Responses to Reviewers Comments

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1. We have moved away from discussing beta-diversity and resources in general because (i) beta-diversity has so many different meaning to different disciplines, and (ii) the reviewers were right to point out that talking about resources in general in a palaeo paper was too vague.
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Other general changes:

- Aifeng Zhou is now a co-corresponding author along with Anson Mackay
- Keywords are more reflective of the revised manuscript

Reviewer 1:

Reviewer 1 has two points of general criticism. First that we should develop the assumption that temporal changes in diatoms are linked to lake-catchment resource availability, which in itself is related to climate variability. Second, that we show no other palaeolimnological data such as TOC.

The first set of comments are really interesting, and have highlighted us to new literature by Rimet et al. 2019, and Passy & Larson 2019, including the role that turbulence may play in influencing alpine diatom communities. We have taken on board other factors that may influence diatom communities in an alpine setting throughout the text. Rather than providing a new suggested paragraph on temporal beta diversity (linked to Korhonen et al. 2010), we have provided greater clarification on the form of beta-diversity used in this study. In fact, as now stated in the text, we have chosen to discuss our data in the form of compositional turnover, to avoid the confusion that the term beta-diversity can now have, given all its different meanings (*sens*u Anderson et al. 2011).

Specific comments have all been addressed:

Page 2, line 56: for consistency with the rest of the manuscript, use Medieval Climatic Anomaly (not Optimum)

- Done

Page 3, line 76: delete “however”

- Done

Page 3, lines 82-83: rephrase such as:: : : but provide their habitats to many iconic species that are also vulnerable

- Done, P3, Line 73-74

Page 3, line 86: : : :where long-term historical and/or instrumental records are

- Done

Page 4, line 102: add a reference about the driver of the NH cooling

- Done. Marcott et al. 2013, P4, Line 107

Page 4, line 108: correct spelling of climatic

- Done

Page 4, line 115: spell in full Asian Summer Monsoon (ASM) as it here mentioned for the first time in the text

- Done

Page 5, lines 127-128: from where this big assumption comes from? Is diatom diversity always linked to resources? Also need to be more specific about the resources: is it just nutrients, light? What about the other factor: habitat availability, grazing by invertebrates?

- Response: we have deleted the sentence related to this assumption, as the reviewer is right, it is a very big assumption, and we have not demonstrated its validity.

Page 5, line 144: (in legend for Fig. 1): change central Asia by central China.

- Done

Are subalpine meadow (as written in the text, line 141) and tundra the same type of vegetation?

- Response: No they are different; we have deleted "tundra" from the legend of Figure 1

Page 6, line 163: From what it is written I assume that the core was sliced at 1-cm intervals: please specify and also give the actual number of samples analysed

- Done

Page 7, line 167: it's divinylbenzene (DVB), not bivinyl

- Done

Page 7, line 168: the concentration unit should be in nb of spheres per volume, ml or cm3 but not cm2, right?

- Correct – this should have been spheres/cm^3

Page 7, line 171: add the registered symbol ® after Naphrax, Zeiss Axiostar Plus

- Done

Page 7, line 184: siltation is also an important factor that promote motile benthic diatoms over attached forms (e.g. Battegazzore et al. 2004; Dickman et al. 2005).

- Response: We have added in reference to siltation, using the Battegazzore reference: P8, Line 196

Page 7, line 192- 193: a log-linear contrast PCA. I'm not familiar with this technique, please explain in one sentence how different it is from "conventional" PCA and what are the advantages

- Response: Into P8, Lines 205-206, we have added in the clause, which also necessitates a new reference: "(appropriate for closed relative abundance data (Lotter and Birks,1993)) was undertaken…"

Page 8, line 207: give a reference for the C2 program

- Done: added in Juggins 2014)

Page 10, line 228: *Puncticulata* is a redundant generic name. Use *Lindavia* (see Nakov et al. 2015).

- Done

Page 10, line 250: you forgot a few words: : : :while high profile and motile diatoms are persistently

- Done

Page 11, line 256 (legend of Fig. 3): rephrase such as: Only diatoms with abundance greater than 3% are shown

- Done

Page 12, Figure 3: It would be useful to group the diatom species according to their ecological guild.

- Done

In Fig 3, Correct spelling of Staurosira construens, change Puncticulata to Lindavia

- Done

Page 14, Fig.5: correct spelling for "centered"

- Done

Page 15, line 303: : : :dominated by species belonging to the Fragilariaceae

- Done

Page 15, line 304: replace "growing well" by "dominating the assemblages"

- Done

Page 15, line 306: on the abundance of fragilarioids:

- Done

Page 15, line 307: add "(Russia)" after "Eastern Sayan mountains"

- Done

Page 15, lines 310-319: This explanation about the decline of Stauroforma is not entirely convincing. First the catchment of the lake appears treeless as it is located above the treeline (as shown on Fig. 1). In that case, how the mentioned shift from a deciduous-conifer forest to a steppe forest would have impacted the soils of the lake catchment if no forest was there in the first place?

- Agreed: we have removed this sentence

Then you need to be more specific than just saying "related to the provision of resources linked to catchment changes around the lake". Could the reduced input of DOC may be linked to deeper, longer permafrost instead of shift in catchment vegetation? (as the authors have suggested themselves on lines 423-424 but for the upper part of the record).

- Response: we have tried to be more nuanced here, and have made the observation that highest Stauroforma and TOC occur together, so its presence may be linked to the lake being dystrophic at the time. See new text in Section 4.1, P 15, Lines 329-338

Page 16, line 329: use replaced instead of replacing

- Done

Page 16, line 341: Why are you comparing your results with winter temperature? Summer temperature would be more relevant for benthic diatoms. Also note that summer temperature may have been relatively high in Northern China during the "Roman Warm Period" as suggested by the pollen reconstruction by Stebich et al. (2015).

- Response: we had not seen the Stebich et al. 2015 article, so as suggested we have replotted their mean temperature of the warmest month in our multi-archive Figure 6, and included relevant interpretation in the text. (e.g. see P15, Lines 334-335)

Page 17, legend of Fig. 6. Replace "Chinese" by "central China".

- Done

Fig 6: The number for each curves are wrong, should be 6a, 6b, 6c, etc: : : instead of 7a, 7b, 7c:

- Done

Page 17, line 364: correct spelling of climatic

- Done

Pages 18-19: For consistency and to make it easy to found the features that are discussed on the diagrams, please give all the ages in cal yrs BP, not just in CE calendar.

- Done

Page 19, line 419: replace "important" by abundant Page 20,

- Done

Page 20, line 427: give a reference about the ecology of Denticula subtilis

- Done: we have actually re-focused the ecology here, as other studies have found it to be linked to elevated conductivity, e.g. Antoniades et al. (2005): see P22, Lines 463-467

Page 20, line 446: is a bit confusing: was aridity declining or on the contrary increasing, as the curve for reconstructed precipitation (Fig 6d) would suggest?

- Done – sorry, yes aridity was increasing. We have corrected the text

Page 20, line 448: delete "of the" after around the time

- Done

Page 20, lines: 448-450: what about the 2-sample shift from Stauroforma to Lindavia+humidophila?

- Response: We have added in extra discussion at the end related to this period, P 23 Lines 488-492.

Page 21, line 465: rephrase such as: Increased summer precipitation during the MCA as inferred from nearby records (here add references!) resulted in increased diatom fluxes

- Done

General comment on adding in more data.

- Response: unfortunately we do not have any geochemical data, but we do have measurements for total organic carbon, and these have now been added to methods, results, and implications in discussion.

References used:

Antoniades, D., Douglas, M.S. and Smol, J.P., 2005. Benthic diatom autecology and inference model development from the Canadian high arctic Archipelago 1. *Journal of Phycology*, *41*(1), pp.30-45.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F. and Harrison, S.P., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology letters*, *14*(1), pp.19-28.

Juggins S (2014) C2 version 1.7.7: software for ecological and palaeoecological data. University of Newcastle

Lotter, A.F., Birks, H.J.B., 1993. The impact of the Laacher See tephra on terrestrial and aquatic ecosystems in the Black Forest, southern Germany. Journal of Quaternary Science 8, 263-276

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Reviewer 2 comments

Reviewer 2 found some of the interpretation "a bit vague" and lacked a "multiproxy approach". These two broad comments are similar to Reviewer 1, and we have addressed both. The former comment has been tackled by being more explicit what we mean when we talk about diatom responses to changing resources – see comments to R1 above, and changes made throughout the text, highlighted under track changes. And the latter comment has been addressed now by adding in TOC data (see Fig 5c).

Specific comments:

Line 70: Describe what is beta-diversity.

- Response: As identified by R1, we have added in further clarification on beta diversity (eg P3, lines 81-84).
- Because the term now means different things to different groups of scientists, we refer to the data more specifically as compositional turnover (P3, Lines 88-90)

Line 77: What do you mean by elevation-dependent warming?

