 10, with major declines at c. 6.0 and 5.2 kyr BP. N2 values remain low for c. 1000 years, before increasing to almost 8, at c. 4.4 kyr BP, after which they decline to their lowest values (just above 1) at between 1.5 – 1.3 kyr BP. When comparing the Holocene with the latter stages of Termination 1 (ie 15.8 – 11.7 kyr BP), there is no significant difference in diatom richness (N0) (Table 1), but N2 diversity values were substantially higher (MWU test; p=0.000). N2 diversity was less stable prior to 10 kyr BP and during the past 2 kyr, as revealed through coefficient of variation (CV) (Fig 4).

Table 1: Median values for diatom fluxes, diatom BVAR, richness (N0) and diversity (N2), for the Holocene and its preceding Termination period (T1). Differences between medians were assessed using the non-parametric Mann-Whitney U test.

<table>
<thead>
<tr>
<th></th>
<th>Diatom valve flux (x 10⁶ valves/cm²/yr)</th>
<th>Palaeoproduction (BVAR) μm³/cm²/yr</th>
<th>N0 richness</th>
<th>N2 diversity</th>
</tr>
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<tbody>
<tr>
<td>Holocene</td>
<td>0.940</td>
<td>1.46 x10⁶</td>
<td>24.1</td>
<td>5.3</td>
</tr>
<tr>
<td>T1</td>
<td>1.238</td>
<td>2.16 x10⁶</td>
<td>22.7</td>
<td>2.7</td>
</tr>
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</table>
Palaeoproductivity was substantially higher and more unstable during the latter stages of Termination 1 than the Holocene (p=0.000; Table 1), with diatom BVAR (µm/cm²/yr) rapidly increasing at the onset of the Younger Dryas, to reach peak values at c. 12.4 kyr BP (Fig. 3) associated with peaks in *S. acus v. radians* then *A. baicalensis*. Diatom BVAR declined as rapidly, and remained low for the remainder of the Younger Dryas and the start of the Holocene. Palaeoproductivity was generally higher during the early Holocene than the late Holocene, with spring productivity being far more dominant than autumn productivity (Fig 3). After 7 kyr BP, total palaeoproductivity remained relatively low, although the contribution from autumnal blooming diatoms increases (Fig. 3). When we compare the ratio of autumn versus spring productivity, between 1.5 – 1.3 kyr BP autumnal productivity increase to more than ten times that of spring productivity (Fig. 3). CV analyses shows that palaeoproductivity gradually stabilised during the Late Glacial – early Holocene period until c. 7 kyr BP. During the remainder of the Holocene, moderate periods of instability reoccur c. 5 kyr BP and between 2 – 1 kyr BP (Fig. 4). A 1000-yr moving window reveals that during Termination 1, correlations flipped from strongly positive to strongly negative with greatest change observed at the start of the Bølling-Allerød (Fig. 5). But over much of the Holocene correlations coefficients are low, until c. 2.0 – 1.0 – kyr BP, when a strong negative correlation develops.
4. Discussion

