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The indirect response of an aquatic ecosystem to long-term climate-driven terrestrial vegetation in a subalpine temperate lake.

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Abstract:

Aim- To assess whether climate directly influences aquatic ecosystem dynamics in the temperate landscape of Tasmania or whether the effects of long-term climatic change are mediated through the terrestrial environment (indirect climate influence).

Location- Paddy's Lake is located at 1065 m asl in temperate north-west Tasmania, a continental island south-east of mainland Australia (41°15-43°25'S; 145°00-148°15'E).

Methods- We developed a new 13,400 year (13.4 kyr) palaeoecological dataset of lake sediment subfossil cladocerans (aquatic grazers), bulk organic sediment carbon (C%) and nitrogen (N%) and δ^{13}C and δ^{15}N stable isotopes. Comparison of this new data was made with a recently published pollen, geochemistry and charcoal records from Paddy's Lake.

Results- Low cladoceran diversity at Paddy's Lake is consistent with other temperate Southern Hemisphere lakes. The bulk sediment δ^{15}N values demonstrate a significant lagged negative response to pollen accumulation rate (pollen AR). Compositional shifts of dominant cladoceran taxa (*Bosmina meridionalis* and *Alona guttata*) occur following changes in both pollen AR and pollen (vegetation) composition throughout the 13.4 kyr record at Paddy's Lake. The δ^{15}N values demonstrate a significant positive lagged relationship to the oligotrophic:eutrophic cladoceran ratio.

Main conclusions- Long-term changes in cladoceran composition lag changes in both pollen AR and terrestrial vegetation composition. We interpret pollen AR as reflecting climate-driven changes in terrestrial vegetation productivity and conclude that climate-driven shifts in vegetation are the principal driver of the cladoceran community during the last ca. 13.4 kyrs. The significant negative lagged relationship between pollen AR and δ^{15}N reflects the primary control of vegetation productivity over within-lake nutrient status. Thus, we conclude that the effects of long-term climate change on aquatic ecosystem dynamics at our site are indirect and mediated by the terrestrial environment. Vegetation productivity controls organic soil development and has a direct influence over lake trophic status via changes in the delivery of terrestrial organic matter into the lake.

Keywords: carbon and nitrogen**,** climate change, cladocerans, Late Quaternary, long-term fire, nutrient dynamics, Tasmania, terrestrial-aquatic ecosystems

Introduction

Aquatic ecosystems are known to respond both 'directly' and 'indirectly' to climatic change (Battarbee, 2000; Ball *et al.*, 2010). 'Direct' aquatic ecosystem responses to climate change are principally influenced by changes in temperature and lake level on aquatic environments (Schindler, 1997; Smol & Cumming, 2000; Gell *et al.*, 2005), while 'indirect' responses include those that are mediated through the surrounding terrestrial environment via, for example, vegetation change that alters nutrient inputs and pH of watersheds (Huvane & Whitehead, 1996; Korsman & Segerstrom, 1998; Lancashire *et al.*, 2002; Augustinus *et al.*, 2008; Wang *et al.*, 2016). Despite the importance of climate in driving terrestrial ecosystem dynamics, and the clear relationship between terrestrial and aquatic ecosystems (Huvane & Whitehead, 1996; Korsman & Segerstrom, 1998; Engstrom *et al.*, 2000; Augustinus *et al.*, 2008), most research into long-term aquatic ecosystem change focusses on the 'direct' role of climate in driving aquatic ecosystem dynamics. Understanding how and when climate affects aquatic systems through both direct and indirect pathways is important if we are to understand how these systems will respond to the rapid climatic changes the Earth is currently experiencing. To address this knowledge gap, we use multi-proxy palaeoecological data to assess the relationship between climatic change and long-term terrestrial and aquatic ecosystem dynamics in a temperate subalpine lake in Tasmania, Australia.

Direct aquatic ecosystem responses to climate change include changes to water temperature (Schindler et al., 1996; Schindler, 1997, 2001), salinity/lake depth (Gasse et al., 1997; Smol & Cumming, 2000b; Saunders et al., 2007; Tibby et al., 2007; Gell et al., 2012) and water chemistry (Schindler, 2001). Direct responses result in aquatic ecosystem changes that are either synchronous with (Prebble *et al.*, 2005), or independent of (Tibby *et al.*, 2012), changes in the terrestrial environment. In contrast, indirect aquatic ecosystem responses to climate that are mediated through the terrestrial environment are characterised by a lagged response of the aquatic environment to terrestrial change (Fritz *et al.*, 2004; Heggen *et al.*, 2010). Indirect effects of climate change include changes in the type and amount of terrestrial material entering an aquatic system (via erosion and/or vegetation productivity changes), which can alter critical factors such as pH (Whitehead *et al.*, 1989; Pienitz *et al.*, 1999), mixing/turbidity (Lotter, 2001; Augustinus *et al.*, 2012) and the trophic status of water bodies (Engstrom *et al.*, 2000; Heggen *et al.*, 2010; Fritz & Anderson, 2013).

In the cool high rainfall environment of western Tasmania, a combination of low temperatures, high humidity and extreme bedrock oligotrophy have resulted in a landscape blanketed in acid peats (Brown *et al.*, 1982; Jarman *et al.*, 1982; Bowman *et al.*, 1986). As a result, waterbodies in this landscape are uniformly dystrophic, with nutrient inputs largely derived from the acid peat soils (Tyler, 1974, 1992; Vanhoutte *et al.*, 2004). Indeed, the bedrock is so unyielding that the ionic composition of many lakes is identical to sea water (i.e. nearly no input from bedrock sources) (Buckney & Tyler, 1973) and soil development is almost entirely dependent on the extant vegetation (Jackson, 1968; Wood & Bowman, 2012). Despite the tight coupling between vegetation, peat development and water chemistry, there is a dearth of information about how terrestrial ecosystem change influences aquatic ecosystem dynamics in this landscape (Bradbury, 1986). This knowledge gap is critical, as terrestrial systems in western Tasmania are currently experiencing unprecedented changes in response to anthropogenic climate change that are principally manifest as a reduction in rainfall and a concomitant increase in fire activity (McWethy *et al.*, 2013; Fox-Hughes *et al.*, 2014; Mariani & Fletcher, 2016).

Here, we attempt to assess the relationship between long-term climatic change and changes in both aquatic and terrestrial ecosystems in a subalpine temperate environment in Tasmania, Australia. Given the tight coupling between vegetation, peat and water chemistry evident today, we hypothesise that the response of aquatic ecosystems to long-term climatic change in this landscape will be mediated by the terrestrial environment: i.e. 'indirect' response pathways. Further, we hypothesise that the principal pathway for mediation of climate signals through the terrestrial environment will be via vegetation-driven changes of nutrient inputs into the lake. To assess these hypotheses, we developed a new long-term (13,400 year; 13.4 kyr) multi-proxy lake sediment dataset of subfossil cladocerans (as a proxy for aquatic ecosystem dynamics), and organic carbon (elemental and $\delta^{13}C$) and nitrogen (elemental and $\delta^{15}N$) content. We compare our record to an existing record of pollen, charcoal and geochemistry from the same sediment sequence that shows clear climate-driven vegetation dynamics over the last ca. 14.6 kyrs (Beck *et al.*, 2017). To assess our hypotheses, we propose that 'indirect' climate-driven changes in aquatic ecosystem dynamics and nutrient cycling will be mediated by the terrestrial environment and, thus, will lag changes in the terrestrial system; while 'direct' climate-driven aquatic ecosystem dynamics and nutrient cycling will either precede, occur synchronously with, or be independent of changes in the terrestrial system.