- Response: We have provided greater explanation: , "i.e. the amplification of warming at higher altitudes" P3, Lines 69-70

Line 97: Don't really like the term global warmth...is there another way to say this?

- Done: have changed to "globally warmer temperatures".

Line 99: "less monotonic" – is that the right term? Thought monotonic was used to describe sequences...?

- Done – we have simplified this sentence to read "The extent of cooling varied regionally, being most pronounced in the extra-tropical northern hemisphere (Marcott et al. 2013)." (P4, Lines 105-106)

Line 110: Define LIA

- Done

Line 115: Define ASM

- Done

Line 124: What do you mean by ecological guilds?

- Response: This is defined in the methods in Section 2.2, P8-9, Lines 188-198

132: On what account is it a biodiversity hotspot? Describe

- Response: We have added in more detail: "…as a refuge for both Tertiary plants (Zhang et al. 2017) and the vulnerable Giant Panda (Fan et al. 2014). (P5, Lines 134-136)

Line 141: Describe what you mean by Larix forest - what species? what climate/soil conditions do they require? Etc

- Response: we have added in detail – P6, Lines 144-146:

Line 142: More detail on the lake itself would be good. Has the lake ever been studied before? Any more bathymetry of the lake? What is its riparian/shoreline vegetation? Is it in a small, steep catchment? Does it have macrophytes in its shallow waters? Is it dimictic/polymictic etc? Or is knowledge extremely limited here?

- Response: we actually have very little information on the lake, due to its remoteness. We have included what extra info that we have. We observed no shoreline macrophytes (it was winter when the lake was visited, and frozen over), but we measured surface water pH at 6.84, using a YSI ProDSS multiparameter water quality meter. (P6, Lines 146-150)

Line 155: Which country is Beta Analytic?

- Done: USA

Line 224: Don't quite follow the sentence. Do you mean 120 of the species were rare?

- Done: we have rephrased

Line 316: State specifically how and why the change in catchment vegetation would have altered delivery of allochthonous material? Increased or decreased?

- Response: We agree with the statement that more detail needs to be given as to whether allochthonous material increased or decreased with shift in vegetation. But as highlighted in R1 above, the relevance for this for YHC site is not clear – we have deleted this statement therefore

Line 321: Not a clear sentence. Did limiting resources become more limited? Or more resources became more limited?

- Response: We have deleted this sentence

Line 323: "deterministic processes become more important" - more important than what? What do you mean by deterministic processes?

- Response: Here we have clarified that deterministic processes become more important than stochastic ones. Deterministic processes here are ones related to niche selection. See P17, Lines 374-379

Line 330: What "resources"? Be specific.

- Response: we have rewritten and reorganized the start of the Discussion

Line 342: Again, be more specific about what "resources" you mean and why and how this increased the prevalence of high profile diatoms.

- Response: we have rewritten and reorganized the start of the Discussion

Line 387: Is this a worthy comparison if the soils and altitudinal differences are dissimilar? If so, why? This could be a good opportunity to highlight the importance of lake and catchment characteristics is shaping the response of lake ecology to large-scale spatial and temporal drivers of change.

- Response: we have deleted comparison to this other site, as it was a bit random, and given catchments differences, may well not have been a robust comparison to make

Line 395-6: Don't understand what you mean by "several interacting, time-transgressive forcings", please be clear and describe what you mean.

- Response: we have added information: "…, including reduced solar activity during the late 17th century (Shindell et al. 2001), increased volcanic activity during the early 19th century (Brönnimann et al. 2019) and reduced Gulf Stream flow (Lund et al. 2006)." P20, Lines 430-433

Line 411: What is K+ a proxy for? Please describe for readers who may not know

- Response: we have added in extra text + reference - , "…given that potassium is likely sourced from central Asian dust via long-range transport to the Greenland ice sheet (Meeker and Mayewski 2002)" P21, Lines 450-452

Line 414: What do you mean by phenological records?

- Response: we have added "beginning of tree flowering" P20, Line 415

Line 421: What are these conditions? Be specific.

- We have deleted this sentence.

Line 422: How does cold conditions and extended ice cover decrease these planktonic diatoms? Be specific. Changes to turnover events? Nutrient supply?

- We have deleted this sentence

Line 428: What do you mean by "resources" here? Nutrients? Be specific.

- Response: we have actually re-focused the ecology of D. subtilis here, as other studies have found it to be linked to elevated conductivity, e.g. Antoniades et al. 2005): see P22, Line463-465.

Line 434: Again what do you mean by "resources" becoming more available? Be specific.

- Response: we have rephrased as "…increased competition among species (Larson et al. 2016)" P22, Lines 473-474

Line 436: Why is this important? Describe.

- We have deleted this sentence

Line 448: "time of the"..?

- Corrected

Line 453: What is "their"? Be clear

- We have deleted this sentence

References used:

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Brönnimann, S., Franke, J., Nussbaumer, S .U., Zumbühl, H. J., Steiner, D., Trachsel, M., Hegerl, G. C., Schurer, A., Worni, M., Malik, A., Flückiger, J.: Last phase of the Little Ice Age forced by volcanic eruptions. *Nat. Geosci. 12*, 650-656, 2019.

Meeker, L.D. and Mayewski, P.A., 2002. A 1400-year high-resolution record of atmospheric circulation over the North Atlantic and Asia. *The Holocene*, *12*(3), pp.257-266

Stebich,M., Rehfeld,K., Schlütz,F., Tarasov,P., Liu,J., Mingram,J.: Holocene vegetation and climate dynamics of NE China based on the pollen record from Sihailongwan Maar Lake. Quat. Sci. Rev., 124, 275-289, 2015.

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Reviewer 3 comments

Reviewer 3 wanted more information on the lake and it's environmental context (see main comments to reviewer 2 above; what little information we do have, we have now included), and greater interpretation of the diatom changes themselves rather than relying on other papers. Given the responses to Reviewers 1 and 2 above, our interpretation of diatom changes is much tighter throughout the manuscript.

Specific comments:

Line 48: "Here we take…"

- Response: This is still grammatically correct, so no need to change

Line 49: "Multidecadal variability" on what data is this based?

- Response - this phrase has been deleted

Line 49: The dating seems to have a hard water effect (which has not been clearly addressed) and only five AMS dates. Please clarify how you have come up with this multidecadal (55 years) variability

- Response: the reservoir effect in bulk organic dating is common in the lake sediments (Zhou et al., 2015). The Yuhuangchi lake is located in a high altitude area, where organic matter mainly comes from terrigenous organic matter input and the lake's authigenic algae. Terrigenous organic matter often contains the old soil carbon input through to the lake. We also found that has obvious reservoir effect in 10cm dating result. A common way to judge radiocarbon reservoir effect is by using a linear or quadratic regression, and interpret the extrapolated surface of age as a radiocarbon reservoir effect (Hou 2012 QSR).

- Extra text and reference to Hou et al. 2012 have been provided in Section 2.1, P7, Lines 164-165

Line 55: “Important”: : :what does this mean here? Important compared to what?

- We have removed this word

Line 61: Consider to add “productivity” to keywords

- Done

Line 77. Is there a word missing after “sensitive” e.g. “area” or “environment”?

- No – the word sensitive here refers to the regions themselves

Lines 82-83. “..but their habitats to many: : :” I don’t really understand this sentence? Is this needed?

- Sentence has been corrected to “they provide habitats to many…” which is clearer; P2, Line 73-74

Lines 140 and 145: Is the elevation of the lake 3370m asl or 3365m asl?

- Good spot – the elevation has been corrected in the Figure legend to 3370m asl

Line 152. What kind of piston corer did you use? Please specify

- We actually used a homemade piston drill, similar to UWITEC's piston corer, which a plastic core tube with a piston inside and can be hammered into the sediment. So I think we can leave text as is

Line 153. “: : :from the central region of Lake Yuhuang Chi”. Why from the central area, was it the deepest part of the lake? or the main sedimentation area? or had it the longest sediment sequence? Please clarify

- Response: Yes, this was the deepest part of lake and also with flat lake floor

Line 154. Why did you use bulk organic sediment for dating? Where there no terrestrial plant macrofossil in the sediment?

- Response: Yes, that is correct; no macrofossils were found in the sediments. We have made this clear in the text – Lines 159-160

Line 158. Its rather unclear how you came up with the 1340 year reservoir age effect. Please clarify this in sufficient detail and add the number of dates to line 156

- Response – both things done – see P6, lines 160-161

Lines 163-164. What does this sentence mean? How did you came up with a resolution of 55 years considering the uncertainties of the datings? What is the frequency of the diatom samples, 2mm, 5 mm, 1 cm: : :?

- Response: We have added in that diatom analyse were performed on alternate 1cm-thick samples (P7, line 174). The 55 year resolution is got from the age model but seeing as we are still in the methods section we have taken this clause out.

Line 165. Please add a reference(s) after “: : :standard procedures”

- Done: we have added in the reference to Battarbee et al. 2001

Lines 169-170. ": : :such that suitable concentrations could be calculated". What does this mean, please clarify

- Response: we have taken this phrase out; it is not necessary

Line 207. Please add a reference after "C2 Data Analysis Version 1.7.2

- Response: we have added Juggins (2014)

Line 214-> this is a bit odd paragraph as it contains only Table 1 and no written results?