4.1 The climatic record

Our study spans the past 15,800 years, specifically Termination 1 and the Holocene (11.7 kyr – present). Termination periods are defined by the demise of northern hemisphere ice sheets, as the planet transgressed from glacial to interglacial environments (Broecker & Donk 1970). Termination 1, the most recent of these, started in the North Atlantic around 17.5 kyr years ago (Stern & Lisiecki 2014), during which time, temperatures in the northern hemisphere fluctuated by as much as 10 °C in a matter of decades, if not years (Alley 2000). These abrupt temperature changes, linked to iceberg discharge and freshwater surges into the North Atlantic Ocean, caused significant periods of millennial-scale climate variability.
During Termination 1, the first sign of a shift to warmer temperatures occurred with the onset of the Bølling-Allerød interstadial, c. 14.7 kyr BP. The Bølling-Allerød is linked to warm waters deep in the North Atlantic ocean releasing heat (Thiagarajan et al. 2014) which led to the resumption of the Atlantic meridional overturning circulation (AMOC) (McManus et al. 2004) (Fig. 6g), warmer northern hemisphere temperatures (Fig. 6j) (Stuiver et al. 1995) and stronger Asian summer monsoon (Fig. 6f) (Dykoski et al. 2005). Mean pollen-inferred temperatures of the warmest month (July) from neighbouring Lake Kotokel provide an independent climate record for the Lake Baikal region (Fig. 6c), and reveal a 5 °C increase during the Bølling-Allerød (Tarasov et al. 2009). At the same time, pollen-inferred mean annual precipitation records show that rainfall increased from c. 300 mm/yr to c. 460 mm/yr (Fig. 6d). This warmer, wetter climate led to extensive melting of glaciers along the shores of Lake Baikal (Horiuchi et al. 2004), and major expansion of boreal vegetation (Tarasov et al. 2009; Bezrukova et al. 2010; Reshetova et al. 2013).
The Younger Dryas stadial (12.9 – 11.7 kyr BP), is probably the most studied climate disturbance event of the late Quaternary (Broecker et al. 2010). It was caused by an influx of freshwater from Lake Agassiz into the Arctic Ocean (Tarasov & Peltier 2005; Murton et al. 2010) which led to the decline in AMOC (Fig. 6g) (Bond et al. 2001; McManus et al. 2004), and concomitant cooler temperatures across the northern hemisphere (Stuiver et al. 1995) (Fig 7j), and an attenuated Asian summer monsoon (Fig. 6f) (Dykoski et al. 2005). Increased GISP2 K+ concentrations (Fig.7i) indicate that the Siberian High intensified at the start of the Younger Dryas (Mayewski et al. 1997), which accounts for cooler and more arid climate conditions inferred from Lake Kotokel (Tarasov et al. 2009) (Fig. 7 c,d). These cooler, more arid conditions led to a decline in hydrological input into Lake Baikal itself (Fig. 6e; Mackay et al. 2011), and a short-lived expansion of the tundra biome (Tarasov et al. 2009; Bezrukova et al. 2010).

Finally, although millennial scale variability is a feature of Holocene records (e.g. Bond et al., 1997, 2001; Fisher et al., 2002; Mayewski et al. 2004; Nesje et al. 2005; Wanner et al., 2008; Wanner & Bütikofer, 2008), the causes of this variability differs among the early, mid and late Holocene periods (Wanner et al. 2014). During the early Holocene, climate disturbance events are generally associated with pulses of freshwater discharge from northern hemisphere ice sheets, which forced AMOC to decline, resulting in atmospheric cooling (Rasmussen et al., 2006). We use the stacked record of relative abundance of haematite stained grains (%HSG) as tracers of Holocene drift ice in the North Atlantic (Bond et al. 2001), as a proxy for this variability (Fig. 6h). The causes of climate disturbance events associated with millennial-scale variability during the mid- to late- Holocene are less certain, but involve solar and volcanic forcing, often amplified by complex interactions between ocean and the atmosphere (PAGES 2k Consortium 2013; Wanner et al. 2014). Moreover, environmental impacts of mid- late- Holocene events are often not characterised by regional cooling, but by hydrological variability instead. In Lake Baikal, the impact of early-, mid- and late- Holocene climate disturbance events are implicated in understanding Holocene variability in hydrological variability (Mackay et al. 2011) and carbon dynamics in the lake (Mackay et al. 2017). Here we focus on climate disturbance events from the Younger Dryas, and each of the early (10.3 kyr), mid (5.2 kyr) and late (1.4 kyr) periods, as these are concurrent with major shifts in diatom community stability (Fig. 3a).
4.2 Temporal trends in diatom communities, diversity and palaeoproductivity

