Duelling narratives of chironomids and pollen explain climate enigmas during The Last Glacial-Interglacial transition in North Island New Zealand

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ABSTRACT

The Last Glacial-Interglacial Transition (LGIT) was a dynamic stage of Earth’s history, and the difficulty of reconstructing this complex interval may be compounded by divergent proxy records, often collected from the same archive. To overcome this obstacle, we exploit the contrasting biological preferences of chironomids to both summer temperature and degree days (positive) and pollen to both the length of the growing season (positive) and winter duration (negative), recorded by a small lake in the central North Island of New Zealand. The climate proxy records are anchored to shifting zonal boundaries (e.g., southern westerly wind belt) via the hydrogen isotope ratios of leaf wax n-alkanes (Dwax). These results enable us to interrogate the structure of the LGIT and address two fundamental questions: 1) Is there evidence for Holocene-like temperatures during the early deglacial? and 2) Were early Holocene summers cool? Lake sediment Dwax values indicate a poleward retreat of the westerlies around 18,000 calibrated years before present (cal kyr BP), signalling the onset of climate amelioration for the region. Remarkably, the independently derived summer and mean annual temperature reconstructions are anti-phased. Chironomid-inferred summer temperatures surpass modern values by 17.5 cal kyr BP, whereas pollen-inferred mean annual temperatures remain suppressed. Summers cool from 17.5 to 11 cal kyr BP, when they reach a minimum for the record, while winter and mean annual temperatures simultaneously warm to a maximum. The chironomid record generally traces regional insolation, although an Antarctic template imprint on this trend with declining summer temperatures during the Antarctic Cold Reversal (ACR) and warming during the Younger Dryas (YD). Forest development during the early LGIT, on the other hand, is suppressed by cool, dry winters, punctuated by severe frosts, despite being set against a backdrop of overall warming; the successional pattern is best explained by a latitudinal retreat of the westerlies. Our findings underscore the complementarity of multiple bioproxy responses and reveal the importance of seasonal heat and energy distribution during the LGIT.

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1. Introduction

During the Last Glacial-Interglacial Termination (LGIT), commencing 18,000 calibrated years ago (cal kyr BP), climates experienced a major reorganisation, shifting from fully glacial to essentially modern conditions within 10,000 years (Denton et al., 2010). While floral and faunal distributions adjusted to shifting
bioclimatic envelopes, habitats and migratory routes were reshaped by a changing landscape. A deeper understanding of this interval remains a long-standing goal (Lowe et al., 2008; Denton et al., 2010), and paleoecological data offer the opportunity to both identify forcing mechanisms and test physics-based climate models. Here, we aim to exploit the contrasting responses of plants and insects to seasonal signals and gain further insight into the nature of environmental change during the LGIT.

Vegetation and insect remains recovered from lake sediments originate from organisms with different life strategies and are deposited via different taphonomic pathways. Plants generally live on annual to centennial timescales, producing pollen and spores that are ex situ with respect to their final depositional environment. In terms of climate controls, plant species abundances are often associated with mean annual temperature (MAT), length of the growing season, frost tolerance, rainfall, and drought (Wardle, 1991; Leathwick, 1995; Wilmshurst et al., 2007). On the other hand, insects, specifically larvae of the Chironomidae, live on sub-annual to annual timescales, generally produce in situ remains, and typically correlate with summer temperature (Barley et al., 2006; Rees et al., 2008; Massaferrro et al., 2014). The important distinction is that chironomids primarily reflect summer temperature, whereas chironomids also respond to seasonal rainfall and its variation, whereas chironomids obliquely respond to precipitation via correlates such as lake depth. Consequently, it is unsurprising that plant and insect turnover during the LGIT offer different interpretations concerning the timing and magnitude of temperature change.

The difficulty in reconciling proxies holds true in the temperate mid-latitudes of Australasia, where deglacial climate amelioration commenced shortly after the Last Glacial Maximum (Alloway et al., 2004; Vandergoes et al., 2005). Maximum warmth and temperature change. A chironomid-based reconstruction from Boundary Stream Tarn, located in the South Island at 44°S, suggests summer temperatures began to warm around 15.5 cal kyr BP, reverted to cooler conditions between 13.9 and 13.2 cal kyr BP, and then warmed to stable, albeit cooler-than-modern temperatures characterising the early Holocene (Vandergoes et al., 2008). Farther north at Lake Pupuke (38°S), summer temperatures subtly cooled from 14 cal kyr BP to a minimum for the record between 12.5 and 10 cal kyr BP (van den Bos et al., 2018). Across the Tasman Sea, chironomid-based reconstructions in Tasmania suggest summer temperatures were above modern values from about 14.5 to 12 cal kyr BP and then cooled to below modern, remaining so until about 10 cal kyr BP (Rees and Cwynar, 2010). These chironomid-based reconstructions provide new insights into the seasonal dynamics of climate change not previously apparent from palynological evidence.

Here, we present pollen and chironomid temperature reconstructions that encompass the majority of the LGIT and part of the early Holocene from Lake Rangatauaunui, located towards the southern margins of the central North Island volcanic plateau of New Zealand (Fig. 1). We aim to reconcile potentially divergent proxy records by considering the representative signals of each indicator. We specifically try to answer: 1) Is there evidence for Holocene-like temperatures during the early deglacial, here defined as the period between the deposition of Rerewhakaaitu Tephra at 17.5 cal kyr BP and 2) Were summers cool at the onset of the early Holocene 11.5 cal kyr BP? In addition to addressing the divergences between pollen- and chironomid-derived temperature reconstructions highlighted by previous work, these questions are relevant to considerations of recent past analogues to current and projected climate change scenarios and their biotic impacts (e.g., Cole, 2010).

Our results are tied to the migration of the southern westerly winds via the hydrogen isotope ratios of leaf waxes from terrestrial vegetation (δD wax). As the westerlies shift north or south, they direct regional storm tracks (Garreaud et al., 2013), imparting isotopic differences in the δD wax record. This link with the westerlies, the paleoclimate reconstruction from Lake Rangatauaunui takes on broader significance in two fundamental ways. First, the southern westerlies play a critical role in mid-latitude climate but also respond to Northern Hemisphere forcing mechanisms and theoretical drivers of glacial terminations (Denton et al., 2010). Second, empirical and modelling studies have postulated that changes in SWW strength and position have influenced ocean-atmosphere CO2 exchange (Toggweiler et al., 2006) which is a critical part of the carbon cycle and hence climate projections. Together, these data will add to the few quantitative reconstructions that exist for the mid-latitudes of the Southern Hemisphere and help discern between local and far-field drivers of climate change.