- Response: good point; we have added in text to describe the lithology and introduce Table 1 (P9, Lines 226-230)

In Table 1 all +- ages are 30 years, is this correct?

- Yes

Lines 239-240. This sentence could be combined with the previous one as the information is almost the same

- Response: it is not clear what is being meant here so we have chosen to leave sets of info separate

Lines 256-257. The first two sentences of the Figure caption could be e.g "Diatoms with a relative abundance >3% in more than one sample are shown"

- Response: the figure legend has been edited

Line 263. Please add "Relative abundance (%) below the diatom stratigraphy figure

- Response: rather than doing this, we have added in (%) to the Figure legend, making clear what relative abundance refers to

Line 272. Please add "Relative abundance (%) below Figure 4

- Response: rather than doing this, we have added in (%) to the Figure legend, making clear what relative abundance refers to

Line 282. The beta-diversity value of 1.033 SD units is rather low and indicates relative subtle changes in the core (compare e.g. to values in Smol et al. (2005, PNAS))

- Response: I don't think that we need to respond to this just here, as it is a comment. But note from comments above re. beta-diversity, we have moved away from this concept to one that characterizes compositional change

Line 303. Fragilariaceae are also very common in high latitude lakes: : :you may add a reference after this statement

- Response: this is made explicit in the statement: "Fragilarioids are often opportunistic, dominating assemblages in alpine and arctic lakes with a short growing season and long periods of ice cover (Lotter and Bigler 2000)" (P14, Lines 322-324)

Line 329. H. Schmassmannii is not really replacing S. exiguiformis as its relative abundance varies between ca. 10- 15% during this period and S. exiguiformis decreases from ca. 50 to 40%...this does not really seem as a replacement, or? This is a too strong interpretation, please rephrase

- Response: this paragraph has been reinterpreted according to other reviewers comments as well; we no long have one species replacing another as such, but that changes in species are likely linked to changes in lake dystrophy (see P14, Lines 329-338)

Lines 337-338. "..resources stabilised or even increased slightly: : :" How can this be seen in the results? Which species or index is confirming or suggesting this intepretation? At least not the relative abundances of Figs 3 & 4

- Response: we have changed this from "resources stabilized" to "compositional turnover stabilised" - this is now data led rather than an interpretation of resources, which we acknowledge above may have been over-interpreting what these scores can tell us (17, Line 389)

Line 343. High profile G2-diatoms dominate the whole zones 1 & 2 with an relative occurrence around 60% (see Fig. 4)...so there are no real changes here unlike is suggested

- Response: we agree, and the text here has been modified substantially (P16, lines 348-371)

Lines 337-344. This whole paragraph consists of rather vague speculation without much of supporting data from the study. I would suggest you to re-evaluate your results and rewrite this accordingly

- Response: we agree, and the Discussion has been rewritten, moving away from focus on interpretation of resources, which was not clear from the data

Lines 348-353. Please change the numbers of sub-figures to be 6b, 6c, 6d etc

- Response: done

Line 358. Please add "Winter" before "temperature"

- Winter-temperature anomaly graph has now been removed

Lines 368-369. This is not clear in Figure 6c

- Winter-temperature anomaly graph has now been removed

Line 379. "Increasing diatom flux: : :"the relative abundance data does not really support this: : :could there be some problems in counting the diatom flux as the dating results are not very convincing and the sedimentation rate has a large impact on the flux values?
Line 380-381. "Driven mainly by increasing P. bodanica": : :that is not clear when looking at Figure 3: : :P. bodanica seems to have a relative abundance around 20% before and after this period. Please check and re-think

- Response: we have removed the clause "including planktonic species", as reviewer is right, relative abundance data do not show major changes in the planktic guild at this time. Flux rates are of course tied to sedimentation rates, so we're not clear of the point being made. We think the dating is rather robust, with all errors and uncertainty given in the manuscript.

Line 382. Beta-diversity does not increase between 1500-800 cal yrs BP. Please re-phrase

- Response: this has been amended

Line 398. How come beta-diversity is almost zero although in Fig. 3 a relatively diverse diatom population still remains?

- Response: this is because beta-diversity means the change in species composition, not numbers of species per se. But as highlighted above, we have shifted our interpretation away from beta-diversity to compositional turnover which describes the data more accurately.

Lines 421-422. ": : :planktonic diatoms show a distinct decline during the LIA". Where can this be seen? In Fig 3. the P:L ratio does not decrease nor does the abundance of P. bodanica and also the planktonic guild is high in Fig 4? Please clarify

- Response: This statement has been removed from our re-write of the discussion

Lines 425-426. I doubt that the appearance of H. Schmassmannii is due to low water temperature? Do you have any data when this species blooms? Or what its temperature optima is? This species can be found also in high latitude lakes

- Response: the paper by Buczkó et al. 2015 reviews a number of different papers which state that this species is thermophilic, but also mentions at least one at the end which suggests that the species has been found during the younger Dryas at Krakenes, Norway. On balance, it is likely that this species does decline during cooler temperatures – so we have left this statement as it is, but we have augmented by bringing in possibility of other factors such as siltation also being important (P21, Line 463-464)

Line 429. ": : :the lake becoming more shallow due to increased aridity": : :The planktonic species P. bodanica still occurs with a relative abundance of ca. 20%, which could indicate deeper water as it needs turbulence to sustain in the water column. Could one explanation be that the water became clearer due to the frozen ground and less inwash of e.g. DOC/humic substances?

- Response: we suggest the the lake become more shallow due to the appearance of Denticula subtilis which usually occurs in shallow lakes with high conductivity. (P21, Lines 463-465)

Lines 456-472. This whole paragraph is rather general based on other publications instead of your own results. I think this whole paragraph should be re-written so that it reflects the results of this study

- Response: we have made greater reference to our own data in the conclusions

Line 548. Please add the reference for the program C2 here:

- Response: this has been done – Juggins 2014

Lines 659-664. Please switch the alphabetical order of these two references

- Response: done

Line 448. ": : :around the time of the did: : :" please re-phrase

- Response: done

References used

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., Juggins, S., 2001. Diatoms. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Kluwer Academic Publishers, Dordrecht, pp. 155e201.

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Neoglacial trends in diatom dynamics from a small alpine lake in the Qinling Mountains of central China.

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Abstract:

During the latter stages of the Holocene, and prior to anthropogenic global warming, the Earth underwent a period of cooling called the neoglacial. The neoglacial is associated with declining summer insolation and changes to Earth surface albedo. Although impacts varied globally, in China the neoglacial was generally associated with a cooler climate and an attenuated Asian summer monsoon. Few studies in central China, however, have explored the impact of neoglacial cooling on freshwater diversity, especially in alpine regions. Here we take a palaeolimnological approach to characterise multidecadal variability in diatom community composition, ecological guilds, and compositional turnover over the past 3,500 years from the alpine Lake Yuhuang Chi on Mount Taibai in the Qinling Mountains. Diatoms in the high profile guild dominate much of the record from 3,500 – 615 cal yrs BP, which suggests that few nutrients in the lake were limiting overall, and disturbance and herbivory were likely low. After 615 cal yrs BP, low profile and planktic guild diatoms increase, suggesting greater turbulence in the lake, alongside a decline in available nutrients. Diatom turnover highlights periods in the lake history when deterministic processes structured diatom communities. For example, an abrupt decline in turnover is coincident with the shift from high to low profile diatoms at 615 cal yrs BP, and is likely due to the onset of the Little Ice Age in the region. We suggest that Lake Yuhuang Chi become more shallow during peak regional aridity, which led to the short-lived community restructuring observed in the record.

Keywords:

Diatoms, ecological guilds, compositional turnover, productivity, Little Ice Age

1. Introduction

Alpine ecosystems are some of the most sensitive to changing climate, due in part to elevation-dependent warming, i.e. the amplification of warming at higher altitudes (Yan and Liu 2014; Pepin et al. 2015). Understanding how high-altitude ecosystems respond to changing climate is a matter of urgency, because not only do these regions act as 'water towers' supplying water to huge populations downstream (Messerli et al. 2004; Buyteart *et al.*, 2017), they provide habitats to many iconic species that are classified by the IUCN as being vulnerable (Fan et al. 2014). Alpine freshwaters have multiple ecosystem functions (Messerli et al. 2004; Buytaert *et al.,* 2017) and provide many ecosystem services such as freshwater regulation and habitat provision (Grêt-Regamey et al. 2011). Their multifunctionality depends on local species communities, and how species vary through space and time (beta-diversity) driven by ecosystem properties, environmental gradients, and species interactions (Korhonen et al. 2010).