Geographical setting of Tasmania

Tasmania is a continental island with a cool temperate maritime climate (Gentilli, 1971) bisected by north-west—south-east mountain ranges that result in a steep gradient of westerly derived precipitation from 3500 mm p/a west of the ranges to 400 mm p/a in the east (http://www.bom.gov.au/). These ranges create a clear division in the geography of Tasmania manifest as a stark east-west contrast in geology, climate and ecology. Acidic organosols (peat), rain forests and fresh oligotrophic to dystrophic lakes prevail over much of the west, lakes in the east are less acidic, (ultra)oligotrophic, turbid and more saline (Tyler, 1974, 1992; Vanhoutte *et al.*, 2004). The zone of transition between the eastern and western provinces is often referred to as Tyler's line (Figure 1). The rain forests of the Tasmania's west share remarkable taxonomic and physiologic similarities with the temperate rain forests in New Zealand and Chile, the so-called Gondwanan forests that are now restricted to tiny fire refugia in Tasmania (Wood & Murphy, 2011). Fires have decimated rain forest across all these southern regions (Veblen & Ashton, 1982; McGlone, 1989), with more than 30% of Tasmanian subalpine rain forest lost to fire over the last two centuries (Holz *et al.*, 2015).

Cladocerans of subalpine temperate Australasia

Cladocerans are aquatic zooplankton that are an excellent proxy for changes in water temperature, lake level, water quality, trophic status of lakes and food web dynamics (Hofmann, 1998; Lotter *et al.*, 1998; Kamenik *et al.*, 2007; Kattel & Augustinus, 2010; Kattel *et al.*, 2015). In south-east Australia and New Zealand, important taxa include: *Alona guttata* (Sars, 1862), *Alonella excisa* (Fischer, 1854), *Bosmina meridionalis* (Sars, 1904) and *Chydorus sphaericus* (O.F. Müller, 1785) (Green, 1976; Geddes, 1988; Kattel & Augustinus, 2010; Augustinus *et al.*, 2012; Kattel *et al.*, 2015). *Alona guttata* is a cosmopolitan littoral taxon that is reported to be an indicator of wetland hydrology changes and nutrient status (Kattel & Augustinus, 2010; Kattel *et al.*, 2015), as well as, warm climatic conditions (Frey, 1991b; Lotter *et al.*, 2000; Kattel & Augustinus, 2010). *Bosmina meridionalis*, a pelagic cladoceran, is endemic to Australia and New Zealand and is an indicator of relatively clear water and oligotrophic conditions (Green, 1976; Geddes, 1988). *Chydorus sphaericus* is a eurytopic taxa, found in both littoral and pelagic habitats, showing responses to nutrient enriched environments (Frey, 1980; Lotter *et al.*, 1998; Kattel & Augustinus, 2010).

Site description

Paddy’s Lake (41°27’04” S, 145°57’41” E) is a cirque lake situated at ca. 1065 m asl on the Black Bluff massif in north-west Tasmania, Australia (Figure 1). The lake is acidic and dystrophic; with one small, out-flow to the north and a maximum depth of 21.5 m. The local geology is nutrient poor – consisting of quartz dominated Quaternary glacial deposits and conglomerate, with minor surface expressions of slightly more fertile Cambrian volcanics (Seymour & Calver, 1995; Pemberton & McKibben, 2004). Average monthly temperature ranges from ~4.6-14°C, with an annual average of ~12.3°C (Bureau of Meteorology, 2016b, a; Beck *et al.*, 2017). The local vegetation is classified as subalpine heathland (Harris & Kitchener, 2005), with the broader region composed of a complex mosaic of rain forest, *Eucalyptus*-dominant forest, scrub and open communities that reflects a long history of burning (Jackson, 1968; Fletcher & Thomas, 2010).

Materials and Methods

Core collection and chronology

An entire sediment sequence of 291 cm was developed using radiocarbon dating, charcoal and geochemistry from two cores (TAS1401 SC1 and TAS1401 N1) (Beck *et al.*, 2017) retrieved with a Bolivia coring system (a modified Livingstone system; Wright, 1967), and a Nesje coring system (Nesje, 1992). The core chronology was developed using 19 radiocarbon dates calibrated with the Southern Hemisphere calibration curve - SHCal13 (Hogg *et al.*, 2013) (Table 1 in Supporting Information). The age-depth model was produced in R 3.1.1 (R Development Core Team, 2014) using a smooth spline regression with a smoothing factor of 0.5 in the 'clam' 2.2 package (Blaauw, 2010). Full details are in Beck *et al.* (2017).

Cladoceran analysis

Processing for cladocerans followed standard methods (Korhola & Rautio 2001) at a resolution of 1-4 cm (ca. 60-350 yrs). Concentration values were determined using an exotic pollen spike (*Lycopodium* spp.) (sensu Faegri & Iversen, 1989). A total of 100 cladoceran individuals were identified at 100-400X magnification (Kattel and Augustinus 2010). Identification was based on the following resources: Alonso, 1996; Brehm, 1953; Frey, 1991ab; Shiel and Dickson, 1995; Shiel, 1995; Smirnov and Timms 1983;   and Szeroczyńska and Sarmaja-Korjonen, 2007. The oligotrophic:eutrophic ratio was calculated between *Bosmina meridionalis* (oligotrophic) and *Alona guttata* and *Chydorus sphaericus* (eutrophic).

Geochemistry

Organic carbon (C%), nitrogen (N%), δ^{13}C and δ^{15}N were analysed at Australian Nuclear Science and Technology Organisation (ANSTO) at a resolution of 2-4cm (ca. 50-530 yrs) using an Elementar VarioMICRO Elemental Analyser (C% and N%) and an Isotope Ratio Mass Spectrometer (δ^{13}C and δ^{15}N) with a CO_2 trap (NaOH). An absence of carbonates was determined throughout the sequence by testing with HCl. The δ^{13}C results were normalised to an IAEA C8 reference (Le Clercq *et al.*, 1998) and δ^{15}N to IAEA N-2 (Böhlke & Coplen, 1995) and USGS-25 (Böhlke & Coplen, 1995) normalisation references. Values for C% and N% were normalised to 'High Organic Sediment Standard OAS'. Normalised XRF Bromine (Br) data from Paddy's Lake is presented here from published data to demonstrate trends in organic matter (Beck *et al.*, 2017).

Pollen and charcoal analysis

Pollen and *Botryococcus* spp. accumulation rates (AR) were calculated from the existing Paddy's Lake pollen data (Beck *et al.*, 2017). Here, we use the pollen AR to track changes in vegetation biomass, consistent with data linking pollen influx and plant biomass (Sugita *et al.*, 2010; Matthias & Giesecke, 2014). Background charcoal (particles cm^{-2} yr^{-1}) was calculated with CharAnalysis (Higuera, 2009) from Beck et al. 2017 and used as an indicator for local and regional drying. For further pollen and charcoal analysis methods see Beck *et al.* 2017.

Numerical analyses

Detrended correspondence analysis (DCA) and cluster analysis

DCA was performed using the 'vegan' 2.4-4 package (Oksanen *et al.*, 2016) in R on square root transformed cladoceran percentage data with down-weighted rare taxa. Zonation was determined using CONISS cluster analysis (Grimm, 1987) in TILIA 2.0.37 (Grimm, 2013). Zone significance was determined using a broken stick model in R using 'rioja' 0.9-15 (Juggins, 2016). Pollen ordination results (pollen DCA axis 2) from Beck *et al.* 2017 were used to demonstrate the secondary vegetation composition changes on the landscape; primary shifts in the vegetation are dictated by the glacial-interglacial transition period (Beck *et al.*, 2017).