Although community turnover, as indicated by the principal curve (Fig 3a), was rather stable during the latter stages of Termination 1 (Fig 3a), diatom communities were already species-rich (Table 1), indicative that Lake Baikal species were able to tolerate and survive preceding very cold glacial conditions, challenging the notion of an ecological collapse in Lake Baikal during the Last Glacial Maximum (Karabanov et al. 2004). A. skvortzowii thrives in cold water temperatures below 5°C (Jewson et al., 2008), and dominates the cool period prior to the Bølling-Allerød interstadial. To avoid higher surface-water temperatures, it produces a resting stage, or spore. The trigger for the production of spores is phosphate utilisation by other algae (e.g. picoplankton) (Jewson et al., 2008). For A. skvortzowii spores to dominate, phosphate concentrations must have fallen below a threshold level of 15-23 µg/L (Jewson et al., 2008). Prior to the Bølling-Allerød, pigment analyses of Baikal sediments highlight increased productivity from many algal groups (Tani et al. 2002; Soma et al. 2007) which likely caused intensive competition for P during the short, ice-free summer. Nutrient, especially P, limitation may be why we also observe low N2 diatom diversity during Termination 1 (Fig. 3d), i.e. resources available were strongly limited (Interlandi & Kilhman 2001) at this time.

During the early stages of the Bølling, pre- Bølling diatom flora persists, with concomitant low richness and diversity (Fig. 3b,d). Increasing diatom richness (N0) during the Allerød is associated with the presence of littoral diatoms on the Vydrino Shoulder (Fig. 3n), cells of which have to be transported from near-shore environments to the site of the core location. Transport would have been greatly facilitated by increased fluvial input into the south basin, linked to rapidly melting glaciers at the start of the Allerød at c. 14.1 kyr BP (Osipov and Khlystov 2010). Increasing N2 diversity in Lake Baikal during the Allerød suggests an increase in available resources (Interlandi & Kilham 2001), such as Si and P; co-limitation by several nutrients and light allows more planktonic species to co-exist (Burson et al. 2018), which in Lake Baikal at this time includes the heavily silicified endemic A. baicalensis, which needs relatively high concentrations of Si to grow, and a high degree of turbulence to remain in the photic zone (Jewson et al. 2010).
Simultaneous with the onset of the Younger Dryas, principal curve (PrC), and community metrics of species richness and diversity show evidence of an abrupt ecological shift in Lake Baikal (Fig. 3). While changes in stability and richness were almost instantaneous, N2 diversity declined only about 200 years later (Fig. 3d). The decline in N0 in the Younger Dryas is mainly driven by a decline in littoral taxa, which could be related to increased ice cover on the lake and lower littoral productivity. Alternatively, lower N0 may be linked to the decline in fluvial input into the south basin (Fig. 6e) reducing transport of littoral diatoms off-shore. The lag in N2 diversity decline suggests that available resources for diatom growth were not initially limiting; species composition at this time is dominated by the spring blooming *S. acus v. radians* and the autumnal blooming *C. inconspicua* (Fig. 3h,k), and therefore these species may not be directly competing for the same resources (Interlandi & Kilham 2001). The eventual decline in N2 diversity is linked to peak values for *A. baicalensis* for the whole record at c. 12.4 kyr BP (Fig. 3f), which likely caused the decline in *S. acus v. radians*. Silicic acid availability in Lake Baikal is strongly controlled by diatom population changes (Callender & Granina 1995; Jewson et al., 2010; Shimaraev and Domysheva, 2013; Jewson et al., 2015). In particular, when populations of *A. baicalensis* are very high, the availability of silicic acid uptake by other species declines, leading to a drop in their populations, (Jewson et al., 2010; 2015). Being a heavily silicified species, *A. baicalensis* needs a strong period of mixing, which suggests that when abundant, turnover is strong, allowing the recycling of nutrients needed for peak paleo-productivity. Changes in climate and resource availability together (e.g. Huisman et al. 2004) therefore explain the rapid successional changes in planktonic diatoms during the early stages of the Younger Dryas, and concomitant decline in N2 diversity. During the latter stages of the Younger Dryas, increasing N2 diversity reflects an increase in the abundance of *A. skvortzowii* spores, along with autumnal blooming species *C. inconspicua* and *Cyclotella minuta* (Fig. 3).