2. Study site

Lake Rangatauaunui (39.434°S 175.379°E) sits at the southwestern end of the Taupo Volcanic Zone (TVZ), a region of prolific volcanism in the central North Island (Fig. 1). The lake occupies one of two maar craters that were created by phreatomagmatic explosions from a parasitic vent of Mount Ruapehu approximately 30 kyr (Houghton and Hackett, 1984). The catchment geology consists of the Miocene-Pliocene Whanganomona Group, comprising repeat sequences of sandstone, siltstone, shellbeds, and conglomerate, while overlying Quaternary volcanic deposits have developed allophanic soils (Townsend et al., 2008). Proximal deposits above the boundary boulders of the lake are also present on Mount Ruapehu until 18 kyr (Eaves et al., 2016b). Based on coupled energy-ice flow modelling, temperatures during the last glacial were between 5.1 and 6.3 °C cooler than present (Eaves et al., 2016a), which agrees with pollen estimates from the
Griselinia lucida, Olearia spp., following description is largely summarised from Newnham et al. the lake before conversion into pasture in the 19th century. The identical, forest community likely occupied the region surrounding ~5 km to the northwest of Lake Rangatauanui. A very similar, if not Newnham et al., 2017), with the southwestern boundary located persist on the central North Island volcanic plateau (summarised in (Mcglone, 1989). Today, extensive remnants of the original forest continuous forest cover, apart from swamps and alpine areas (McGlone and Topping, 1977; Turney et al., 2003).

Prior to human arrival in New Zealand, c. A.D. 1280 (Wilmshurst et al., 2011), the wider central North Island region supported continuous forest cover, apart from swamps and alpine areas (Mcglove, 1989). Today, extensive remnants of the original forest persist on the central North Island volcanic plateau (summarised in Newnham et al., 2017), with the southwestern boundary located –5 km to the northwest of Lake Rangatauanui. A very similar, if not identical, forest community likely occupied the region surrounding the lake before conversion into pasture in the 19th century. The following description is largely summarised from Newnham et al. (2017).

At altitudes comparable to Lake Rangatauanui, remnant forests are characterised by emergent podocarp, predominantly Prumnopitys taxifolia, Dacrydium cupressinum, and Podocarpus totara, and hardwoods including Metrosideros robusta, Laurelia novae-zelandiae and Knightia excelsa. The lower canopy consists of hardwood tree species dominated by Weinmannia racemosa, Nestegis spp., Elaeocarpus dentatus, and Beilschmiedia tawa. The subcanopy is made up of small trees and large shrubs (e.g., Aristotelia serrata, Brachyglottis repanda, Carpodetus serrat us, Coprosma spp., Fuchsia excorticata, Griselinia lucida, Hedycarya arborea, Melicytus spp., Myrsine spp., Olearia spp., Pennantia corymbosa, Pittosporum spp., Pseudopanax spp., Pseudowintera spp., and Quintinia spp) with lianas and tree ferns (Cyathea spp. and Dicksonia spp.). More poorly drained areas, like those immediately surrounding Lake Rangatauanui, are vegetated by dense stands of Dacrycarpus dacrydioides.

At higher elevation, beech (Fuscospora spp.) becomes more prominent, occurring in pure stands or with red beech (F. fusca). D. cupressinum and Prumnopitys ferruginea. As altitude increases, beech forest may continue, but mountain (F. cliffortioides) and silver (Lophozonia menziesii) beech become dominant, accompanied by mountain cedar (Libocedrus bidwillii). In areas where beech has not taken hold, vegetation consists of a low-canopy alpine podocarp-hardwood forest with Podocarpus laetus and L. bidwillii, with or without D. cupressinum. Progressing into the upper montane to subalpine zones, forest is short-statured, with a canopy of Phyllocladus alpinus, F. cliffortioides, L. menziesii, and W. racemosa. Tree ferns, lianas, and the tall podocarp taxa (i.e., P. totara and Prumnopitys spp.) are absent at these altitudes. Beyond this, stunted mountain beech (F. cliffortioides) forest extends to the treeline (max 1510 m). At these altitudes, poorly drained areas support shrubland often dominated by L. bidwillii, Halocarpus biformis, Halocarpus bidwillii, and Manooa colensoi. Above the treeline, P. alpinus, Lepotsernum scoparium, Dracophyllum spp., and Podocarpus nivalis shrubland eventually gives way to tussock-dominated herbfield, featuring Chionochloa and the alpine herbs Astelia spp., Astereaceae, Apiaceae, and Ranunculus spp. Bare ground with sporadic patches of vegetation occurs within the alpine belt, where conditions become too harsh to support continuous cover.

Present vegetation in the immediate vicinity of Lake Rangatauanui comprises a 50-m wide zone of wetland dominated by Phormium sp., with Typha orientalis, Cordyline, and Lepotsernum scoparium, which gives way to regenerating conifer-hardwood forest, with Dacrycarpus dacrydioides, W. racemosa, Knightia excelsa, Metrosideros robusta, as well as other broadleaved large shrubs and small trees. This forest comprises a small (~58 ha) reserve surrounded by pasture.

The surface area and water depth of Lake Rangatauanui are 2.5 ha and 7 m, respectively. As is often typical of maar lakes, Lake

Fig. 1. Map of study site. Lake Rangatauanui, depicted by the star, is located near the southern margin of New Zealand’s central North Island volcanic plateau.
Rangatauanui is a closed system with no inflowing or outflowing streams, making it well suited to proxy-based reconstructions. The lake sits at an elevation of 580 m asl, roughly 670 m below the contemporary treeline. Mean annual temperature at nearby Ohakune is 11.0 °C, ranging from 16.3 °C in February to 5.6 °C in July, while total annual rainfall is roughly 1310 mm, with minimal variation throughout the year (NIWA, 2017).