Cross Correlation

Cross correlation analysis was performed on 400 year bins of the following data: cladoceran DCA axis 1, cladoceran oligotrophic:eutrophic ratio, bulk sediment δ^{15}N, pollen DCA axis 2 and pollen AR to assess the significance of temporal relationships in the time series data (Green, 1981). Binning is an alternative to interpolation, where data are averaged within a selected age interval to create even time steps without creating non-existent trends (Carstensen *et al.*, 2013; Seddon *et al.*, 2014). Data was first binned using R script written by Seddon *et al.* 2014 then transformed with the standardized method in R using 'analogue' 0.17-0 (Simpson & Oksanen, 2016) to remove any non-stationarity, a violation of cross correlation requirements (Horvatic *et al.*, 2011). Cross correlation was run with four lags of 400 years in R.

Results

Chronology

Radiocarbon results are accessible in Supporting Information, with full details in Beck *et al.* (2017). An age-offset estimate of 223.5 yrs was applied to all samples in the age-depth model and two dates (200 cm and 225 cm) were out of stratigraphic sequence and identified as outliers (Figure 2) (see Beck *et al.*, 2017).

Cladoceran analysis

A total of 13 cladoceran taxa were identified throughout the Paddy's Lake record. Cladoceran diversity was very low; however, not abnormal for a Tasmanian alpine lake (pers. comm. A. Kotov & R. Shiel). Seven significant CONISS zones were produced and Table 1 lists the taxonomic trends in each zone.

Geochemistry

All C%, N%, δ^{13}C, and δ^{15}N results are the mean of replicate analyses, the standard deviation of the replicates are ≤± 0.3 for all δ^{13}C and ≤ ± 0.4 for all δ^{15}N results. These organic geochemical indicators show a distinct shift at ca. 13.4 ka (Figure 4). C%, N% and C/N are extremely low prior to ca. 13.4 ka followed by an increasing trend ca. to maximum values by ca. 8 ka with relatively stable trends to present. High values of δ^{13}C occur prior to ca. 13.4 ka (maximum=-23.5 ‰) then decline to persistently low values. High δ^{15}N values (~2 ‰) occur prior to ca. 13.4 ka, then decline at ca. 13 ka and ca. 12 ka. δ^{15}N values peak at ca. 8.5 ka (~2.2 ‰) and ca. 6 ka (~2.3 ‰), a rise at ca. 2.5 ka is followed by stable values until present (Figure 4h&5e). Trends in XRF Br demonstrate very low values before ca. 13.4 ka, followed by a sharp increase to ca. 12 ka then decline to ca. 11 ka. From ca. 11 to 8 ka Br increases with a declining trend from ca. 8.5 to 6 ka. At ca. 6 ka values drop with a stable trend until present (Figure 4h&5a).

Pollen and charcoal analysis

Grass and herb pollen and woody plant percent pollen show opposite trends of high (low) values before ca. 13.3 ka, then a shift to decreasing (increasing) abundance for the remainder of the record (Figure 4g&f). The pollen AR increases from ca. 13.3 to 12.3 ka, ca. 6 to 4.5 ka, and ca. 3 ka to present. From ca. 9 to 6 ka high variability in pollen AR occurs (Figure 5h). Background charcoal remains relatively low from ca. 13.4 to 6 ka, followed by an increase to a maximum at ca. 4.3 ka. Values decline at ca. 4.3 ka with two more increasing trends at ca. 3 ka and 2 ka.

Numerical analyses

Detrended correspondence analysis

Trends in the cladoceran DCA axis 1 scores (explained variance=25.1%) follow changes in the pelagic taxa *Bosmina meridionalis* (Figure 3&5e). DCA axis 2 (explained variance=14.3%) shows high stability throughout the entire record with high values from ca. 9.1 to 6.4 ka. The DCA biplot can be found in Figure 1 of the Supporting Information. The pollen DCA axis 2 scores follow opposing trends to the pollen AR from ca. 13.4 to 6 ka with an increasing trend from ca. 6 ka to present.

Cross correlation

Pollen AR has a positive correlation with $\delta^{15}N$ (-1600 to 400 yr lag). A negative response in $\delta^{15}N$ occurs prior to an increase in pollen accumulation. Cladoceran DCA axis 1 shows a positive response with pollen composition (Pollen DCA axis 2) prior to increase in cladoceran DCA 1 (-400 to 1600 yr lag). The oligotrophic:eutrophic cladoceran ratio show a positive correlation with $\delta^{15}N$ (400 to 1200 yr lag) (Figure 6).

Discussion

Vegetation change and lake nutrient dynamics

We observe a significant negative lagged relationship between pollen AR and the $\delta^{15}N$ content of organic matter within Paddy's Lake throughout the last ca. 13.4 kyrs (Figure 6a). A linear relationship between pollen ARs and plant biomass has been shown in temperate systems in the Northern Hemisphere (Sugita *et al.*, 2010; Matthias & Giesecke, 2014), and anecdotal evidence suggests that this relationship occurs in subalpine Tasmanian ecosystems (Fletcher *et al.*, 2014). We interpret the negative lagged relationship between pollen AR and $\delta^{15}N$ as reflecting increased input of terrestrially derived ^{14}N into the lake as terrestrial vegetation productivity increases. When available ^{14}N stocks are high, aquatic organisms discriminate against ^{15}N, resulting in organic matter low in $\delta^{15}N$. Once vegetation productivity decreases (reduced pollen AR), available ^{14}N decreases and aquatic organisms are forced to use ^{15}N – classic Rayleigh Distillation (Talbot & Johannessen, 1992; Talbot, 2001) – resulting in an increase in organic matter $\delta^{15}N$ values.

While the negative lagged relationship between pollen AR and $\delta^{15}N$ is significant over the entire ca. 13.4 kyr sequence, we observe an apparent decoupling of these variables after ca 3.4 ka (Figure 5f&h). This decoupling is manifest as persistently high $\delta^{15}N$ values (Figure 5f) despite an increase in pollen AR (Figure 5h). We note that this decoupling is coeval with the establishment of both sclerophyll-dominant vegetation around the lake (Figure 5b) and a marked increase in the colonial algae *Botryococcus* spp. (Figure 5c). *Botryococcus* spp., likely *Botryococcus braunii* (Kütz.), [$\delta^{15}N$

signature of 4-7 **‰** (Heyng *et al.*, 2012)] is an algae common in oligotrophic waters that prefers shallow littoral environments (Aaronson *et al.*, 1983; Clausing, 1999). We interpret this shift as reflecting increased nutrient consumption by *Botryococcus* spp. that depleted ^{14}N stocks within the lake. The shift toward sclerophyll-dominant vegetation was driven by successive fires beginning at ca. 6.3 ka (Beck *et al.*, 2017). Elsewhere, similar fire-driven vegetation shifts from pyrophobic rain forest communities to pyrophytic sclerophyll associations are marked by changes in both carbon and nitrogen content of lake sediment organic matter (Fletcher *et al.*, 2014). Sclerophylly is an adaptation to nutrient deficiency (Beadle, 1966, 1968) and the nutrient content of soils under sclerophyllous vegetation in Tasmania is lower than under rain forest vegetation (Jackson, 1968; Orians & Milewski, 2007; Wood *et al.*, 2011). It is possible, then, that the invasion of the catchment by sclerophyllous plant taxa lowered the nutrient status of the catchment organosols (Br and C/N; Figure 4c&h), lowering the available nutrient pool within the lake and favouring the increase in *Botryococcus* spp.. The combination of reduced terrestrial nutrient input and increased aquatic nutrient demand would, thus, result in a rapid consumption of ^{14}N stocks, forcing aquatic organisms to use ^{15}N and, thus, increasing the δ^{15}N value of deposited organic matter.