Although our data highlight a rapid decline in diatom richness and diversity from the start of the Holocene to 11.3 kyr BP (Fig. 3b,d), coincident with tracers of increased drift ice in the North Atlantic (stacked record of haematite-stained grains; Fig. 6h) (Bond et al. 1997; 2001) here we focus on the period of abrupt ecological change that occurred between 10.5 – 10.2 kyr BP, (Fig. 3a). Just before this period, it is useful to note that peak June isolation (Fig. 6k) resulted in increasing mean annual precipitation in the region (Fig. 6d) (Tarasov et al. 2009), which, alongside glacier melt, will have contributed to peak Holocene hydrological input into Lake Baikal (Fig. 6e) (Mackay et al. 2011). Then at c. 10.5 kyr BP, we have this record of
rapid diatom successional changes, with distinct multidecadal variability (Fig. 3). The decline in community metrics for richness and diversity (Fig. 3d) are concurrent with a slow-down in AMOC (Bond et al. 2007; IRD7) (Fig. 6h) concurrent with a very intense Siberian High (Fig. 6i) (Mayewski et al. 1997). Together, these resulted in regional aridity and cooler temperatures, which led to the decline in river flow into the south basin of Lake Baikal (Fig. 6e) (Mackay et al. 2011). Diatom community instability (Fig. 3a) reflects rapid switches in dominance between spring blooming S. acus and A. skvortzowii, alongside increasing autumn blooming C. inconspicua. S. acus has one of the highest cell division rates of all the Lake Baikal phytoplankton (Jewson et al. 2015), which allows it to respond rapidly to changes in resource availability. Large blooms of S. acus will have utilised resources, including P, which then would have stimulated A. skvortzowii to produce resting cells (Jewson et al. 2008). The increase in C. inconspicua is indicative of a shift in balance towards autumnal production, perhaps due to sustained ice cover during this cool event leading to a decline in spring diatoms.

Another notable period of community instability occurs between 6 – 5 kyr BP, with a major decline in community turnover occurring at 5.2 kyr BP (Fig. 3a). Globally, this period marks the transition from Holocene Thermal Maximum to the Neoglacial, as northern hemisphere summer insolation levels declined (Steig 1999; Wanner et al. 2008). Again, increased diatom instability is concurrent with a major slow-down in AMOC, as reflected in the large increase in haematite stained grains (Fig. 6h) (IRD 4; Bond et al. 2001) and the end of a period of more intense Siberian High (Mayewski et al. 1997). In general, regions around the world became cooler (see Magny et al. 2006 for a review), but some also became wetter (e.g. Ireland; Roland et al. 2015) while in central and southern Asia they became more arid (see Magny et al. 2006). Terrestrial ecosystem changes in northeast China have also been attributed to the weakening of the East Asian winter monsoon (Wu et al. 2019). In Lake Baikal, there is little overall change in diatom richness at this time (Fig. 3b), although N2 diversity declines, reflecting a shift from spring to autumn diatom communities (Fig. 3d).

Tentatively, we conclude that this period of ecological change was likely extrinsically forced (Williams et al. 2011; biome reconstruction in the Easter Sayan Mountains show an increase in steppe grasslands from c. 6.0 kyr BP, indicative of more arid conditions (Mackay et al. 2012), while maximum taiga biome reconstructions occurred at c. 5.0 kyr BP, after which they declined, again indicative of cooler, more arid climate in the Lake Baikal region (Bezrukova et al. 2005; Prokopenko et al. 2007). Further afield in the Altai Mountains, there...
is also strong evidence for a marked increase in aridity after 6.0 kyr BP (Blyakharchuk et al. 2007; Rudaya et al. 2009) (Fig. 1), while glaciers advanced across Europe, North America and mountain regions of central Asia (reviewed in Mayewski et al. 2004).