Beta-diversity links biodiversity at regional and local scales, and may take the form of non-directional variation, or directional turnover (Anderson et al. 2011). Long-term records of beta-diversity commonly focus on the amount of compositional turnover over time, which provides important information on ecosystem functioning (Birks 2007). For example, estimating species turnover assumes that species are lost and gained over time in response to resource availability, competition, historical events and environmental factors (Korhonen et al. 2010), over both recent (Smol et al. 2005) and long timescales (Leprieur et al. 2011). However, because the concept of beta-diversity has so many meanings to different disciplines, we take the approach of Felde et al. (2019) and just focus on directional compositional turnover, appropriate for palaeolimnological datasets from a single lake.

Natural archives are an important resource for reconstructing past environments where long-term historical and/or instrumental records are either scarce or absent. In central China, speleothems provide exceptional, high resolution records of monsoon intensity, allowing periods of multiannual and multidecadal drought to be determined (Wang et al. 2005). Yet there are relatively few studies (Liu et al. 2017) which have explored multidecadal records of biodiversity change over similar timescales, leaving a fundamental gap in understanding as to how biodiversity in freshwater ecosystems, especially at higher altitudes, responded to periods of climate variability. Reconstructing the impacts of past climate on freshwater ecosystems is fundamental to understanding how freshwater biodiversity may respond to future climate, especially during periods of rapid change. Here we focus on the neoglacial, which spans at least the past c. 3,500 years.

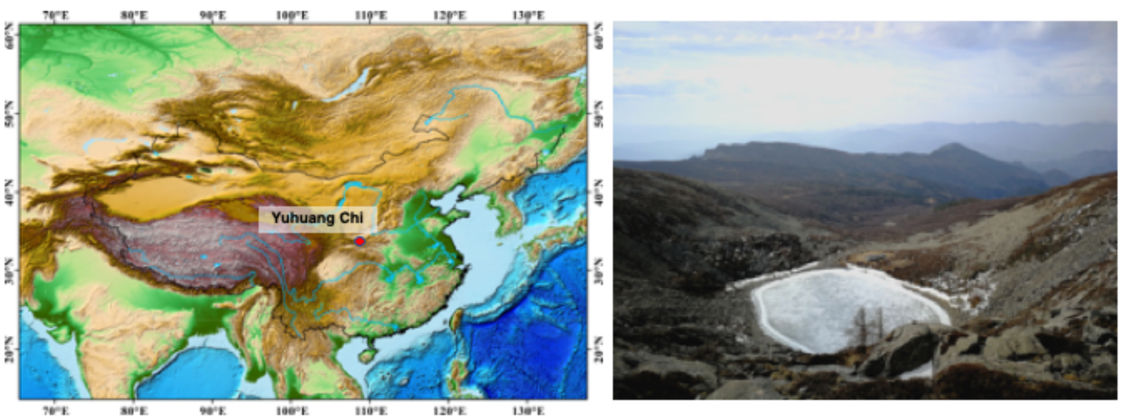
The neoglacial, characterised by increasingly cooler temperatures, follows on from globally warmer temperatures of the early- to mid-Holocene. The extent of cooling varied regionally, being most pronounced in the extra-tropical northern hemisphere (Marcott et al. 2013). The most important driver of northern hemisphere cooling was declining summer insolation (ibid.) in conjunction with changes in albedo on the Earth's surface, linked to feedbacks from vegetation and snow / ice. In China, the neoglacial resulted in the persistent decline in monsoon intensity in southern China (Wang et al. 2005) and rapid decline in precipitation in northern China (Chen et al. 2015a) leading to increased aridity and major shifts in vegetation communities (Zhou et al. 2010). Superimposed on the insolation-driven neoglacial were notable periods of sub-Milankovitch, centennial-scale climatic events (e.g. Mayewski et al. 2004; Mann et al. 2009; Wanner et al. 2014), including the 2,800 yr BP event (Hall et al. 2004), the Medieval Climatic Anomaly (MCA) (c. 1000-1300 AD) and the Little Ice Age (LIA) (c. 1300 – 1850 AD). The latter two events are well expressed throughout China; Medieval temperatures were generally warmer than the following centuries spanning the LIA (Cook et al. 2013; Chen et al. 2015b). However, while the LIA generally resulted in periods of aridity (e.g. Wang et al. 2005; Tan et al. 2011; Chen et al. 2015a), in depth research highlights a more heterogenous response across China (e.g. Cook et al. 2010), with some central and southern regions becoming wetter due to interplays between the Westerly jet stream and the Asian summer monsoon (ASM) (Tan et al. 2018).

Freshwater ecosystems in the Qinling Mountains of central China provide natural capital and ecosystem services for local and regional populations, and understanding the impact of monsoon variability on ecosystem functioning has the potential to add insight into how freshwater biodiversity may respond to future climate change, and predicted increases in mean annual precipitation (Guo et al. 2017). In this study, we reconstruct neoglacial trends in diatom community composition, their ecological guilds, and compositional turnover at a multidecadal resolution over the past 3500 years.

1.1 Study region

The Qinling Mountains are widely recognised for their conservation importance and as a biodiversity hotspot; they are a refuge for many Tertiary plants (Zhang et al. 2017) and vulnerable species such as the Giant Panda (Fan et al. 2014). The region is climatically very sensitive, as it separates the northern subtropical zone of China from the country's central warm-temperate zone (Figure 1). Mount Taibai (34°N, 108°E; 3767 m), is the highest mountain in the range, with a timberline at c. 3,370 m, and treeline at c. 3,600 m (Liu et al. 2002). The mountain is classified as a glacial heritage site because Quaternary glaciations are well preserved, especially the last glaciation (Yang et al. 2018). On Mount Taibai there are several clusters of cirque lakes, and our study site, Lake Yuhuang Chi (YHC), is found in one of these clusters. It is a cirque and moraine lake at 3370 masl, placing it in the *Larix* forest - subalpine meadow ecotone. Specifically, *Larix chinensis* Beissn, grows in podzolic soils between 2,000 m to 3,500 m, and is associated with cold, arid climate. Regional annual average temperature is below 8°C and annual precipitation is c. 840-960 mm. Lake Yuhuang Chi has a maximum depth of 21.5m and an area of c. 23,600 m². No shoreline macrophytes were observed during coring, but it was winter when the lake was frozen. Using a YSI ProDSS multiparameter water quality meter, surface water pH was measured at 6.84 pH units.

Figure 1: Regional position of Lake Yuhuang Chi in the Qinling Mountains of central China. The photograph of the frozen lake to the right shows the small catchment with few trees.



2. Methods:

2.1 Coring, Age model, Total Organic Carbon

A 135 cm sediment core (YHC15A) was collected in 2015 CE using a 6cm diameter piston corer from the central region of Lake Yuhuang Chi. The highly humified lake sediments contained no sizable macrofossils for radiocarbon analyses. Radiocarbon dating was instead carried out on five bulk organic sediment samples using accelerator mass spectrometry (AMS) at Beta Analytic, USA. There is a radiocarbon reservoir effect evident in the data (likely from old soil carbon input from the catchment), so we used a quadratic extrapolation to determined reservoir ages (Hou et al. 2012). All the radiocarbon dates were quadratic fitted ($^{14}CAge = 0.0693depth^2 + 17.31depth + 1340$, $R^2 = 0.9994$), so we determined the top (0cm) with a 1340 year reservoir age effect. An age-depth model was developed with smooth fit using CLAM 2.2 (Blaauw, 2010) in *R*, using Intcal13 (Reimer et al., 2013) calibration curve. Total organic carbon (TOC) provides an estimate of the amount of organic carbon that escapes remineralisation before being incorporated into lake sediments. TOC was measured on contiguous 1cm samples using an elemental analyser (Flash EA 1112).

2.2 Diatoms

Diatom analysis was performed on alternate 1cm-thick sediment samples. Approximately 0.1g of wet sediment from each sample was prepared using standard procedures outlined in Battarbee et al. 2001. Organic matter was removed by heating each sample in 30% H_2O_2, before 10% HCl was added to remove carbonates and any excess H_2O_2. Diatom concentrations were calculated through the addition of divinylbenzene (DVB) microspheres (concentration 8.02 x 10^5 spheres/cm^3) to diatom suspensions, and diatom fluxes calculated using sediment accumulation rates. Diatom suspensions were diluted and then pipetted onto coverslips to dry before being fixed onto microscope slides with Naphrax®. Using a Zeiss Axiostar Plus® light microscope, diatoms were counted at x1000 magnification under an oil-immersion objective and phase contrast. A minimum of 300 diatom valves (min 331, max 591) were counted for each of the 67 samples. Diatoms were identified using a variety of flora including Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Williams and Round, 1987; Lange-Bertalot, 2001.