Vegetation change and aquatic ecosystem dynamics

Our results reveal a significant relationship between terrestrial vegetation and aquatic ecosystem (cladoceran) change throughout the last ca. 13.4 kyrs at Paddy's Lake (Figure 6b). Importantly, shifts in terrestrial vegetation precede changes in cladoceran community composition, reflecting a clear link between terrestrial and aquatic ecosystem change through time. Long-term vegetation change at Paddy's Lake inferred from pollen data closely tracks long-term shifts in regional hydroclimate identified from raft of local and regional palaeoecological and palaeoclimatic data (Macphail, 1979; Markgraf *et al.*, 1986; Fletcher & Moreno, 2012; Fletcher *et al.*, 2014; Stahle *et al.*, 2016; Beck *et al.*, 2017). Our results confirm that the influence of climate-driven changes in vegetation (composition and productivity) over nutrient delivery into the lake supersedes any direct influence of climatic change over aquatic ecosystem dynamics in this lake system. We, thus, tentatively accept our hypothesis that long-term aquatic ecosystem dynamics respond indirectly to climatic change in this landscape via changes in the terrestrial environment.

Whilst changes in hydroclimate could be expected to drive changes in lake level and a concomitant change in pelagic taxa (e.g. *B. meridionalis*)(Korhola *et al.*, 2000; Kattel & Augustinus, 2010), we find no consistency between regional hydroclimatic trends and changes in pelagic cladoceran taxa at Paddy's Lake (Figure 3). Critically, we do observe a significant lagged relationship between δ^{15}N and the oligotrophic:eutrophic cladoceran ratio through the last ca. 13.4 kyrs, indicating that changes in cladoceran composition at Paddy's Lake clearly tracks lake trophic status (oligotrophic:eutrophic ratio). Increases in the abundance of cladocerans usually classed as 'littoral' (Kattel & Augustinus, 2010) reflect characteristic of cosmopolitan communities (*A. guttata* and *C. sphaericus*: low DCA axis 1 values) preferring a wide gradient of trophic status (mesotrophic to eutrophic) in lakes (Kattel & Augustinus, 2010) (Figure 5e&g). Increases in pollen AR and pollen compositional change (pollen DCA axis 2) at Paddy's Lake occur during phases of elevated relative moisture, low regional fire activity and an increase in regional forest cover (Fletcher & Moreno, 2012; Stahle *et al.*, 2016; Beck *et al.*, 2017; Mariani *et al.*, 2017). These shifts in pollen AR and pollen DCA axis 2 are simultaneous with decreasing organic δ^{15}N values and an increase in the important occurrence of littoral cladocerans within the lake (Figure 5f&g).

In contrast, 'pelagic' cladocerans (e.g. *B. meridionalis*) at Paddy's Lake favour oligotrophic lake conditions (Green, 1976; Geddes, 1988) and increases in these taxa occur during phases of low relative moisture, reduced regional forest cover, increased regional fire activity (Fletcher & Moreno, 2012; Stahle *et al.*, 2016; Beck *et al.*, 2017; Mariani *et al.*, 2017), consistent with reduced terrestrial organic matter inputs (Br: Figure 5a) and δ^{15}N enrichment of organic matter within the lake: i.e. oligotrophic lake water (Figure 5f). Our results, then, reveal a shift toward more oligotrophic tolerant cladoceran community (dominated by *B. meridionalis*) that precedes δ^{15}N enrichment of organic matter within the lake, reflecting (1) a shift toward oligotrophic tolerant taxa due to reduced terrestrial nutrient input influencing the diet of these aquatic grazers, (2) a depletion of available ^{14}N stocks and (3) a subsequent δ^{15}N enrichment of within lake organic matter.

Given our established link between terrestrial vegetation productivity and lake nutrient stocks, we interpret our results as indicating an aquatic ecosystem response to climate-driven changes in terrestrial nutrient inputs. Vegetation productivity decreases (increases) during relatively dry (wet) climate phases (Figure 5), resulting in a decrease (increase) in terrestrial nutrient inputs. Consumption (replenishment) of available nutrients by aquatic grazers leads to the development of a more (less) oligotrophic lake environment that favours an increase (decrease) in the abundance of cladoceran species, such as *B. meridionalis,* that prefer lower nutrient environments. During phases of low terrestrial nutrient delivery, the eventual depletion of ^{14}N stocks forces aquatic organisms to use ^{15}N – Rayleigh Distillation (Talbot & Johannessen, 1992; Talbot, 2001) – enriching organic matter in this isotope. Our results imply that cladoceran community dynamics respond indirectly to climatic change via the influence of temperature and precipitation over changes in terrestrial vegetation composition dynamics, as well as, their influence over lake nutrient status with no evidence of a direct climate response.

Conclusion

In our study system, time-series analysis of multi-proxy lake sediment data identified an indirect relationship between climatic change and aquatic ecosystem dynamics manifest as a lagged response of aquatic ecosystem change to terrestrial vegetation dynamics. Climate-driven terrestrial vegetation change exerts control over both within-lake nutrient cycling and cladoceran community composition, due principally to the low bedrock nutrient content promoting landscape-wide dominance of peat and associated dystrophy in fresh water systems. A fire-driven shift from rain forest to sclerophyll-dominant vegetation at ca. 3.4 ka is associated with a decoupling of vegetation productivity and lake nutrient cycling. Sclerophyll plants in this landscape produce peat with low nutrient content relative to rain forest, thus, lowering the within-lake nutrient status and favouring an increase in *Botryococcus* spp.. The increase in *Botryococcus* spp. and reduction in terrestrial nutrient input, then, depleted nutrient stocks irrespective of changes in vegetation productivity. The increase in fire activity in western Tasmania over the last century is unprecedented throughout the last 12 kyrs and many Tasmanian rain forest systems are under threat of extinction in response to fire and invasion by fire-promoting plant species (Fletcher *et al.*, 2014; Holz *et al.*, 2015). Our results indicate that aquatic ecosystem dynamics in subalpine western Tasmania are closely linked to climate-driven rain forest dynamics, and that fire-driven vegetation change has the potential to radically alter within-lake nutrient dynamics and aquatic ecosystem composition. All southern temperate rain forest systems are under threat of climatic and fire regime change and the lack of emphasis on how terrestrial and aquatic ecosystems are linked across these systems exposes a critical knowledge-gap that must be addressed if we are to successfully manage aquatic ecosystems of the region into the future.

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Supporting Information

Appendix S1 Radiocarbon laboratory results table for Paddy’s Lake.

Appendix S2 Cladoceran Detrended Correspondence Analysis (DCA) biplot with overlapping zones for axis 1 and 2.

Appendix S3 Pollen stratigraphy of Paddy’s Lake

Biosketch

Kristen K. Beck is a palaeoecologist with a particular interest in the complex relationship between terrestrial-aquatic ecosystems and the climatic forces that drive their long-term dynamics. She is currently completing her PhD research.

KK Beck, M-S Fletcher and G Kattel conceived ideas for this research; KK Beck and M-S Fletcher collected and analysed data; KK Beck, M-S Fletcher and G Kattel led the writing of this manuscript; PS Gadd, H Heijnis, L Barry, GE Jacobsen, and KM Saunders contributed to laboratory and data analysis, as well as, manuscript writing and ideas.

Editor: Brian Huntley

Tables with their legends above

Table 1: Summary of significant CONISS cladoceran zones (N=7) from Paddy's Lake, displayed by age (ca. ka) and sample depths (cm). Key taxa are reported with their approximate mean, maximum and minimum percent abundance.