During the late Holocene, diatom communities were increasingly dominated by the autumnal blooming Cyclotella minuta (Fig. 3l), leading to increasing ratio of autumn versus spring diatom communities (Fig. 3o). This increasing ratio is concurrent with declining June insolation (Fig. 6k) which may be an wide-scale ecosystem response to long-term orbital forcing. The final peak in C. minuta comes first of all at the expense of the cosmopolitan S. acus, then by the endemic A. baicalensis. Between c. 1.7 – 1.2 kyr BP, the pelagic community consists almost of only C. minuta to such an extent that N2 diversity reaches some of their lowest values (Fig. 3d), comparable to diversity during the Bølling-Allerød. Even more striking is the development of autumnal productivity between 1.48 – 1.32 kyr BP, which is unique for the 15,800 year record, and reaches almost 60 times that of spring productivity at c. 1.40 kyr BP (Fig. 3q). This dominance of autumnal productivity is concurrent with the Dark Ages Cold Period (DCAP) (CE 400 – 765) (Helama et al. 2017), a climatically cool period, linked to changes in ocean circulation (IRD1; Bond et al. 2001), and solar & volcanic activity (Helama et al. 2017). C. minuta is currently the only pelagic diatom to bloom during the autumn in Lake Baikal in substantial numbers. Because this species can tolerate surface water temperatures up to 11 °C, cells can persist in the surface waters for longer during summer stratification, so that when stratification breaks down in the autumn and nutrients are regenerated, cells of C. minuta are retrained into the photic first, giving them a strong competitive advantage (Jewson et al., 2015). From the available evidence, it is still not clear why C. minuta should dominate over all other species at this time. It may be that cold conditions associated with the DCAP led to extended ice cover such that growth of spring blooming species was inhibited, allowing C. minuta to exploit available resources. For the past 1000 years, spring blooming diatoms once more dominate communities.

To further investigate Lake Baikal’s resilience, we specifically tested whether total, spring and autumn productivity, and N2 diversity, were different for the three centuries immediately before and after the three Holocene climate disturbance events using the non-parametric Kruskal-Wallis one-way analysis of variance (Table 2).
Table 2: Kruskal-Wallis one-way analysis of variance for measures of palaeoproductivity and N2 diversity

<table>
<thead>
<tr>
<th></th>
<th>TotValve BVAR</th>
<th>Spring BVAR</th>
<th>Autumn BVAR</th>
<th>N2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>10.3 kyr BP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chi-Square</td>
<td>5.343</td>
<td>6.150</td>
<td>.130</td>
<td>5.343</td>
</tr>
<tr>
<td>Asymp. Sig.</td>
<td>.021</td>
<td>.013</td>
<td>.718</td>
<td>.021</td>
</tr>
<tr>
<td><strong>5.2 kyr BP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chi-Square</td>
<td>1.058</td>
<td>.659</td>
<td>.949</td>
<td>2.550</td>
</tr>
<tr>
<td>Asymp. Sig.</td>
<td>.304</td>
<td>.417</td>
<td>.330</td>
<td>.110</td>
</tr>
<tr>
<td><strong>1.4 kyr BP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chi-Square</td>
<td>3.552</td>
<td>1.464</td>
<td>12.052</td>
<td>19.221</td>
</tr>
<tr>
<td>Asymp. Sig.</td>
<td>.059</td>
<td>.226</td>
<td>.001</td>
<td>.000</td>
</tr>
</tbody>
</table>

Productivity and diversity show only minor or no lasting difference during the early- and mid- Holocene climate disturbance events. Only during the late Holocene climate event at 1.4 kyr BP are autumnal productivity and N2 diversity very different (higher and lower respectively), suggesting perhaps of lowered ecosystem resilience at this time.