### 3. Methods and materials

#### 3.1. Coring and chronology

Lake Rangatauanui is a repository for tephras originating from the andesitic Tongariro and Taranaki, as well as the rhyolitic Taupō volcanic centres. Several cores were collected in 2007 from the deepest part of the lake using a 40-mm diameter Livingstone piston corer, and prominent tephras markers were used for cross-correlation. Due to restricted sample volumes available from individual cores, one was dedicated to volcanological analysis of the many andesitic layers while another was used for proxy analysis. A separate manuscript will detail the tephrostratigraphy, so we restrict our inclusions to data that provide age control for the proxy records presented here.

Tephras were analysed for major element composition of volcanic glass shards using a JEOL JXA-840 electron microprobe equipped with a Princeton Gamma Tech Prism 2000 Si(Li) EDS x-ray detector. We selected an accelerating voltage of 15 kV, an 800-pA beam-current, and an 800-pA beam of 10 µm in diameter for glass shard analyses to minimize Na-migration. Analytical conditions were regularly calibrated using a 100-s live time count and applied a defocused beam of 10 µm.

**Table 1**

<table>
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<tr>
<th>Tephor</th>
<th>Unit K</th>
<th>Whakatane</th>
<th>Mamaku</th>
<th>Rotoma</th>
<th>Okupata</th>
<th>Waihou</th>
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<td>6</td>
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</tr>
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</table>

¹ Means and standard deviations (in parentheses) of n analyses (individual glass shards) normalised to 100% loss-free (wt%). Analyses were conducted on a JEOL JXA-840 electron microprobe equipped with a Princeton Gamma Tech Prism 2000 Si(Li) EDS x-ray detector. We selected an accelerating voltage of 15 kV, an 800-pA beam-current, and a 100-s live time count and applied a defocused beam of 10–20 µm in diameter for glass shard analyses to minimize Na-migration. Analytical conditions were regularly calibrated using an ASTIMEX albite standard.

The second core collected from Lake Rangatauanui, correlated to the first by tephrostratigraphy, x-ray imaging, and physical characteristics (e.g., colour and texture), was dedicated to proxy analysis. To constrain the seasonal temperature regime during the LGIT, we coupled chironomid and pollen sampling at 5-cm resolution. Pollen was extracted from 1 cm³ of sediment using standard potassium hydroxide (KOH), hydrofluoric acid, and acetolysis treatments (Moore et al., 1991). Grains were suspended in silicone oil on a glass slide and counted at 400× magnification until a minimum of 200 dryland pollen grains were identified following standard texts (Pocknall, 1981b; Large and Braggins, 1991; Moar, 1993). Chironomid head capsules were collected from 1.5 cm³ of sediment that was disaggregated with 10% KOH at 70 °C and sieved through 95-µm meshes (Walker et al., 1991). Head capsules were picked from the residue with fine forceps, mounted on a slide, and identified at 400× magnification following a guide by Dieffenbacher-Krall et al. (2008); the minimum counting effort was 50 whole head capsules (Heiri and Lotter, 2001; Larocque, 2001).

To track the influence of the southern westerlies over Lake Rangatauanui, we measured the hydrogen isotope ratios of long-chain n-alkanes produced by terrestrial vegetation. In the contemporary setting, moisture originating from the north of New Zealand is enriched in deuterium relative to southern sources (Ehtesham et al., 2013). Therefore, predominantly subtropical hydroclimate regimes will result in less negative δD values for precipitation, whereas predominantly Southern Ocean hydroclimate regimes will result in more negative δD values. Shifts in δDwater can also reflect changes in overall moisture balance (e.g., Aichner et al., 2010), vegetation type (e.g., Chikaraishi and Naraoka, 2007), and other factors (e.g., Machado and Froehner, 2017).

To isolate leaf wax n-alkanes, 2–10 g of dry, homogenized sediment was weighed into Teflon containers. Lipids were extracted in a CEM Microwave Accelerated Reaction System (MARS 5) with a 9:1 mixture of dichloromethane (DCM) and methanol, then filtered. Total lipid extracts were separated into different polarity fractions and deuterium ages from the dated tephas (Lowe et al., 2013) using Bacon (Blaauw and Christen, 2011). Radiocarbon dating was undertaken to supplement the chronology; however, a lack of terrestrial macrofossils necessitated bulk sediment dating. Complications arising from this approach resulted in discarding radiocarbon ages from the final model (see Appendix A for details).
classes using Sepra\textsuperscript{TM}NH2 (Phenomenex) solid phase extraction, with the hydrocarbon fraction eluted in hexane. Due to the presence of elemental sulphur, acid-treated copper was added to samples before column chemistry. Hydrocarbon fractions were further purified using Discovery\textsuperscript{TM} Ag-Ion (Supelco) solid phase extraction to separate saturated from unsaturated compounds.

To identify and quantify compounds, the saturated hydrocarbon fractions were analysed on a ThermoScientific Trace gas chromatograph (GC) equipped with a ZB-5ms (Phenomenex) column and a PTV injector. From the GC, samples were split between a ThermoScientific TraceDSQ mass spectrometer and a flame ionisation detector (FID). The GC oven was held at 100 °C for 1 min, ramped to 320 °C at 10 °C/min, and held for 10 min. The PTV injector was ramped to 350 °C for 5 min, then held at 320 °C for the duration of the run. Compounds were identified through mass spectral comparison with library data. Abundances were calculated by comparing FID peak areas of compounds of interest with an internal standard (palmitic acid isobutyl ester, PAIBE) and assuming identical response factors for all analytes.

Hydrogen isotope ratios of \( n \)-alkanes were measured on a ThermoScientific TraceGC coupled to a Delta XP isotope-ratio mass spectrometer (IRMS) with a pyrolysis interface operated at 1430 °C. Peaks were identified based on relative heights and elution times compared to those measured on the GC-MS. GC run parameters were similar to those of the GC-MS. To calibrate isotope ratios, peaks of a CH\(_4\) reference gas (\( \delta^D = -151.9\%\)) were inserted throughout sample runs, including before, after, and in between sample peaks of interest. Repeat measurements of the PAIBE internal standard yielded an average \( \delta^D \) of \(-198.0 \pm 2.5\%\) (\( n = 64 \)). All \( \delta^D \) values are reported as permil deviations from the VSMOW isotopic standard. The \( H_2 \) factor correction was calibrated daily using an \( H_2 \) reference gas with known isotopic composition, following the method of Sessions et al. (2001). This correction and other data processing were done in the Isodat v2.5 software.