Diatom species were categorised according to ecological guilds commonly associated with the abundance of available resources (e.g. light, nutrients) and disturbance (e.g. grazing and turbulence) (after Passy 2007; Rimet and Bouchez 2012). The low profile guild includes diatoms which attach themselves to substrates in erect, prostrate, and adnate forms, are very slow moving (Passy 2007), and are generally adapted to low nutrient conditions. High profile guild diatoms are those of tall stature (e.g. they are filamentous, or chain-forming, or found in mucilage tubes), and are generally adapted to high nutrients and low levels of disturbance (Passy 2007). Motile diatoms are relatively fast-moving species, tolerant of high nutrients (Passy 2007) and siltation processes (Battegazzore et al. 2004). A new planktic guild was determined by Rimet and Bouchez (2012) which includes centric species able to resist sedimentation in lake ecosystems.

2.3 Multivariate analyses

The magnitude of diatom turnover was initially estimated using detrended correspondence analysis (DCA), with square root transformation of the species data to stabilise variance and rare species downweighted. The axis 1 gradient length was 1.44 standard deviation units, so diatom abundances were reanalysed using principal components analysis (PCA). A log-linear contrast PCA was undertaken (appropriate for closed, relative abundance data (Lotter and Birks 1993)), with symmetric scaling of ordination scores so that scaling of both samples and species were optimised. Species compositional turnover was estimated using detrended canonical correspondence analyses (DCCA), with the diatom data constrained using dates from the calibrated age model (Smol et al. 2005). We used DCCA to estimate compositional turnover because sample scores are scaled to be standard units through the process of detrending by segments and non-linear rescaling (Birks 2007). Sample scores can therefore be interpreted as the amount of species turnover through time, making them ecologically useful and ideal for estimating compositional turnover. Ordinations were undertaken using Canoco5 (Šmilauer and Lepš 2014). Breakpoint analysis, a form of segmented regression analysis, was used to determine major points of change in diatom guilds and turnover, using the segmented package in R v. 3.5.1 (Muggeo 2008). Stringent p-values were adopted ($p<0.001$) when determining any major changes observed. All stratigraphical profiles shown were constructed using C2 Data Analysis Version 1.7.7 (Juggins 2014), and zones determined using stratigraphical constrained cluster analysis by incremental sum of squares (CONISS) and broken stick analysis using the rioja package in R v. 3.5.1 (Juggins 2017).

3. Results

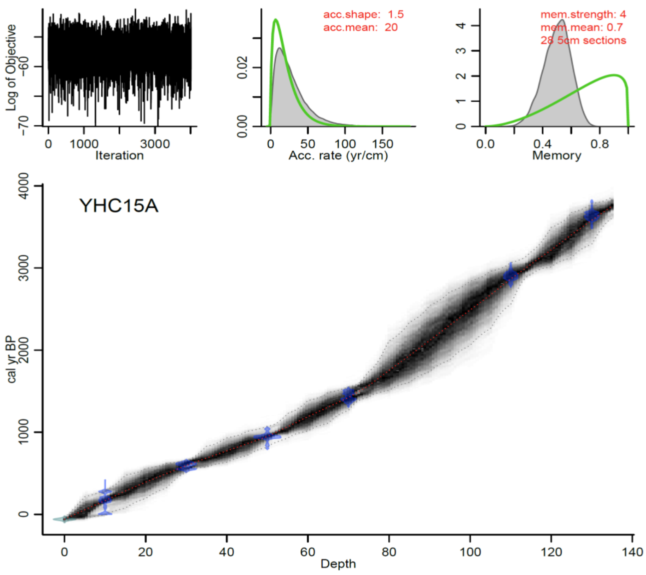
3.1 Core Description and Age Model

The lithology of the 135 cm-long YHC15A core consisted entirely of grey-brown, highly humified gyttja. Radiocarbon dates of TOC are given in Table 1, and an age-depth model determined using CLAM 2.2 (Blaauw, 2010), shown in Figure 2. Sediment rates are lower during the early part of the record, before c. 1,400 cal yrs BP (0.28mm/yr) than sediments deposited during the past 1,400 years (0.48mm/yr).

Table 1: AMS-^{14}C radiocarbon dates from Lake Yuhuang Chi (core YHC15A)

Lab No.	Depth (cm)	Material	$\delta^{13}C$ (‰ VPDB)	^{14}C date ±error (yr BP)	^{14}C date minus 1340 reservoir age (yr BP)	Weighted calibrated age（No error）(cal yrs BP)
Beta-425231	10	Bulk organic	-24.6	1530±30	190±30	168
Beta-425232	30	Bulk organic	-24.7	1920±30	580±30	595
Beta-425233	50	Bulk organic	-24.9	2370±30	1030±30	949
Beta-417757	70	Bulk organic	-24.8	2870±30	1530±30	1423
Beta-425234	110	Bulk organic	-24.8	4140±30	2800±30	2868
Beta-417758	130	Bulk organic	-24.9	4730±30	3390±30	3584

Figure 2: The age model determined on 5 radiocarbon dates of organic bulk sediments from core YHC15A. The age-depth model was developed with smooth fitting, using CLAM 2.2 (Blaauw, 2010).



3.2 Diatoms

A total of 170 species of diatom were identified from Lake Yuhuang Chi, with the majority (120 species) being only of low occurrence (< 1% in one or more samples). For much of the stratigraphy, diatoms were dominated by fragilarioids and naviculoids up to c. 930 cal yrs BP, [1020 CE] after which they decline, to be replaced by monoraphid and *Gomphonema*-type taxa alongside the centric *Lindavia*. Stratigraphically constrained cluster analysis by incremental sum of squares analyses (CONISS) on diatom relative abundance data reveals three zones. Zone 1 (c. 3550 – 2300 cal yrs BP), Zone 2 (c. 2300 – 615 cal yrs BP), and Zone 3 (c. 615 cal yrs BP – present) (Fig 3, 4). Zone 1 is dominated by diatoms in the high profile guild (Fig 4), notably fragilarioids *Stauroforma exiguiformis* and *Staurosirella pinnata*. Diatoms in the motile guild are well represented by the naviculoid *Humidophila schmassmannii*, together with *Diadesmis gallica*, *Mayamaea atomus* and *Mayamaea fossalis*. The decline in *S. exiguiformis* at the top of the zone is accompanied by an increase in *Pseudostaurosira brevistriata*, and decline in motile diatoms e.g. *M. atomus*. In Zone 1, there is a gradual decline in compositional turnover and PCA1 samples scores. Zone 2 is marked by a notable increase in the planktic *Lindavia bodanica* and increasing *P. brevistriata* and *Pseudostaurosira pseudoconstruens*. Diversity in zone 2 exhibits a rather stable, flora, dominated by *P. brevistriata*, *P. pseudoconstruens* and *L. bodanica*, while *Gomphonema olivaceoides* and *Karayevia suchlandtii* appear in the record for the first time at c. 1400 and 1070 cal yrs BP, respectively. Motile diatoms become persistently lower than the mean at this time during zone 2, while low profile diatom abundances increase to fluctuate about the average (Fig 4). Zone 3 occurs just before a major change in diatom turnover (Fig 3). Several species decline from the record altogether including *S. exiguiformis* and *H. schmassmannii*, while other species reach peak abundance for the whole profile, including *L. bodanica* and *G. olivaceoides*, and diatoms which occupy low profile guild status in general (Fig 4). *Denticula subtilis* appears in the record for the first time at c. 400 cal yrs BP (1550 CE). During zone 3, low profile and planktic diatoms increase to their highest values for the whole record, while high profile and motile diatoms are persistently lower than the mean. Diatom fluxes range from 0.07 – 7.02 (mean 1.85) valves x10^6 cm^{-2} yr^{-1}. When centred around the mean, fluxes are highest in zone 2, between c. 1500 - 800 cal yrs BP (450 – 1150 CE), but decline at c. 800 cal yrs BP (1150 CE), to lowest values from c. 600 cal yrs BP (1350 CE) to the present (Fig 3). %TOC values are low, and range from 2.6 – 4.3% (mean 3.45%). TOC values were highest in zone 1, declined in zone 2, and reached lowest values, coincident with lowest values for compositional turnover, c. 1645 CE.

Figure 3: Only diatoms with abundance greater than 3% in more than one sample are shown. Diatom species are shown as relative abundances (%), and grouped according to ecological guild. Also shown are PCA axis 1 sample scores, diatom compositional turnover values, planktonic-benthic (P/B) ratio data, and mean-centered diatom fluxes. Zones were delimited using CONISS – see text for details.