Zone	**Age (ca. ka)**	**Sample Depths (cm)**	**Key Taxa**	**Mean % Abundance**	**Maximum % Abundance**	**Minimum % Abundance**
1	> 13.4	177.5	*Alona guttata*	89.3	-	-
			Bosmina meridionalis	9.7	-	-
			Chydorus sphauricus	1.0	-	-
2	13.3-12.8	174.5-165.5	*Alona guttata*	8.2	10.7	6.7
			Bosmina meridionalis	88.8	92.4	82.5
			Chydorus sphauricus	1.9	3.9	0.0
			Simocephalus spp.	1.0	2.9	0.0
3	12.7-11.6	163.5-147.5	*Alona guttata*	57.6	81.4	39.8
			Bosmina meridionalis	9.9	16.5	4.3
			Chydorus sphauricus	30.6	46.6	10.8
			Simocephalus spp.	1.9	4.8	0.0
4	11.3-8.9	114.5-118.5	*Alona guttata*	10.6	17.0	5.6
			Alona quadrangularis	0.1	1.0	0.0
			Bosmina meridionalis	83.0	90.4	72.0
			Chydorus sphauricus	3.1	7.7	0.0
			Diaphanosoma cf. unguiculatum	0.2	1.0	0.0
			Simocephalus spp.	2.2	10.0	0.0

			Unknown	0.8	2.6	0.0
5	8.7-6.4	116.5-92.5	*Alona guttata*	49.4	80.0	15.3
			Alona quadrangularis	0.1	1.0	0.0
			small *Alona* sp.	0.2	2.4	0.0
			Alonella excisa	0.2	2.0	0.0
			Alonella sp.	0.2	2.4	0.0
			Biapertura intermedia	0.1	1.0	0.0
			Bosmina meridionalis	38.9	76.9	13.6
			Chydorus sphauricus	3.0	7.9	0.0
			Daphnia spp.	0.2	1.9	0.0
			Diaphanosoma cf. unguiculatum	0.4	3.0	0.0
			Simocephalus spp.	7.3	17.3	1.0
			Unknown	<0.1	1.2	0.0
6	6.2-0.3	90-6.5	*Alona guttata*	17.7	51.0	4.4
			small *Alona* sp.	0.1	1.0	0.0
			Bosmina meridionalis	80.3	94.7	45.9
			Chydorus sphauricus	0.8	3.5	0.0
			Daphnia spp.	<0.1	1.0	0.0
			Pleuroxus spp.	0.1	2.0	0.0
			Simocephalus spp.	0.9	3.7	0.0
			Unknown	0.4	1.7	0.0
7	< 0.1	2.5	*Alona guttata*	92.6	-	-
			Bosmina meridionalis	1.9	-	-
			Chydorus sphauricus	1.9	-	-
			Simocephalus spp.	3.7	-	-

List of Figure Legends

Figure 1: Digital elevation map of Tasmania and location of Paddy’s Lake (yellow dot), on the right, featuring Tyler’s Line (Tyler, 1992) determined by precipitation (solid blue line), rain forest boundary (dotted blue line) and the dolerite edge (blue dashed line). On the left a photograph of Paddy’s Lake.

Figure 2: Age-depth model of Paddy’s Lake, Tasmania with a smooth spline model (factor=0.50; goodness-of-fit of 83.38) calibrated using SHCal13 (Hogg *et al.*, 2013). Outlier dates are marked in red (Beck *et al.*, 2017).

Figure 3: Stratigraphy of Paddy’s Lake cladoceran taxa. Cladoceran species are presented as percentage composition and grouped by Pelagic (blue), Littoral (green) and Eurytopic (yellow) taxa. The DCA axis 1 (variance= 25.1%) and 2 (variance= 114.3%) scores estimate trends in the cladoceran percentage data. Red dashed lines indicate breaks in the seven significant CONISS zones.

Figure 4: Summary figure of Paddy’s Lake vegetation types and nutrient indicators. a) δ^{15}N (‰); b) δ^{13}C (‰); c) C/N ratio; d) sediment Nitrogen percentage; e) sediment Carbon percentage; f) percent woody plant pollen (grey) with a weighted average (black, window width=5); g) percent grass and herb pollen (grey) with a weighted average (black, window width=5); and h) Bromine ($kcps_n$ x 10^3)(grey) and weighted average (dark green, window width=61) (Beck *et al.*, 2017).

Figure 5: Summary figure of aquatic and terrestrial ecosystem changes at Paddy’s Lake. a) Bromine ($kcps_n$ x10^3)(grey) with a weighted average (dark green, window width=61) (Beck *et al.*, 2017); b) percent sclerophyll pollen (grey) with a weighted average (black, window width=3) (Beck *et al.*, 2017); c) *Botryococcus* spp. AR (grains/cm^{-2} yr^{-1} x 10^{-3})(light green) with a weighted average (black, window width=3); d) Pollen DCA axis 2 (grey) with a weighted average (black, window width=5); e) Cladoceran DCA axis 1 (blue); f) δ^{15}N (‰) (orange); g) oligotrophic:eutrophic cladoceran taxa ratio (green); h) pollen AR (grains/cm^{-2} yr^{-1} x 10^{-4})(grey) with a weighted average (black, window width=5); and i) background charcoal particles/cm^{-2} yr^{-1} (red) (Beck *et al.*, 2017). Shaded background colours indicate generic climate transitions.

Figure 6: Cross correlation analysis of Paddy’s Lake data with four lags of 400 year bins for: a) δ^{15}N vs. pollen AR; b) pollen DCA axis 2 vs. cladoceran DCA axis 1; and c) δ^{15}N vs. oligotrophic:eutrophic cladoceran ratio.