3.3. Numerical analysis

We reconstructed quantitative mean annual temperature (MAT) from fossil pollen samples using the transfer function developed by Wilmshurst et al. (2007), which employs the Modern Analogue Technique. This transfer function calibrates samples from a pre-settlement pollen database against modern climatic metrics. In terms of performance, the model has a bootstrapped coefficient of determination (\( R^2_{\text{boot}} \)) and root mean squared error of prediction (RMSEP) of 0.82 and 1.51 °C, respectively. We estimated summer temperatures from square-root transformed chironomid abundances using the weighted averaging partial least squares (WA-PLS) model from Dieffenbacher-Krall et al. (2007). This model has a \( R^2_{\text{boot}} \) of 0.80 and a RMSEP of 1.27 °C.

We used principal components analysis (PCA) to summarise major groupings in the biological proxy data. PCA is a robust exploratory technique that highlights major trends in the data. Pollen and chironomid counts were independently converted into percentages, and sample scores were calculated from the combined dataset. We only plotted taxa with contributions to principal component (PC) 1 and PC2 greater than a threshold, which corresponds to the expected value if contributions were uniform across taxa. Contributions were determined using the factoextra package (Kassambara and Mundt, 2017) in R v3.3.2 (R Core Team, 2016).

Finally, we illustrated the uncertainties of our reconstructions by resampling ages from Bacon-derived accumulation rate probability densities and resampling temperatures from normal probability densities with a mean equal to the reconstructed value and the model error equalling two standard deviations. Consequently, each chironomid and pollen estimate is represented by a cloud that can vary along the x- and y-axes. The percentage of overlap between clouds was estimated using the overlapping package (Pastore, 2018) in R v3.3.2 (R Core Team, 2016).

4. Results

4.1. Stratigraphy and chronology

The sediment core is 4.5 m long and consists of green-grey silt at the base, which grades into brown silty organic lake mud at 2.7 m and transitions to dark brown organic lake mud at 1.8 m. At least 70 individual tephra layers are preserved within the core, ranging from 1 to 12 mm in thickness and from fine ash to lapilli in grain size. Based on the age-depth model (Fig. 2), which was strictly developed from tephras, the lithological transition at 2.7 m corresponds to 16.6 cal kyr BP, occurring shortly after deposition of the Rerewhakaitu, whereas the transition at 1.8 m coincides with 11.4 cal kyr BP, roughly coeval with the onset of the Holocene. Sediment accumulation in the lake basin is relatively linear between 18 and 9 cal kyr BP, with an average of 1.7 cm per century (Fig. 2).

4.2. Environmental reconstructions

We focused on the time interval between 18 and 9 cal kyr BP to answer the two questions posed in the introduction: is there evidence of Holocene-like temperatures in the early LGIT? and were early Holocene summers cool? The PCA of the chironomid and pollen stratigraphies demonstrates clear groupings of samples younger than 11.4 cal kyr BP, samples older than 15.8 cal kyr BP, and a transitional cluster intermediate between the two (Fig. 3). These zones broadly link to the early deglacial and early Holocene, the time frames emphasised by our research questions.

The bioproxy records are complemented by hydrogen isotope ratios. GC/MS analyses revealed abundant \( n \)-alkanes from \( C_{21} \) to \( C_{33} \) with strong odd-over-even predominance (OEP ~3). Alkanes from \( C_{21} \) to \( C_{27} \) have concentration and \( \delta^D \) profiles that are distinct from those of \( C_{25} \) to \( C_{33} \). We attribute the former group to aquatic...
macrophytes, and their hydrogen isotopic compositions are thus difficult to interpret because the hydrologic balance of Lake Rangatauanui is not well understood over time. The aquatic macrophyte-derived n-alkanes are described in Appendix B but not considered here. The latter group (C₁₉ to C₃₃) is attributed to terrestrial leaf waxes and is discussed below in relation to the chironomid and pollen records.

4.2.1. Early deglacial (18—15.8 cal kyr BP)

Early deglacial samples plot to the top right quadrant of the PCA (Fig. 3), characterised by Fuscospora, Phythlocadus, Coprosma, Halocarpus, and Poaceae as the main pollen taxa (Fig. 4a). The abundance of these cool climate indicators for this locality wanes around 16.5 cal kyr BP. In the chironomid record, dominated throughout by Corynocera, the oldest assemblages include abundant cold-adapted taxa like Chironomus and the Marcropelopini tribe (Fig. 4b).

The mean annual and summer temperature reconstructions possess a low degree of overlap during the early part of the phase; however, this trend quickly devolves as summer temperatures approach modern values by 16.5 cal kyr BP, whereas mean annual temperatures remain low (Fig. 5e and f, 6). δDmax (from C₂₅ and C₃₃ n-alkanes) values are between −170 and −180‰ at the onset of the record, then sharply increase by >15% between 17 and 16 cal kyr BP (Fig. 5d). The timing and magnitude of this shift corresponds to changing terrestrial vegetation assemblages.

4.2.2. Early deglacial—Holocene transition (15.8—11.4 cal kyr BP)

This transitional phase predominately occupies the bottom half of the PCA (Fig. 3), demarking the switch from a Coprosma and Halocarpus montane shrubland to a podocarp forest with abundant Prumnopitys taxifolia and P. ferruginea (Fig. 4a), Corynocera, Polyplegium, and Ablabesmyia characterise the chironomid assemblage until 14.5 cal kyr BP, when cold-adapted taxa, like Tanytarsus funebris-types C and A and Chironomus, reappear (Fig. 4b).

Summer temperatures cool while mean annual temperatures warm between 15.8 and 12.9 cal kyr BP, whereas δDmax values plateau after a total early deglacial rise of >20‰ (Fig. 5d,e,f, 6). After 12.9 cal kyr BP, summer temperatures begin to warm while mean annual temperatures stabilise (Fig. 5e and f, 6).

4.2.3. Early Holocene (11.4—9.2 cal kyr BP)

Early Holocene samples occupy the top-left quadrant of the PCA (Fig. 3). P. taxifolia, P. ferruginea, and Podocarpus are replaced by Dacrydium cupressinum (Fig. 4a), whereas cold-adapted chironomid taxa are abundant, but nevertheless coexist with warm types like Naonella kimihia and Corynocera (Fig. 4b).