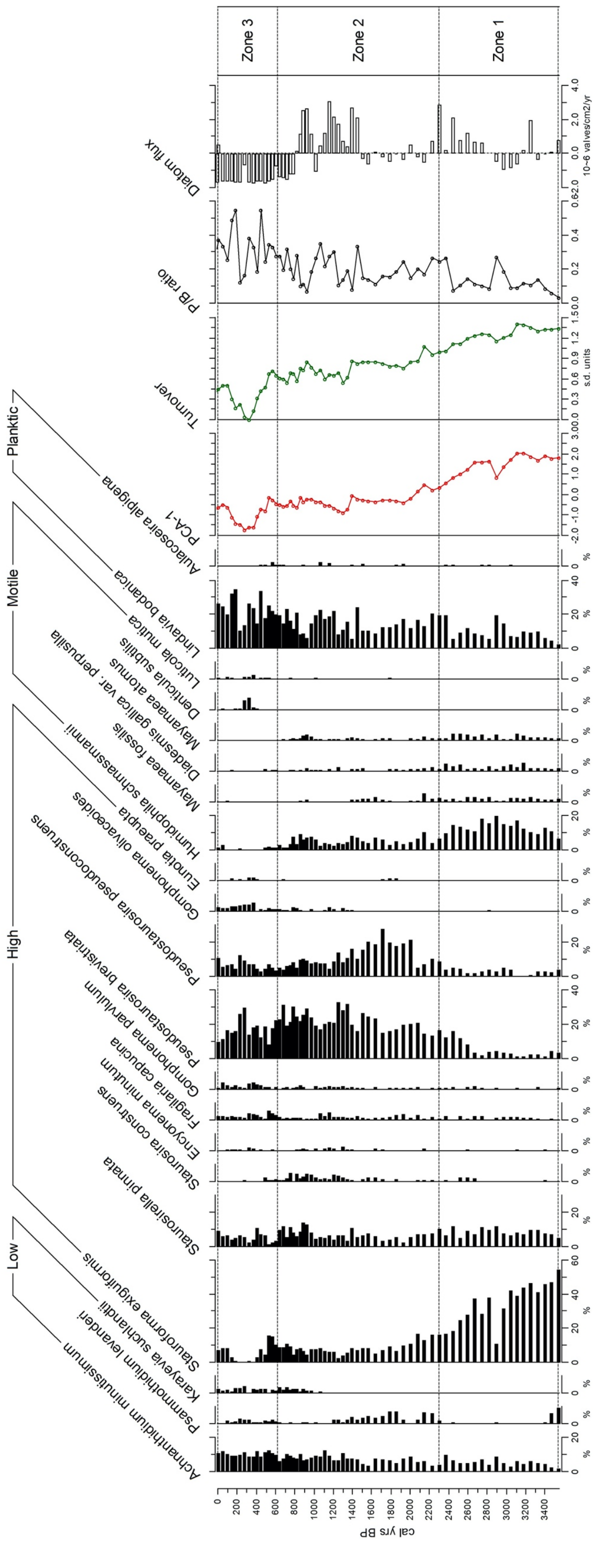
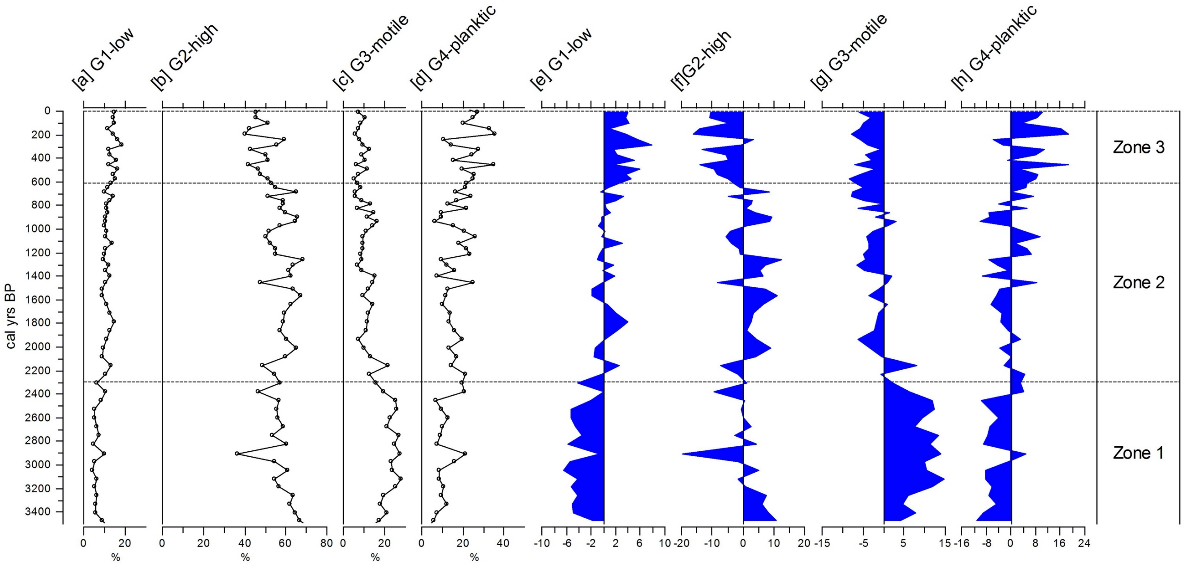


Figure 4: All diatoms were classified into one of four guilds (after Passy 2007, and Rimet and Bouchez 2012): low profile (guild 1), high profile (guild 2), motile (guild 3) and planktic (guild 4). Guilds are presented as relative abundances (%) to the left, and deviations around the mean to the right.



PCA highlights a very strong first axis gradient which accounts for over 45% of variation in the diatom data. Trends in PCA-1 are most clearly seen in Fig 5, as deviations around the mean. Breakpoint analysis indicates major ($p<0.001$) change in PCA axis 1 scores (Table 2), close to the transition when PCA values switch from being higher than the mean, to being lower than the mean, and low values persist for the rest of the record. Diatom compositional turnover (estimated from DCCA; 1.033 SD units) shows a similar pattern to PCA-1, with breakpoints identified at c. 515 cal yr BP ± 40 years, (c. 1435 CE) and 335 cal yr BP ± 33 years (c. 1615 CE) (Table 2; Fig 5).

Figure 5: Ordination and biodiversity trends shown as deviations around the mean.

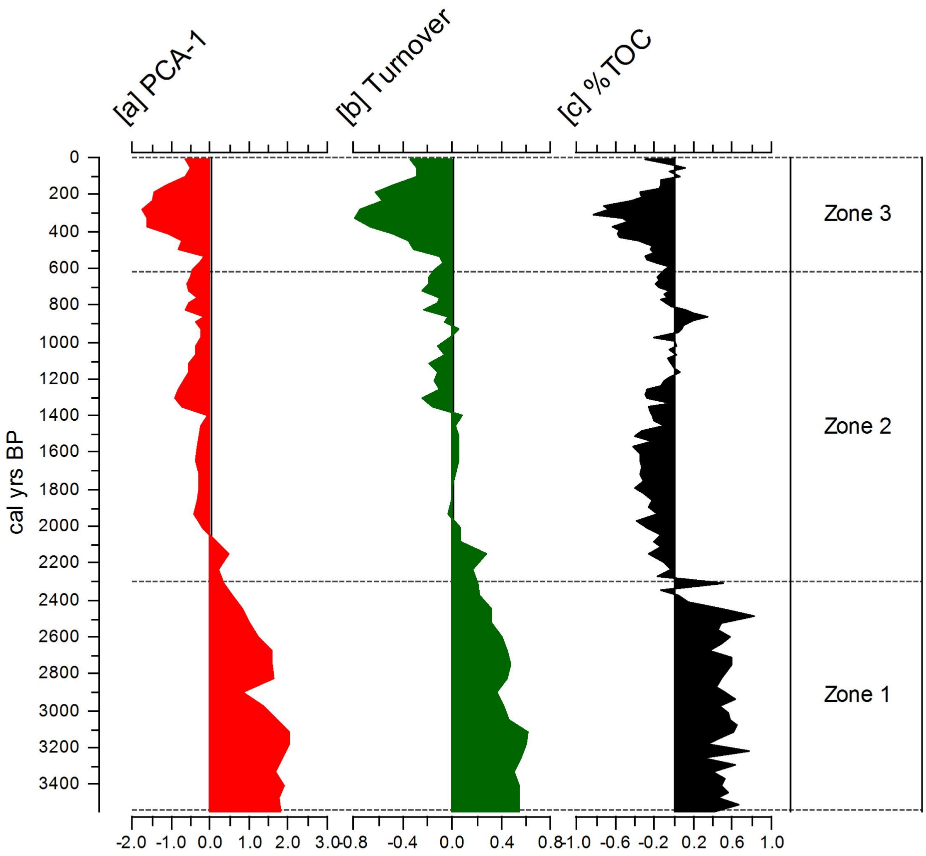


Table 2: Significant breakpoints in diatom trend data; p < 0.001).