Embedded Figures

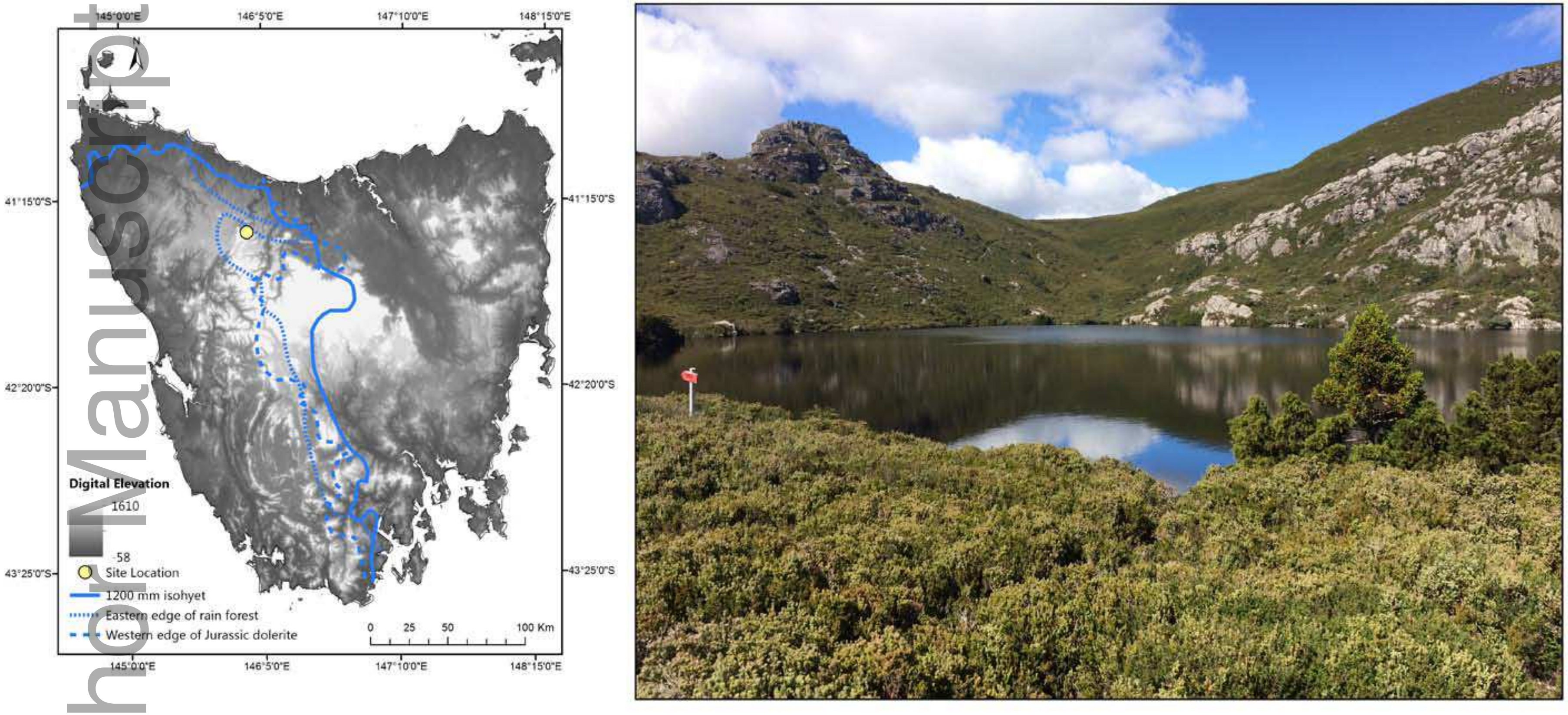


Figure 1:

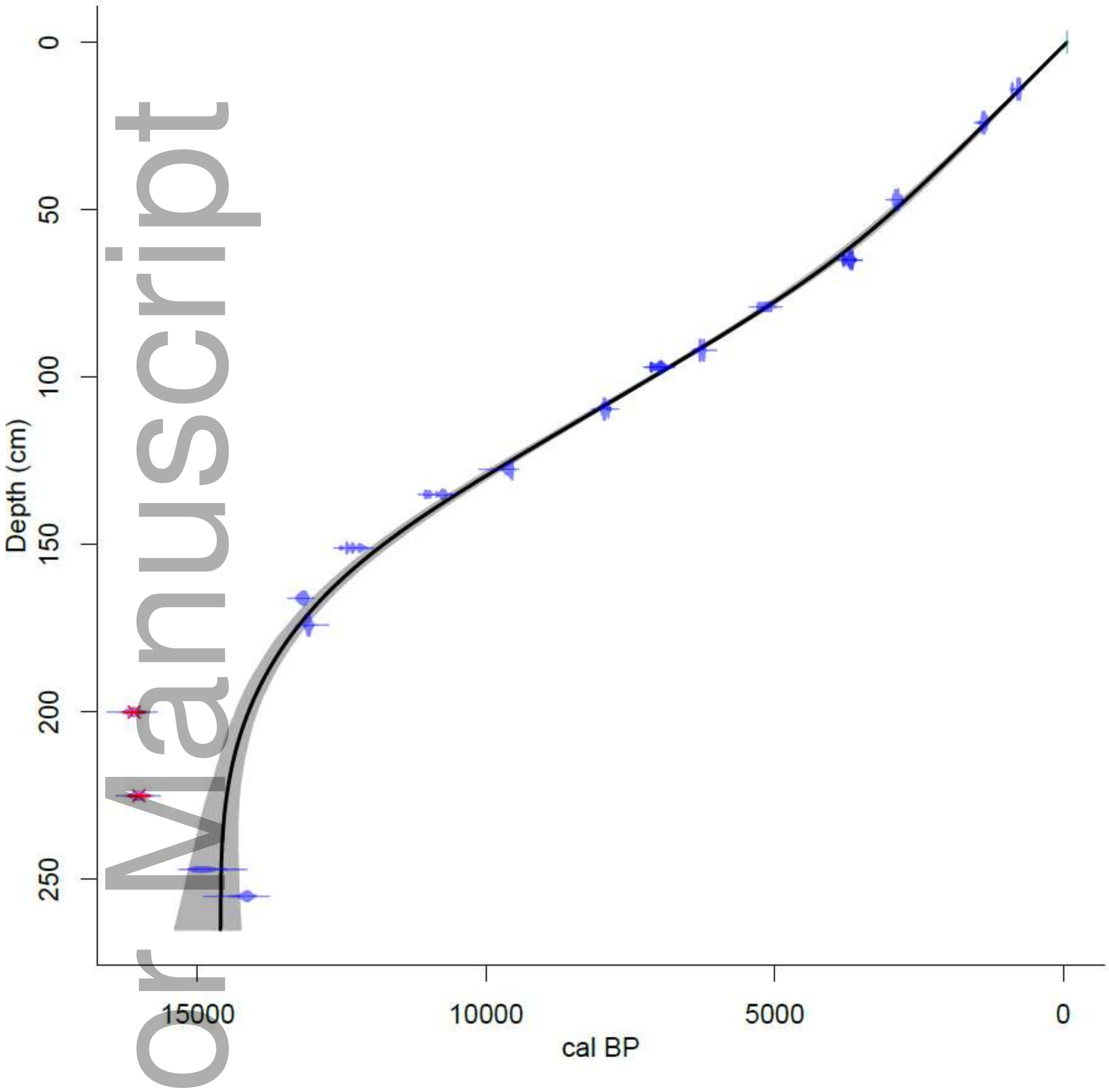


Figure 2:

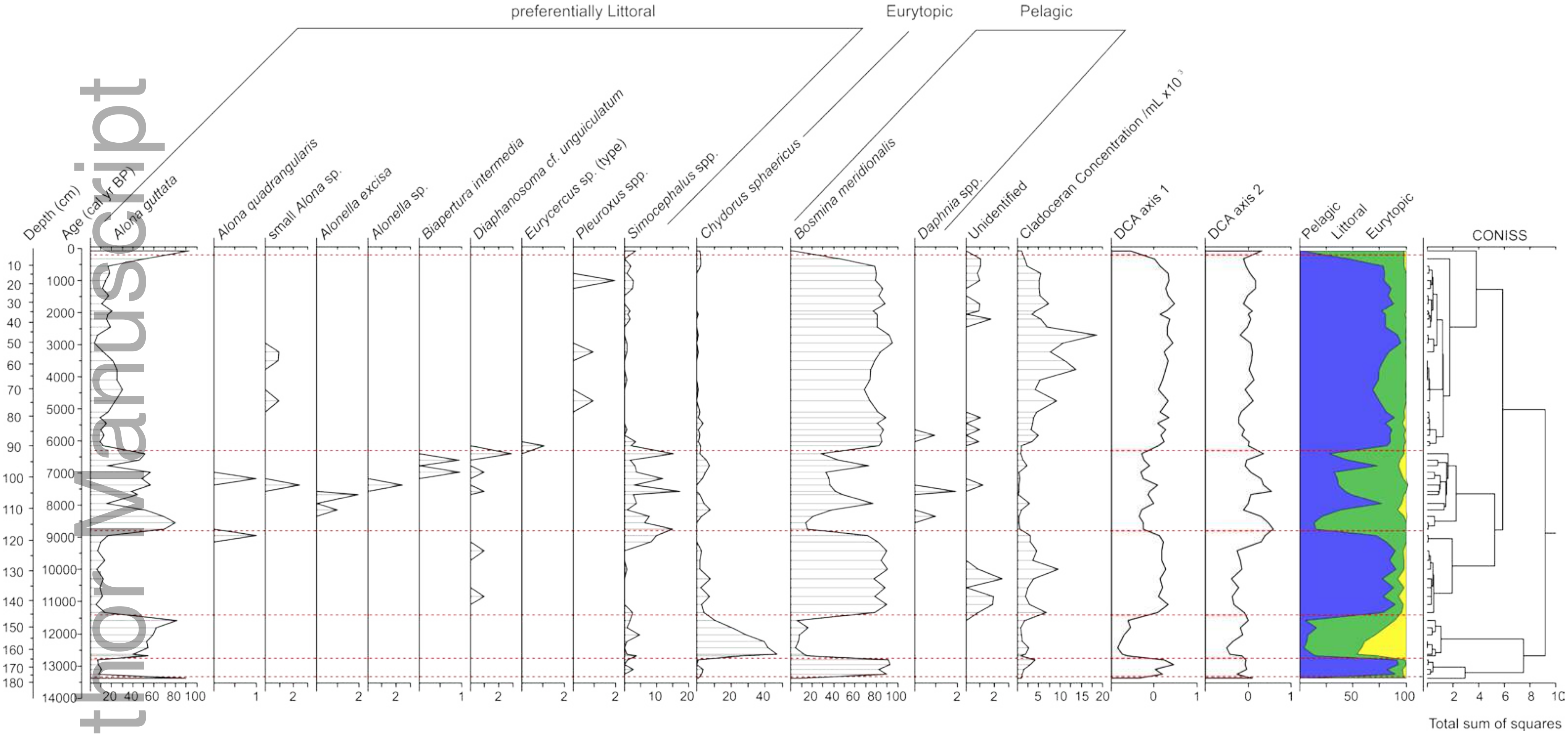

preferentially Littoral
Eurytopic
Pelagic
Depth (cm)
Age (cal yr BP)
Alona guttata
Alona quadrangularis
small Alona sp.
Alonella excisa
Alonella sp.
Biapertura intermedia
Diaphanosoma cf. unguiculatum
Eurycercus sp. (type)
Pleuroxus spp.
Simocephalus spp.
Chydorus sphaericus
Bosmina meridionalis
Daphnia spp.
Unidentified
Cladoceran Concentration /mL x10 ³
DCA axis 1
DCA axis 2
Pelagic
Littoral
Eurytopic
CONISS
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
20 40 60 80 100
1
2
2
2
1
2
2
2
10 20
20 40
20 40 60 80 100
2
2
5 10 15 20
0 1
0 1
50 100
2 4 6 8 10
Total sum of squares

Figure 3:

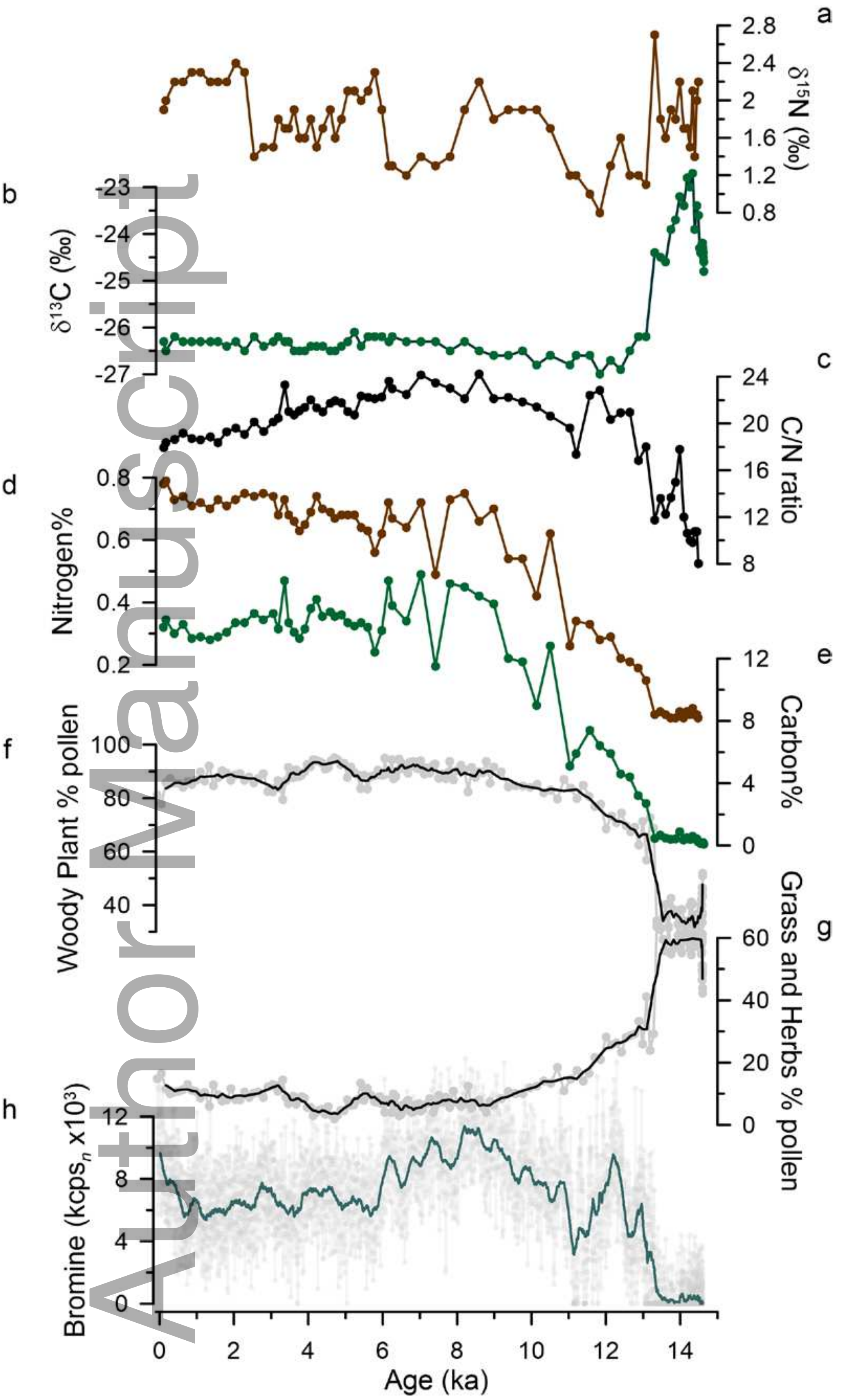
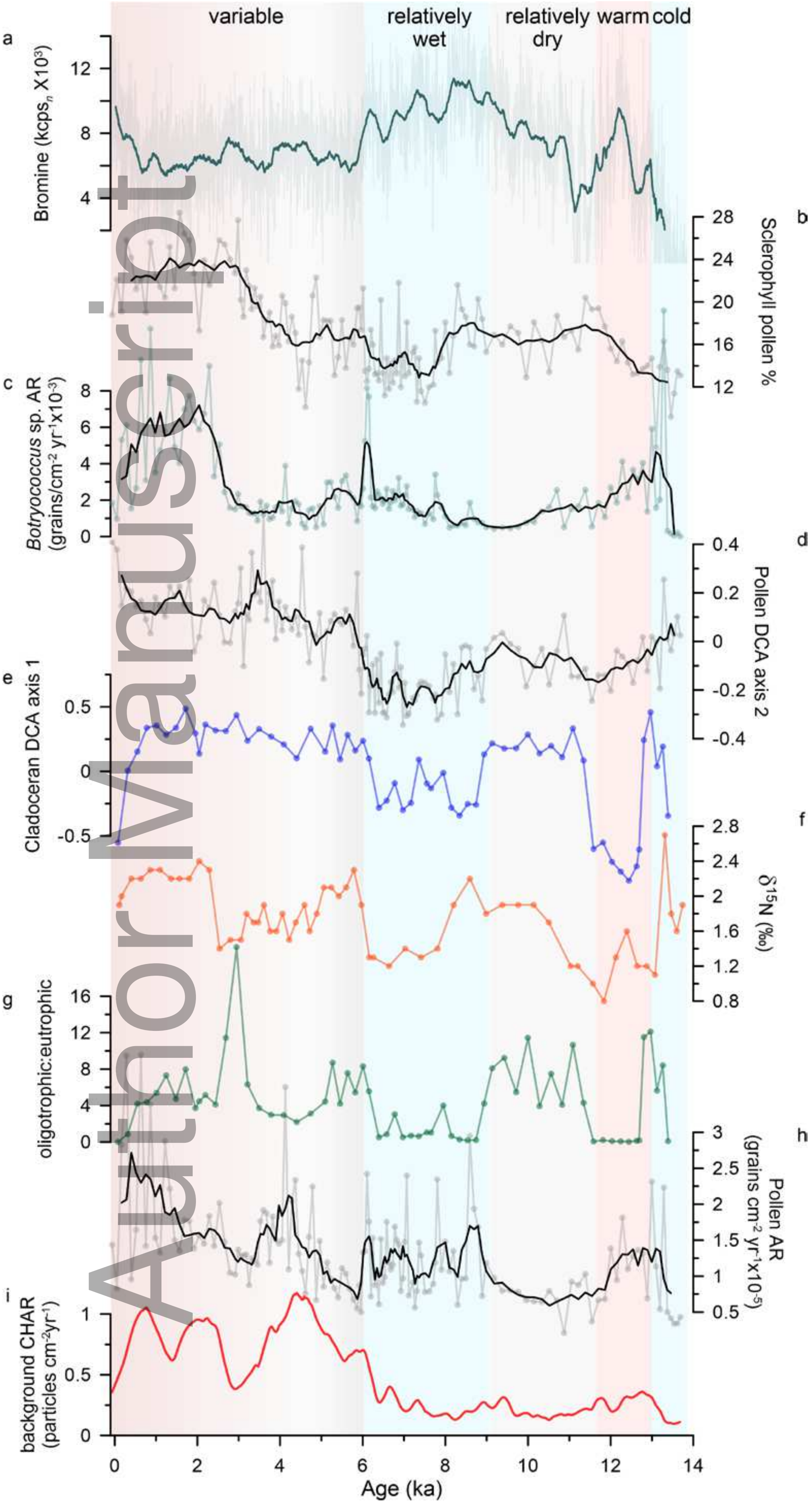