Overall, community metrics for richness and biodiversity suggest that over much of the record, the ecosystem of Lake Baikal has also shown considerable ecological resilience (Holling 1973). Despite repeated impacts on diatom communities from disruptive climate events, diversity recovers to higher N2 values than reached previously (Fig. 3d), at least until the start of the Neoglacial. The impact-recovery response occurs in a saw-tooth pattern, similar to the trapezoidal model of Dansgaard-Oeschger (D-O) cycles (Schulz 2002), where recovery takes hundreds of years (Pimm 1984). Our palaeoecological analyses highlight that succession of planktonic flora in Lake Baikal has always been very dynamic, such that shifting patterns of dominance indicate low stability, but strong resilience. Our analyses also highlight that despite successive abrupt ecological responses to rapid climate change, Lake Baikal planktonic diatoms contain considerable plasticity that has allowed them to tolerate major changes to their aquatic environment for the majority of the Holocene (Hof et al. 2011).

4.3 Relationship between diversity and stability of ecosystem functioning

N2 diatom diversity is highest (Fig. 3d) when there is both strong spring and autumnal productivity during the middle Holocene (Fig. 3p), indicative of optimal growing conditions.
throughout the year. When growing conditions are optimal, productivity and diversity are not
strongly coupled during much of the Holocene (10 – 2.5 kyr BP (Fig 5), indicating that while
species fluctuations respond rapidly to changing resources (Fig. 3, the ecosystem function of
primary production is relatively resilient. This is likely because of the “insurance effect”
described by (Yachi and Loreau 1999), with different plankton playing similar functional
roles in pelagic Lake Baikal.

During periods when diversity was less stable (e.g. during the period before 10 kyr BP),
productivity is also unstable, for example, prior to 10 kyr BP, and again during 1-2 kyr BP
(Fig. 5). The tightly coupled productivity – diversity relationship (PDR) during Termination
1 is likely down to climate disturbance events having direct impact on resource availability.
For example, as the regional climate warmed up, new resources become available, and
nutrients could be transported to the lake through increased river flow from melting glaciers
(Osipov and Khlystov 2010). Shorter ice duration on the lake will also have led to an increase
in productivity due to a lengthening of the growing season. The switch to a strong negative
relationship between 2 – 1.2 kyr BP, likely reflects a complex set of processes linked to both
extreme ecosystem disturbance (eg increased ice cover and duration), and a reduction in
resource heterogeneity (Interlandi & Kilham 2001) due to severe limitation by a single
resource, indicative of a disturbed system (Interlandi & Kilham 2001). For example, silicon is
likely limiting during the Younger Dryas due to massive increases in the abundances of A.
baicalensis (Fig. 3) (Jewson et al., 2010; 2015). During 1.6 – 1.2 kyr BP, autumnal diatoms
are in greater proportion than spring diatoms, concurrent with a strong negative correlation
between palaeoproductivity and N2 diversity. This is also indicative of a reduction in
resource heterogeneity (Interlandi & Kilham 2001), with silicon availability again being a
likely contender.

Conclusions

This study provides many new insights into the development of primary producer
communities in Lake Baikal. That diatom communities are very dynamic, they respond
quickly to disturbance, but they also recover. These observations may hold insights into the
unfolding changes occurring in recent decades; for example the decline in heavily silicified
endemic taxa and the growth of the cosmopolitan S. acus (Roberts et al., 2018). That this
change has occurred earlier in the Holocene suggests that the lake is very resilient, and such changes may be, in the context of long timescales, temporary. However, what our record cannot provide information on is the resilience of the lake’s flora to multiple stressors such as human driven climate change and anthropogenic nutrient enrichment, which is currently impacting the lake’s littoral communities.

In relation to the wider ecological picture, our study has provided important insights into our understanding of productivity-diversity relationships (PDR). We show that diatoms communities and palaeoproductivity are sensitive to extrinsic drivers of climate change. These drivers operate at different time scales, from abrupt events during the Termination1, resulting in a tight coupling between palaeoproductivity and diversity, to slower changes in boreal insolation linked to orbital forcing, leading to gradual changes in seasonal productivity as the Holocene unfolds. We therefore provide important perspective to complement existing short-term observational (Dodson et al. 2000) and experimental (Winfree et al. 2015) approaches. Diatom responses (i.e. stability and diversity) to abrupt events are instantaneous, and although recovery occurs at a slower rate (which may be because resources take time to be replenished, or that disrupted food webs take longer to re-establish), N2 diversity tends to be higher than before the disturbance, indicative of strong resilience (McCann 2000), at least in freshwater ecosystems not damaged by environmental pollution.