Summer temperatures cool during the early Holocene, while mean annual temperatures attain a maximum for the record (Fig. 5e and f, 6). Though data are limited, δDmax increases by ~10‰.

5. Discussion

5.1. Is there evidence for Holocene-like temperatures during the early deglacial?

A duelling narrative emerges from the bioproxies preserved at Lake Rangatauanui. Palynological evidence suggests climate amelioration began shortly after deposition of Rerewhakaaitu Tephra, 17.5 cal kyr BP, though conditions remained colder and drier than present. Other sites from the central North Island archive similar histories (McGlone and Topping, 1977), which in turn are echoed farther afield in Tasmania and some parts of Chile (Macphail, 1979; Colhoun et al., 1999; Moreno and Leon, 2003; Moreno, 2004). Likewise, Antarctic ice cores generally suggest a warming climate just prior to 17.5 kyr, but conditions were still cooler than today (EPICA Community Members, 2004; 2006; WAIS Divide Project Members, 2013) (Fig. 5a).

Chironomid-inferred temperatures, however, reveal Holocene-like conditions shortly after deposition of Rerewhakaaitu Tephra. The sole published chironomid reconstruction encompassing the late glacial in New Zealand, from Boundary Stream Tarn at 44°S (Vandergoes et al., 2008), exhibits summer temperatures that vary between modern and 2.4 °C cooler than modern. Importantly, there is no distinct warm interval shortly after 17.5 cal kyr BP at Boundary Stream Tarn. Across the Pacific in Chile, a chironomid reconstruction from Huelmo mire, 41°S, demonstrates a rapid 3 °C warming between 17 and 16 cal kyr BP (Massaferrro et al., 2014). Meanwhile in Mount Field National Park, at 42°S in Tasmania, chironomid-inferred temperatures are around modern at the inception of Eagle and Platypus tarns, roughly 16 cal kyr BP (Rees and Cwynar, 2010). These Chilian and Tasmanian records support the seasonally warm signal identified at Lake Rangatauanui, with peak summer temperatures around 16 kyr BP.

Turning to other proxies, direct dating and glacier modelling studies show that mountain glaciers on nearby Tongariro and Ruapehu volcanoes and both sides of the Southern Alps underwent considerable retreat between 18 and 15 kyr in response to a temperature increase of roughly 3—4 °C (Putnam et al., 2013; Eaves et al., 2016b, 2017, 2019; Barrell et al., 2019). For instance, Putnam et al. (2013) demonstrated rapid glacier retreat in the Rakaia Valley, South Island of New Zealand, based on beryllium surface-exposure ages; those authors argued for a 4.65 °C warming during the LIGT, 86% of which occurred between 17.84 and 15.6 kyr BP. Barrows et al. (2007a) described rapid postglacial warming evidenced from marine cores off the western and eastern coasts of the South Island of New Zealand, along with another core from the Indian Ocean. Temperatures inferred from foraminiferal
assemblages and alkenones in all cores revealed Holocene-like temperatures by 15 kyr. Along the southern coast of mainland Australia, De Deckker et al. (2012) linked warm and cold phases, inferred from planktonic foraminiferal assemblages, to the presence and absence of the Leeuwin Current (Fig. 5c), whose southern invasion depends on the position of the Subtropical Front (STF). Poleward retreat of the STF bathes southern Australia in the warm waters of the Leeuwin Current, coinciding with Northern Hemisphere cold events like the Younger Dryas and Heinrich Stadial 1.

The differing bioproxy response at Lake Rangatauanui prompts a critical question — why do the chironomid- and pollen-inferred temperatures so drastically diverge? Considering the biology of the organisms, the chironomid lifecycle is predominantly driven by summer temperature and degree days (Armitage et al., 1995). In the marine realm, the vast majority of foraminifera export occurs during spring blooms (King and Howard, 2001, 2003), while alkenone flux takes place in late spring to summer, often followed by another significant flux in late summer to autumn (King and Howard, 2001, 2003; Sikes et al., 2005, 2009). With respect to glacier retreat, variations in glacier length closely follow temperature during the ablation season, namely summer (Anderson and Mackintosh, 2006). Given these common drivers, it is unsurprising that the marine proxies and glacial records generally align with the chironomid-based temperature reconstruction at Lake Rangatauanui.

From this weight of evidence, it seems clear that forest growth at Lake Rangatauanui during the early LGIT was suppressed against a backdrop of dry conditions and overall warming temperatures. Terrestrial evidence north of 39°C (including loess and paleosol sequences (Birrell and Pullar, 1973), aggradation terraces and subsequent downcutting (Eden et al., 2001), along with palynology indicates rapid climate amelioration no more than 1000 years post Rerewhakaaitu Tephra deposition (17.5 cal kyr BP) (Newnham et al., 2003). At the same time, reduced rates of terrestrially-derived quartz are reported from marine sediments to the east of northern New Zealand (Stewart and Neall, 1984; Fenner et al., 1992; McGlone, 2001). These trends march southward throughout the LGIT, hinting at a latitudinally-modulated driver controlling succession into the Holocene.

The suppression of Holocene-type forest until 11.5 cal kyr BP at Lake Rangatauanui therefore likely relates to the position of the westerlies. An equatorward position of the westerlies during the early LGIT (Denton et al., 2021) and expanded polar vortex would have facilitated irregular outbreaks of dry cold air in winter and spring, having a devastating effect on tall trees (e.g., Bannister, 2003). Indeed, evidence from off the southeast shore of the North Island suggests the spread of podocarp-dominant forest occurred between 15 and 11 14C kyr BP, well after the rise in sea surface
temperature (SST) inferred from foraminiferal assemblages (McGlone, 2001). Rather than responding to the onset of warming, podocarp expansion coincided with an abrupt abatement of aero-

csol quartz influx and a decline in productivity at the site, hypothesised to correspond with a southward contraction of westerly windflow. The long-chain \( n \)-alkanes from Lake Rangatauanui, representing meteoric water uptake by local terrestrial vegetation, highlight gradual deuterium enrichment that culmi-

nates around 14.5 cal kyr BP (Fig. 5d). Based on the D/H isoscapes of precipitation around New Zealand (Ehtesham et al., 2013), rain-

water from a northerly moisture source, corresponding to south-

ward retreating westerlies, could explain the enrichment of deuterium in the leaf wax \( n \)-alkanes.