	Breakpoint 1(cal yrs BP)	p value	Breakpoint 2 (cal yrs BP)	p value
Species PCA	1850 ±200	p<0.001	none	
Compositional turnover	515 ± 97	p<0.001	335 BP ± 33	p<0.001
Guild 2 – High profile	2910 ± 127)	p<0.001	1565 BP ± 175	p<0.001
Guild 3 – Motile	2880 ± 69	p<0.001	1960 BP ± 128	p<0.001

4. Discussion:

4.1 Diatom assemblage change

Sedimentary diatom assemblages in Lake Yuhuang Chi are dominated by species in the Fragilariaceae (Fig 3) from 3,500 - 615 cal yrs BP. Fragilarioids are often opportunistic, dominating assemblages in alpine and arctic lakes with a short growing season and long periods of ice cover (Lotter and Bigler 2000). For example, July air temperature and ice cover duration have both been shown to have significant influence on the abundance of fragilarioids in the European Alps (Schmidt et al. 2004), while in a sub-alpine lake in the Eastern Sayan mountains (Russia), insolation and northern hemisphere air temperatures played a strong role on modulating fragilarioid responses through the Holocene (Mackay et al. 2012). The early part of our record is dominated by *Stauroforma exiguiformis*, a species common in dystrophic lakes (Flower et al. 1996). Its high abundance may be related to relatively high carbon sequestration during the very early part of the record in Zone 1 (Fig 5c).The decline in *S. exiguiformis* is concomitant with the increase in *Humidophila schmassmannii* and may be indicative of Lake Yuhuang Chi becoming less dystrophic (Buczkó et al. 2015), perhaps linked to progressively cooler (Stebich et al. 2015) and more arid (Chen et al. 2015a) climate (Fig 6) leading to increasingly frozen soils, reducing the supply of allochthonous carbon. The decline in *H. schmassmannii* after c. 2800 cal yrs BP further tracks the switch to a progressively cooler and more arid climate (Wang et al. 2005; Chen et al. 2015b).

Growth of the planktic diatom *L. bodanica* in oligotrophic lakes is related to increased mixing depth (Saros and Anderson 2015), because it can tolerate relatively low light levels and take advantage of increased nutrient availability (Malik and Saros 2016). As the neoglacial progressed therefore, mixing of the lake may have increased gradually, allowing this taxon to eventually dominate for most of the past 615 years, even though diatom fluxes (Fig 3) and %TOC (Fig 5) were relatively low, indicative of overall low diatom productivity.

4.2 Diatom traits

Even though we do not have quantitative estimates of nutrients in this remote lake, we can start to make inferences about nutrient availability from the traits exhibited by the diatom communities themselves. For example, fragilarioids identified at Lake Yuhuang Chi can be classified as high profile diatoms (i.e. of tall stature), able to compete effectively for resources such as nutrients and light. However, their tall stature also makes them susceptible to disturbance (Passy 2007) including turbulence in alpine lakes with short water-residency times (Rimet et al. 2019). Their dominance at Lake Yuhuang Chi from 3500 - 615 cal yrs BP suggests that nutrients and light were not limiting (Passy and Larson 2019) for much of the sequence. Herbivory was likely low as well (ibid.), because high profile diatoms are not well adapted to high grazing pressures, which are generally low in alpine lakes (Rimet et al. 2019).

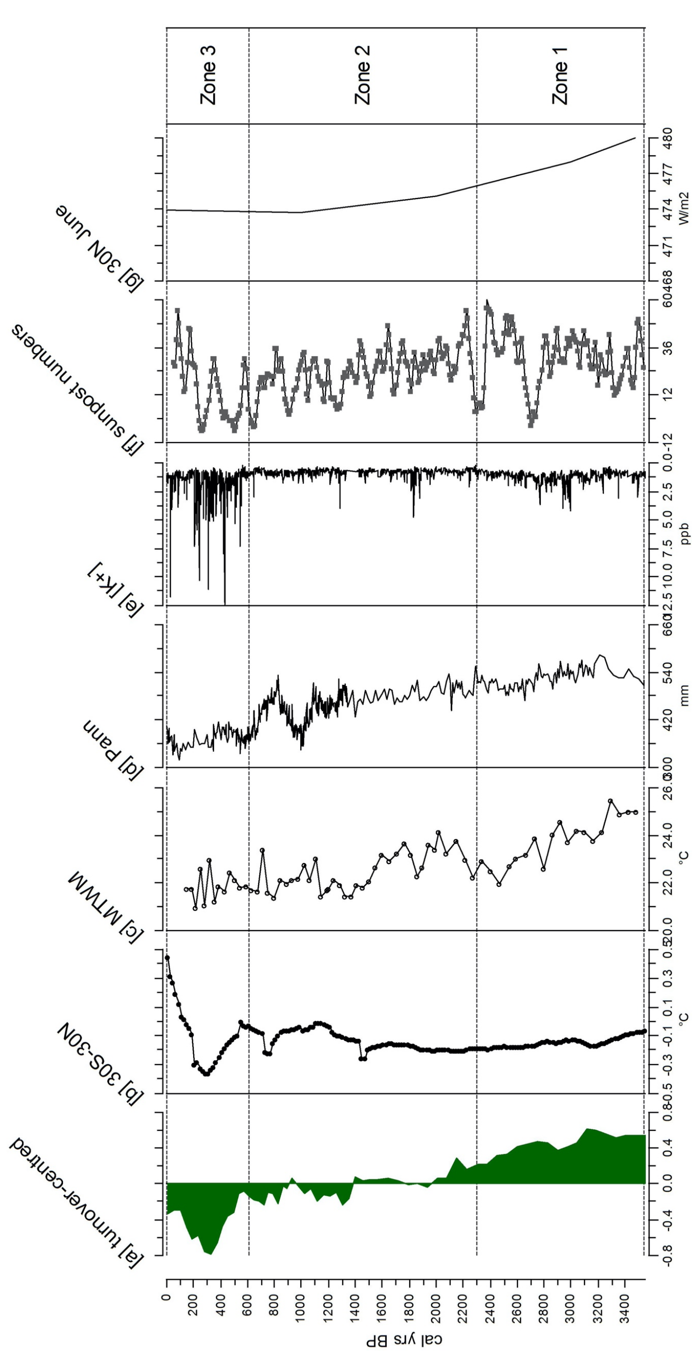
The decline in high profile guild values with concomitant increase in low profile and planktic guilds since 615 cal yrs BP suggests that environmental conditions in Lake Yuhuang Chi changed. Diatoms belonging to the low profile guild attach themselves to substrates in erect, prostrate and adnate forms (Passy 2007), which means that although they are able to tolerate relatively high disturbance, they also need to withstand an increase in the number of resources that becomes limiting to them, i.e. they are well adapted to low nutrient concentrations (Berthon et al. 2011). The planktic guild was proposed by Rimet et al. 2012 alongside the high, low and motile guilds determined by Passy (2007), as diatoms able to resist sedimentation through the water column, and in our lake, this guild is dominated by *L. bodanica*. That *L. bodanica* can tolerate low light conditions, and through turbulence of the water column obtain the nutrients that it needs to grow, again indicative of resources such as nutrients becoming more limiting since the middle of the 14th century.

4.3 Diatom compositional turnover

In aquatic environments, when disturbance increases, or the number of limiting resources increases, such as the decline in nutrient and / or light availability, deterministic processes become more important than stochastic ones in structuring aquatic communities (Chase 2010). Increasing deterministic processes leads to a decline in compositional turnover because disturbance or stress can act as environmental filters (Larson et al. 2016), through niche selection. The decline in turnover between 3,100 – 1,900 cal yrs BP is gradual, and reflects the slow, long term change in low profile guild diatoms increasing, and motile guild diatoms declining. An increase in low profile diatoms hints at increasing disturbance and / or declining nutrients (Passy 2007), while a decline in motile diatoms may be indictive of a decline in siltation processes within the lake (Battegazzore et al. 2004). Over this time period our data also show a marked decline in TOC sequestration to the bottom sediments (Fig. 5c). We suggest therefore the diatom and TOC data both point to a reduction in dissolved organic carbon in Lake Yuhuang Chi, concurrent with cooling regional temperatures and increased aridity (Chen et al. 2015a).

There are also periods when compositional turnover stabilised or even increased slightly during the neoglacial, e.g. between c. 1,900 – 1,400 cal yrs BP (Fig 6a). This period coincides with distinctly warmer Arctic and European temperatures (PAGES 2k Consortium 2013), commonly referred to as the 'Roman Warm Period'. Precipitation in central China is closely tied to the intensity of the Asian summer monsoon (ASM) (Chen et al. 2015a), and at this time the summer monsoon was rather stable (Fig. 6d). Diatoms were dominated by high profile species, indicative that nutrients were not in limited supply, perhaps being washed in from the catchment with summer monsoon rains.