Author Contributions:
Study was conceived by AWM and PR. Diatom counting was undertaken by DM. Age modelling was done by NP. Data analyses was undertaken by AWM, VF and AS. AWM led the paper writing with significant contributions from AS and GEAS. All authors made comments on earlier drafts of the paper.

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Figure Legends:

Fig. 1: Map showing location of the Lake Baikal (inset), together with the coring location on the Vydrino Shoulder, where the main sediment core analysed in this study was taken from. Also shown are selected sites which have been impacted by rapid climate change events during the past 15.8 kyr. These include a suite of cores taken from other locations in Lake Baikal, including the Academician Ridge (Watanabe et al. 2009), and from the Buguldieka Saddle, opposite the shallow waters of the Selenga Delta which separates the south and central basins (Prokopenko et al. 2007). Also shown are sites analysed east of Lake Baikal, including lakes Kotokel and Arakhlei, and to the west of the lake, including Lake ESM-1, Lake Hosvgol and Hoton-Nur in Mongolia, and lakes in the Ulagan Plateau in the Western Sayan Mountains.

Fig. 2: ‘Bacon’ Age-depth model (Blaauw & Christen, 2011) for Vydrino box (CON01-605-05) and piston cores (CON01-605-03) of radiocarbon AMS dates calibrated using IntCal13 radiocarbon calibration curve (Reimer et al., 2013).

Fig. 3: Diatom data determined for sediments spanning the past 15.8 kyr BP from Vydrino Shoulder, Lake Baikal. (a): principal curve component 1; (b-d) Hill’s N0, N1 and N2 indices; (e) – (m) major planktonic species; (n) all littoral diatoms grouped into the ‘benthic’ habitat guild. Planktonic diatoms which grow mainly before summer stratification are coloured blue, while those that grow after summer stratification are coloured green. Planktonic diatoms have been ordered according to their ordination score for axis 1. (o): The proportion of diatoms that bloom in the autumn versus those that bloom in the spring; (p): estimates of palaeoproductivity derived from spring (light blue) and autumn (black line) diatom biovolume accumulate rates (BVAR um3/cm2/yr); (q): the ratio of autumnal / spring palaeoproductivity. Three major time periods have been highlighted: the Bølling-Allerød (B-A) interstadial, the Younger Dryas stadial and the Holocene Epoch.

Fig. 4: Coefficient of Variation (CV) plots against time (cal yrs BP) for N2 diversity (lower chart) and log diatom BVAR as a proxy for palaeoproductivity (upper chart).

Fig. 5: Changes in the relationship (correlation coefficient) between diversity (N2) and palaeoproductivity over time as assessed though a 1000-year moving window analyses; (c) mean pollen-inferred annual
precipitation from Lake Kotokel, with smooth line representing the mean 3-point moving average (Tarasov et al. 2009); (d) mean pollen-inferred temperature of the warmest month from Lake Kotokel, with smooth line representing the mean 3-point moving average (Tarasov et al. 2009); (e) $\delta^{18}O_{\text{diatom}}$ record from Vydrino Shoulder piston-core CON01-605-05 (Mackay et al., 2011); (f) $\delta^{18}O$ values of Dongge Cave stalagmite D4 (Dykoski et al. 2005); (g) North Atlantic core GGC5 231Pa/230Th meridional circulation data; (h) four stacked records of relative abundance of haematite-stained grains (%HSG) in North Atlantic sediments (Bond et al., 2001); (i) K+ ion concentrations (ppb) from GISP2 D core (Mayewski et al., 1997); (j) $\delta^{18}O$ values of NGRIP ice core (Rasmussen et al. 2006); (k) July insolation 50° N (W/m²; Berger & Loutre, 1991). Light blue zones denote climate disturbance events at the Younger Dryas, and at c. 10.3, 5.2, and 1.4 kyr BP.