The temperature gradient between lower and higher latitudes would have diminished with rapid warming of the Southern Ocean from 18 kyr (Barrows et al., 2007a), both reducing the intensity of westerly wind circulation and triggering a poleward migration (Sime et al., 2013; Saunders et al., 2018). The Holocene-like temperatures inferred from the chironomid assemblages post-

Rerewhakaaitu Tephra suggest Lake Rangatauanui is located at a critical latitudinal and elevational threshold for the westerlies ca.

16 cal kyr BP, whereby destructive cold outbreaks and frosts pre-

cluded forest growth during winter and shoulder seasons, but se-

vere weather retreated south of the site during summer. This paradigm explains the co-existence of suppressed forest develop-

ment and a warm-adapted chironomid fauna. Regional insolation during the early deglacial would amplify the bioproxy response to this climatic con

figuration.

February (austral summer) insolation intensity at 39\(^\circ\)S is elevated though declining post-Rerewhakaaitu Tephra (17.5 cal kyr BP), while August (austral winter) insolation intensity is lowered but increasing (Fig. 5g). Given previously argued faunal adapta-

tions, one would predict chironomid-inferred temperatures to broadly follow February insolation. Further, the summer tempera-

ture reconstruction is consistent with terrestrial and marine

vegetation.
records from elsewhere in New Zealand and the Southern Hemisphere. Taking the chironomid reconstruction as true and using measurements from the nearby Ohakune meteorological station, contemporary February temperatures at 16.5 cal kyr BP coupled with mean annual temperatures 3.5 °C cooler imply August temperatures roughly 3 °C lower than present. August insolation at 16.5 cal kyr BP is close to modern (Fig. 5g), so the pollen reconstruction must be underestimating MAT. Cold, dry air masses infiltrating the central volcanic plateau, promoted by equatorward-positioned westerlies and an expanded polar vortex, provide a mechanism for underestimation. While local insolation has previously been proposed as an important driver during phases of some Southern Hemisphere proxy records (e.g., Vandergoes et al., 2005; Fogwill et al., 2015), a direct insolation-temperature relationship is likely too simplistic here, as evidenced by the late-glacial climate reversal at Lake Rangatauanui.

5.2. Expression of late-glacial climate reversal at Lake Rangatauanui

A range of evidence from New Zealand has been reported for a late-glacial temperature reversal broadly synchronous with the ACR (Putnam et al., 2010; Barrell et al., 2013; Lowe et al., 2013). For example, geomorphological evidence indicates one or more glacial readvances on nearby Mount Ruapehu between 14 and 11 cal kyr BP (Eaves et al., 2019). At Lake Rangatauanui, summer temperatures cool from 14.5 to a trough at 12.9 cal kyr BP, before rising to a peak at 11.7 cal kyr BP (Fig. 5e). Meanwhile, rising mean annual temperatures are interrupted by a plateau from ~14 to 11.5 cal kyr BP, broadly corresponding with the ACR. (Fig. 5f). Together, the trends in summer and mean annual temperatures produce a slight bulge in the percent overlap of the two profiles from about 14 to 13 cal kyr BP (Fig. 6) driven by cooling summer and stable, though still below modern, mean annual temperatures.

Following the ACR, the YD time frame marks an interruption of declining summer temperatures at Lake Rangatauanui (Fig. 5e), with a return to near modern values. Evidence from New Zealand’s terrestrial and marine realms generally characterise the period coincident with the YD by resumed warming (e.g., Turney et al., 2003; Barrows et al., 2007b; Kaplan et al., 2010); however chronological constraints can render timings of millennial-scale events equivocal.

The competing explanations for the muted signal in the vegetation record reflect the complexity of the LGIT and the indirect relationship between pollen and MAT. Clearly, neither proxy reconstruction perfectly matches records of possible causal mechanisms, like Antarctic warming (Fig. 5a) and rising CO2 (Fig. 5b), and nowhere is this more evident than during the late-glacial reversal. While there is robust evidence for cooling in New Zealand during the ACR (Putnam et al., 2010; Pedro et al., 2016), influence diminishes with increasing distance from the Southern Ocean (Newnham et al., 2012). At Lake Rangatauanui, summer temperatures decline at the onset of the ACR, only to rebound during the Younger Dryas (YD), evidently taking on an Antarctic imprint. On the other hand, mean annual temperatures peak partway through the ACR and decline into the YD, remaining low until the early Holocene. This pattern in the vegetation is consistent with other North Island records, which often archive a late-glacial signal that intersects the ACR and YD (Newnham and Lowe, 2000; Newnham et al., 2012).

Interestingly, elemental and n-alkane hydrogen isotope ratios from Lake Hayes, located in New Zealand’s South Island (45°S), suggest relative strengthening of the westerlies and increased southerly-sourced precipitation from 14.7 to 13.0 kyr, followed by drier conditions during the YD time frame (Hinojosa et al., 2019). Taken in tandem with Lake Rangatauanui’s δDmax record, these indicate the equatorward incursion of the SSW butes the South Island but did not impinge on the central North Island volcanic plateau. A transect of temperature and moisture-source proxy records that intersect the zone of westerly influence is required to properly deconvolve climate drivers during this dynamic interval.

5.3. Were early Holocene summers cool?

Early Holocene temperatures at Lake Rangatauanui continue the contrasting trend of insect and vegetation proxies. The recurrence of cold types, like Tanytarsus funebris and Chironomus, results in summer temperatures that are on average 2.2 °C cooler than present between 11.5 and 9 cal kyr BP, which are in excellent agreement with Southern Alps glacier records (Putnam et al., 2012; Doughty et al., 2017). Chironomid-inferred summer temperatures during the early Holocene were the coolest for the entire 14-cal-kyr-BP record at Lake Pupuke, Auckland (van den Bos et al., 2018), which accords with the two Tasmanian chironomid-based reconstructions (Rees and Cwynar, 2010). At Boundary Stream Tarn, summer temperatures subtly decrease after about 11.2 cal kyr BP (Vandergoes et al., 2008), whereas temperatures in Chile increase after the Huelmo-Mascardi Cold Reversal, between 12 and 11 cal kyr BP (Massaferro et al., 2014).