Figure 6: Compositional turnover plotted alongside internal and external climate forcings: mean temperature stack records for low latitude temperature anomalies (Fig 6b; Marcott et al. 2013); NE China pollen-inferred mean temperature warmest month (July) (Fig 6c; Stebich et al. 2015); trends in pollen-inferred mean annual precipitation (Fig 6d; Chen et al. 2015a); K+ concentrations in the GISP ice core (Fig 6e; Mayewski et al. 2004); sun spot numbers (Fig 6f; Solanki et al. 2004); June solar insolation at 30 N (W m^{-2}) (Fig 6g; Berger and Loutre 1991)



Between 1400 – 615 cal yrs BP (550 - 1335 CE), turnover although lower than average (Fig 6a), did not decline (Fig 3), indicative of increased competition between species (Larson et al. 2016). This period coincides with the Medieval Climatic Anomaly (MCA), sometimes referred to the Medieval Warm Period. Sub-decadal isotopic records from a stalagmite from Buddha cave in the Qinling Mountains indicate a period of warm, wet climate between c. 985 – 475 cal yrs BP (965 – 1475 CE) (Paulsen et al. 2003), while phenological records, including the beginning of tree flowering along the Yellow and Yangtze rivers, show that winter half-year temperatures were high between 1380 – 640 cal yrs BP (570 – 1310 CE) (Ge et al. 2003). Increased presence of *Quercus* and *Betula* pollen on Taibai Mountain also suggest warm, wet conditions (Li et al. 2005; Wang et al. 2016) with temperatures perhaps being as much as 2 °C warmer than mean annual temperatures observed today (Li et al. 2005). These local climate indicators tie in well with regional monsoon patterns; monsoon strength was higher in central (Paulsen et al. 2003; Chen et al. 2015b; Wang et al. 2016) and north east China (Chen et al. 2015a,b) than north west China (Chen et al. 2015b), while globally, low latitude temperatures increased (Fig 6d).

4.4 Abrupt ecological change during centennial-scale cold events

Against a backdrop of low northern hemisphere summer insolation (Fig 6g), amplified by centennial-scale oceanic variability (Renssen *et al.*, 2006), late Holocene cold events were caused by several “overlapping” factors (such as volcanic eruptions and solar minima) (Wanner *et al.*, 2014). The most recent wide-scale cold event is the period commonly known as the Little Ice Age approximately 1300 – 1850 CE, caused by several interacting, time-transgressive forcings, including reduced solar activity during the late 17th century (Shindell et al. 2001), increased volcanic activity during the early 19th century (Brönnimann et al. 2019) and overall reduced Gulf Stream flow (Lund et al. 2006). It is the cooling event that we focus on in this study, because cluster analyses of diatom assemblages delineate the boundary between zones 2 and 3 at 615 cal yrs BP (1335 CE) and there are two significant breakpoints in compositional turnover including when turnover is at its lowest in the whole record at c. 335 – 330 cal yrs BP (1615-1620 CE) (Table 2).

Describing the Little Ice Age as a period characterised by cooler climate and glacier readvance is rather simplistic, but one that has proven quite resilient, even as its complexities are better understood (e.g. Matthews and Briffa 2005). As more regions are investigated, impacts extend to changes in aridity as well as temperature. For example, Chen et al. (2015b) demonstrated that by and large, regions north of 34° latitude (where our study site is located) were generally drier than regions further south, with the extent of aridity being affected by ocean-atmospheric interactions, such as ENSO, and its teleconnections to SE Asia. The LIA is especially characterised by a strengthened Siberian High (SH), a semi-permanent anticyclone centred over Eurasia which strengthens intensively every winter. A strong Siberian High results in a strong East Asian Winter Monsoon (EAWM) (Zhang et al. 1997). K^+ concentrations in the GISP ice core clearly show that the Siberian High was especially strong between c. 550 – 150 cal yrs BP (1400 – 1800 CE) (Fig 6f), given that potassium is likely sourced from central Asian dust via long-range transport to the Greenland ice sheet (Meeker and Mayewski 2002). Concurrent with increased aridity, global low latitude temperature records show rapid cooling at this time (Fig 6b; Marcott et al. 2013), which in China led to very low winter anomalies (Ge et al. 2003), and lowest summer pollen-inferred temperatures in NE China (Fig 6c).

Very low diatom fluxes characterise the past 800 years at Lake Yuhuang Chi (Fig 3), indicative of reduced diatom productivity, coincident with prevailing colder climate. Lowest compositional turnover at c. 335 – 330 cal yrs BP (1615-1620 CE), linked to the disappearance of *S. exiguiformis*, may be due to enhanced frozen soils, leading to reduced carbon transport to the lake, while the disappearance of *H. schamassmannii* may be because it cannot tolerate such low water temperatures (Buczkó et al. 2015), alongside other factors such as a decline in siltation (Battegazzore et al. 2004). *Denticula subtilis* is a very motile diatom, and in the Canadian High Arctic is characteristic of shallow lakes with elevated conductivity (Antoniades et al. 2005). It may therefore be reflective of the lake becoming more shallow due to increased aridity. Elsewhere, precipitation minima were reconstructed from nearby by Gonghai lake (Chen et al. 2015a), and at neighbouring Lake Sanqing Chi, high *Larix* and *Ephedra* pollen frequencies are interpreted as being indicative of cold, dry conditions (Wang et al. 2016). That minimum turnover and highest values for low profile diatoms are observed at this time, indicates nutrient limitation and / or significant disturbance has led to specialised diatoms to occupy niches where competition was very low (Larson et al. 2016). Following harshest conditions for diatom growth in Lake Yuhuang Chi during the early 17th century turnover increases once more, indicative of increased competition among species (Larson et al. 2016).

While cold and arid climate during the LIA had a major impact on diatom diversity in Lake Yuhuang Chi, impacts from previous centennial-scale cold events such as the 2,800 yr BP event, are less conclusive. Like the LIA, the event dated at c. 2,800 yr BP is concurrent with a deep, abrupt reduction in solar activity (Fig 6f), which led to a decline in surface water temperatures in the North Atlantic (Andersson *et al.*, 2003), weaker meridional overturning circulation (Hall *et al.*, 2004) and sea-ice expansion (Renssen et al. 2006). But although these events led to a rapid weakening in ASM intensity in southern China (Wang et al. 2005), reconstructed precipitation from Gonghai Lake in northern China suggests that aridity was already increasing from c. 3,100 cal yrs BP (Fig 6d) (Chen et al. 2015b). There is a small increase in GISP2 K^+ concentrations, which suggests that the Siberian High during the time of the 2,800 yr BP event did not reach the strengths observed during the LIA (Fig 6e), but still led to regional summer time cooling (Fig 6c, Stebich et al. 2015). At Lake Yuhuang Chi, these changes in climate may have caused both the small, temporary decline in both compositional turnover and total diatom flux, but also a significant decline in high profile diatoms, concomitant with an increase in *L. bodanica*. This may suggest increased water column instability and turbulence in the lake (Saros and Anderson 2015).

5. Conclusions

Diatom turnover in the Qinling mountains of central China demonstrates strong directional change. The decline in turnover over the past 3,500 years mirrors declining low latitude June insolation, which drives overall low latitude cooling (Marcott et al. 2013). This suggests a strong link between orbitally-forced climate change and increasingly deterministic processes affecting aquatic ecosystems in this high altitude region of central China. Over the last 1300 years, impacts related to the Medieval Climatic Anomaly and the Little Ice Age are also expressed in the palaeolimnological records from Lake Yuhuang Chi. Increased diatom fluxes (Fig. 3) are coincident with increased regional summer precipitation during the MCA (Chen et al. 2015a). Colder, more arid conditions during the Little Ice Age, linked to a very strong Siberian High, led to lowest diatom turnover and carbon sequestration for the past 3,500 years, possibly due to the lake becoming more shallow at this time. Our study highlights the value of interpreting diatom changes through compositional turnover, and ecological trait analyses of their growth forms.

6. Author contribution

BC, JC & QZ designed the study. BC undertook the diatom analyses, and AZ the radiocarbon dating. JA provided assistance with statistical analyses, and AWM prepared the manuscript with contributions from all authors.

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Figure Legends

Figure 1: Regional position of Lake Yuhuang Chi in the Qinling Mountains of central Asia. The lake is situated 3370m asl, and was formed by glacial activity. The photograph of the frozen lake to the right shows the small catchment and tundra vegetation.

Figure 2: The age model determined on 5 radiocarbon dates of organic bulk sediments from core YHC15A. The age-depth model was developed with smooth fitting using CLAM 2.2 (Blaauw, 2010).

Figure 3: Diatoms shown greater than 3% in more than one sample. Diatom species are given as relative abundances. Also shown are PCA axes 1 scores for species and genera, compositional turnover values, planktonic-benthic (P/B) ratio data, and mean-centered diatom fluxes. Zones were delimited using CONISS – see text for details.

Figure 4: All diatoms were classified into one of four guilds (after Passy 2007, and Rimet and Bouchez 2012): low profile (guild 1), high profile (guild 2), motile (guild 3) and planktic (guild 4). Guilds are presented as relative abundances (%) to the left, and deviations around the mean to the right.

Figure 5: Ordination, compositional turnover, and TOC trends shown as deviations around the mean.

Figure 6: Compositional turnover (deviations around the mean) plotted alongside internal and external climate forcings: mean temperature stack records for low latitude temperature

anomalies (Fig 6b; Marcott et al. 2013); NE China pollen-inferred mean temperature warmest month (July) (Fig 6c; Stebich et al. 2015); trends in pollen-inferred mean annual precipitation (Fig 6d; Chen et al. 2015a); K+ concentrations in the GISP ice core (Fig 6e; Mayewski et al. 2004); sun spot numbers (Fig 6f; Solanki et al. 2004); June solar insolation at 30 N (W m^{-2}) (Fig 6g; Berger and Loutre 1991)