The expansion of Dacrydium cupressinum at Lake Rangatauanui around 11.5 cal kyr BP drives a rise in MAT to 1 °C below modern values. Again, the succession of vegetation during the early Holocene is consistent with local (McGlone and Topping, 1977; Horrocks and Ogden, 1998; Turney et al., 2003) and regional trends (Newnham and Lowe, 2000; McGlone et al., 2004; Vandergoes et al., 2005; Jara et al., 2015). A warmer-than-present early Holocene is evidenced from many New Zealand vegetation records (Wilmshurst et al., 2007); adjacent marine isotopic, faunal, and alkenone proxies (Phahne et al., 2003; Bostock et al., 2013); and speleothem analyses (Hellstrom et al., 1998; Williams et al., 2005; Lorrey et al., 2020).

Evidence from the marine realm east of New Zealand indicates that peak early Holocene warmth was restricted to areas south of the STF, resulting in a STF gradient of ~2 °C between marine cores MD97-2121 and MD97-2120 compared to the modern ~6 °C gradient – the southern South Ocean warmed faster than its northern counterpart (Prebble et al., 2017). The shallower gradient across the STF is consistent with weakened westerly winds during the early Holocene, a mode that is strongly reinforced by records from across the Southern Hemisphere (Moreno et al., 2010; Fletcher and Moreno, 2012; Rees et al., 2015; Jara et al., 2017; Hinojosa et al., 2019). Additionally, the more positive δDmax values support an increased influence of subtropical moisture, consistent with a reduction in westerly-carried, isotopically depleted southern sources. In the Tasman Sea to the west of New Zealand, the STF moved south with retreating westerlies around 11 kyr concurrent with a southward expansion of the East Australian Current (Bostock et al., 2006). This oceanic setting was coupled with low seasonality, and shorter summers and winters lengthened the growing season. In conjunction with a warmer Tasman Sea upwind, peak
atmospheric CO₂ concentration (Fig. 5b), and weakened westerly cir-
culation, the climate of the early Holocene was ideally con-
figured to trigger lowland forest expansion around Lake Rangatauanui. Despite compatible climate, forest was absent or reduced from current limits in some regions of New Zealand (Rogers and McGlone, 1989), and where forest was present, it was not higher in elevation than modern treeline (Ogden et al., 1997; McGlone and Bashier, 2012; Jara et al., 2015). Together with the presence of frost-
sensitive taxa like Ascarina lucida at Lake Rangatauanui and nearby Gibson’s Swamp (Horrocks and Ogden, 1998), winters must have been milder and summers cooler during the early Holocene. The co-
ocurrence of A. lucida, Dacrydium cupressinum, and tree ferns implies the North Island volcanic plateau was wet during the early Holocene. Combined with drier conditions in the east, like Hawkes Bay where lacustrine and peat sediments did not start accumu-
lating until 6.5 kyr (McGlone, 2002), and weakened westerly cir-
culation, overall rainfall must have been reduced by at least a third (McGlone and Wood, 2019).

Cooler summer temperatures fit well with the chironomid as-
essemblages though are harder to explain with respect to synoptic climate. One potential explanation invokes weakened and south-
wardly migrating westerlies during early Holocene summers, which would facilitate the incursion of easterlies moderated by cool ocean waters off the east coast of New Zealand’s North Island. An alternative explanation is that chironomid fauna primarily responded to regional insolation, modulated by Earth system feedbacks — an assertion that is supported by the general corre-
spondence between trends in local summer insolation/energy and temperature at Lake Rangatauanui (Fig. 5).

6. Synthesis and conclusions

Temperatures inferred from the LGIT chironomid and pollen assemblages at Lake Rangatauanui present duelling narratives that are best understood as complementary proxy-specific responses. To answer the questions posed in the introduction, the LGIT pos-
sesses Holocene-like summers by 17 cal kyr BP, though mean annual temperatures remain suppressed due to severe colds during winter and spring seasons; the opposite temperature trend is true for the early Holocene. Interestingly, the independently derived smoothed summer and mean annual temperature reconstructions are conspicuously anti-phased.

Summer temperatures are near or above modern values by 17 cal kyr BP, decrease at the onset of the ACR, resurge during the YD, and finally cool to a record minimum during the early Holocene. This trend can neither be explained by a template that in-
vokes latitudinally shifting zonal layers nor the hemispheric redistribution of heat implicit to the bipolar seesaw. Indeed, the overall trend in chironomid-inferred temperatures broadly matches regional summer insolation. However, there is an Ant-
artic imprint during the ACR and YD, so if the faunal community is primarily driven by insolation, the relationship is not a simple one. More records need to be developed across a latitudinal transect of the Southern Hemispheres to interrogate these signals.

The same argument could be made for Lake Rangatauanui’s vegetation community, namely that winter insolation, with some Antarctic modulation, governs reforestation during the LGIT. Considering the evidence from other New Zealand pollen records, however, it seems more likely that vegetation is latitudinally controlled by the westerly winds and associated storm track. Reforestation by lowland podocarps occurs in northern sites contemporaneously with the deposition of Rerewhakaitu Tephra (17.5 cal kyr BP) and only at or after the onset of the Holocene in southern South Island locations. At Lake Rangatauanui, Southern Ocean influences submit to subtropical counterparts, based on δDwax — a trend that aligns with the CO₂ from the Antarctic ice cores.

This study highlights the power of a multi-proxy approach and the importance of interpreting biological proxy-based reconstructions with ecological preferences. Hopefully, these types of data can be expanded to cover latitudinal transects and better feed into data assimilation projects, which fine-tune climate model simulations with paleoecological observations.

Author’s statement

All authors have made substantial contributions to this submission entitled, “Duelling narratives of chironomids and pollen explain climate enigmas during The Last Glacial-Interglacial tran-
sition”. All authors have approved the final version of the manu-
script. Detailed contributions follow: Andrew Rees: Conceptualisation, Methodology, Formal analysis, Investigation, Writing — original draft, Writing — review & editing, Visualisation, Funding acquisition; Katherine Holt: Conceptualisation, Methodology, Formal analysis, Investigation, Writing — original draft, Writing — review & editing, Visualisation; Katherine Holt: Conceptualisation, Methodology, Formal analysis, Investigation, Writing — original draft, Writing — review & editing, Visualisation, Funding acquisition; Jessica Hinojosa: Conceptualisation, Methodology, Formal analysis, Investigation, Writing — original draft, Writing — review & editing, Visualisation, Funding acquisition; Rewi Newnham: Conceptualisation, Writing — original draft, Writing — review & editing, Supervision; Shaun Eaves: Conceptualisation, Writing — original draft, Writing — review & editing; Marcus Vandergoes: Conceptualisation, Methodology, Writing — review & editing, Resources; Alex Sessions: Methodology, Writing — review & editing, Resources; Janet Wilmshurst: Methodology, Writing — review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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script. This work was funded by the Massey University Research Fund (MURF) and NZ Natural Hazards Research Platform through the “Learning to Live with Volcanic Risk” programme.
Appendix A. Radiocarbon dating

Limited chronological constraints during the early deglacial at Lake Rangatauanui prompted sieving for radiocarbon targets from core 1 — the core used for tephrochronology. Due to a lack of terrestrial macrofossils, we defaulted to bulk sediment dating (Table A-1). Bulk sediment is notoriously unreliable because various fractions are affected by different reservoirs. We nevertheless developed and age-depth model including the radiocarbon dates (Fig. A-1). Critically, calibrated radiocarbon ages between 300 and 230 cm imply a nearly instantaneous deposition of 70 cm of sediment. Neither the tephrochronology nor the stratigraphy supports such a rapidly deposited event. Further, the reversal at 300 cm conflicts with a robust anchor represented by the Rerewhakaaitu Tephra, which was identified by distinctive geochemistry and is coherent with the tephra-based age-depth model and palynological signature. Given that half of the radiocarbon dates are spurious, we decided to remove all from the final chronology.

Appendix B. Alkane analyses

The hydrocarbon fraction of solvent extracts contained a range of mid-to long-chain n-alkanes from C21 to C33 (Fig. B-1). Concentrations were measured via FID by comparison to an internal standard (palmitic acid isobutyl ester) and ranged from 1 to 25 µg/g dry weight (Fig B-2) with a moderate odd-over-even predominance (OEP = –3). We find no evidence for any significant contamination of lake sediments by petroleum hydrocarbons. C21 and C23 n-alkanes were too low in abundance to measure in every sample and are not considered here. Due to the presence of low amounts of alkanes and other compounds that potentially coelute with the analytes of interest, extracts were further purified via silver-ion SPE yielding very clean n-alkane fractions (Fig B-1).

The C23, C25, and C27 n-alkanes exhibited similar concentration patterns, being highest in the bottom half of our core and lowest in the top half (blue colours in Fig B-3). Values of δD for these compounds were also similar, being most enriched (~120 to ~140‰) at the base of the core and decreasing monotonically to values of ~160 to ~170‰ at 40 cm depth (Fig B-4). δ2H values for C23 then return to higher values in the top 30 cm of the core, while those for C25 and C27 remain low. Mid-chain n-alkanes (i.e., C23 and C25) are commonly attributed to aquatic macrophyte plants and algae (Ficken et al., 2000; Sachse et al., 2004). Although n-C27 is often attributed to terrestrial leaf waxes, in this setting we infer an aquatic source similar to C23 and C25 based on the similarity of concentration and isotopic profiles. The δD values of these compounds should reflect those of lake water (Sauer et al., 2001; Gao et al., 2011); however, the hydrologic balance of Lake Rangatauanui is not well understood through time. With no inlets or outlets, supply is entirely via groundwater, and while some evaporative enrichment must occur, we have no means to quantify this even in the present state, much less over the last 20,000 years. Consequently, we do not attempt to interpret these data, although future insight into the hydrologic history of Lake Rangatauanui might enable such a use.

The C29, C31, and C33 n-alkanes exhibit a distinctly different pattern of abundance, being high but variable throughout the core, with low concentrations across the bottom ~80 cm (Fig B-2). Isotopic compositions are also distinct from the previous group across the lower ~150 cm. Based on these differences, we attribute the long-chain n-alkanes to terrestrial leaf waxes in the Lake Rangatauanui watershed and discuss the significance of their isotopic compositions in the main text.

![Fig. A-1. Age-depth model derived from eight rhyolitic and one andesitic tephras and four radiocarbon dates (Table A-1). The model was developed using Bacon (Blaauw and Christen, 2011) and radiocarbon dates were calibrated with SHCal20 (Hogg et al., 2020). The greyscale represents the 95% confidence intervals of the calibrated ages, while the dotted red line represents the weighted mean ages across the horizons sampled for proxy analysis. Notably, inclusion of radiocarbon implies a nearly instantaneous 70-cm sediment deposit, which is neither corroborated by the tephrochronology nor stratigraphy.](image)

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<th>Sample</th>
<th>Description</th>
<th>¹⁴C age (yr BP)</th>
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<th>95% C.I. (min)</th>
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<td>11,268 12,202</td>
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<td>13,708 ± 65</td>
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<td>18,160 ± 100</td>
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Fig. B-2. Concentrations of \( \text{n-alkanes} \) (\( \mu \text{g/g} \) dry weight) extracted from lake sediments as a function of depth. \( \text{C}_{23} \) to \( \text{C}_{27} \) \( \text{n-alkanes} \) are interpreted as deriving from aquatic plants (or mixed sources) and are plotted in shades of blue; \( \text{C}_{29} \) to \( \text{C}_{33} \) \( \text{n-alkanes} \) are likely derived from terrestrial leaf waxes and are coloured green. 150 cm depth corresponds to ~10 kyr.

Fig. B-3. Relative concentrations of \( \text{n-alkanes} \) as a function of depth. 150 cm depth corresponds to ~10 kyr.

Fig. B-4. \( \text{n-alkane} \) \( \delta D \) values as a function of depth. Error bars represent 1\( \sigma \) standard deviation of replicate analyses. 150 cm depth corresponds to ~10 kyr.

Fig. B-1. GC/MS total ion chromatograms of a typical hydrocarbon fraction (F1) of solvent-extractable lipids from sample 5a. Panel A is prior to silver-ion SPE clean-up, whereas panel B is after. \( \text{n-alkanes} \) are marked by their carbon numbers; IS is the internal standard (palmitic acid isobutyl ester).

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