a
δ15N (‰)
2.8
2.4
2
1.6
1.2
0.8
b
δ13C (‰)
-23
-24
-25
-26
-27
c
C/N ratio
24
20
16
12
8
d
Nitrogen%
0.8
0.6
0.4
0.2
e
Carbon%
12
8
4
0
f
Woody Plant % pollen
100
80
60
40
g
Grass and Herbs % pollen
60
40
20
0
h
Bromine (kcps$_n$ x10^3)
12
8
4
0
Age (ka)
0
2
4
6
8
10
12
14

Figure 4:


variable
relatively wet
relatively dry
warm
cold
a
Bromine (kcps$_n$ X10^3)
12
8
4
b
Sclerophyll pollen %
28
24
20
16
12
c
Botryococcus sp. AR (grains/cm^{-2} yr^{-1}x10^{-3})
8
6
4
2
0
d
Pollen DCA axis 2
0.4
0.2
0
-0.2
-0.4
e
Cladoceran DCA axis 1
0.5
0
-0.5
f
δ^{15}N (‰)
2.8
2.4
2
1.6
1.2
0.8
g
oligotrophic:eutrophic
16
12
8
4
0
h
Pollen AR (grains cm^{-2} yr^{-1}x10^{-5})
3
2.5
2
1.5
1
0.5
i
background CHAR (particles cm^{-2}yr^{-1})
1
0.5
0
0
2
4
6
8
10
12
14
Age (ka)

698 Figure 5:

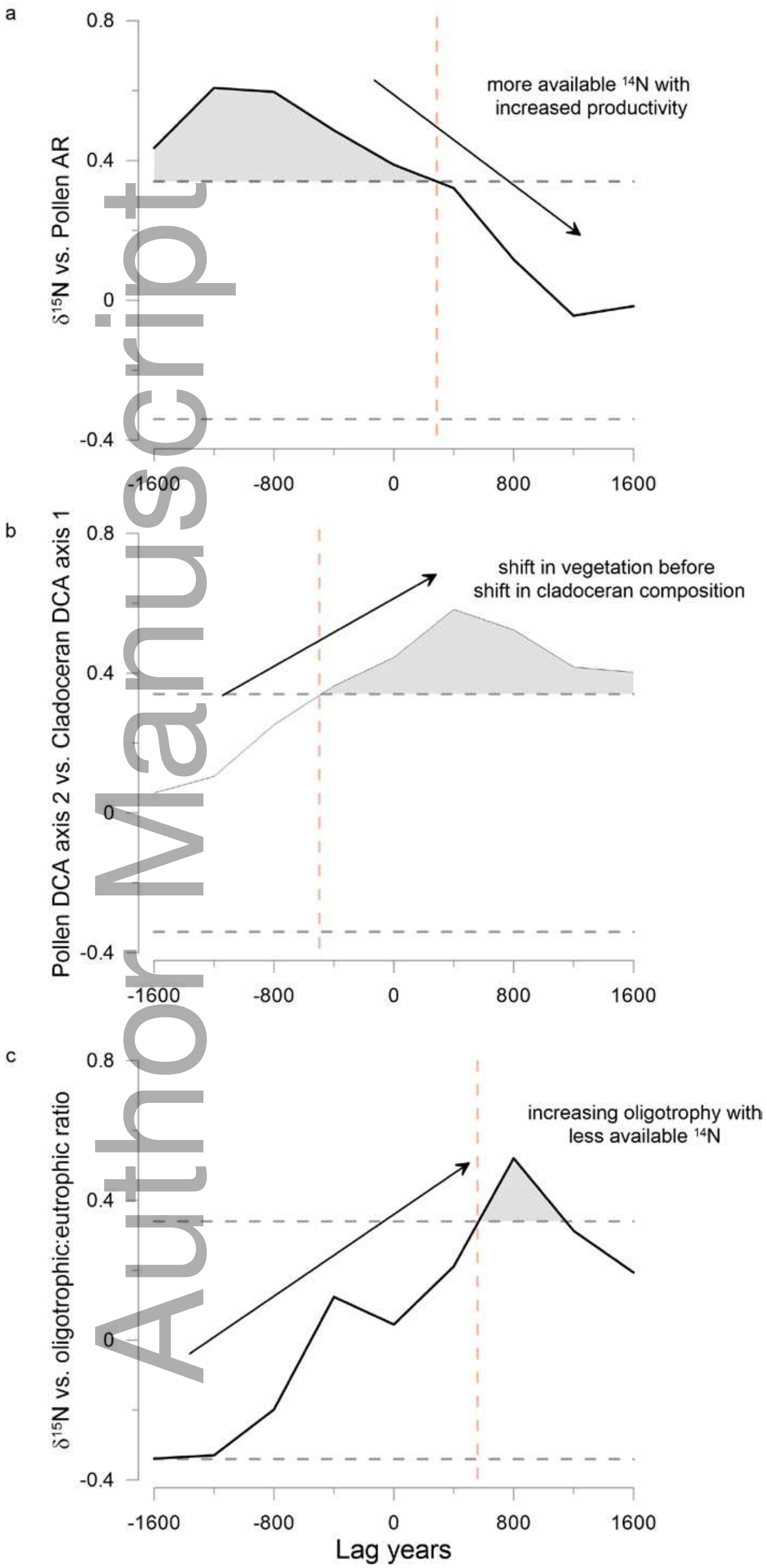
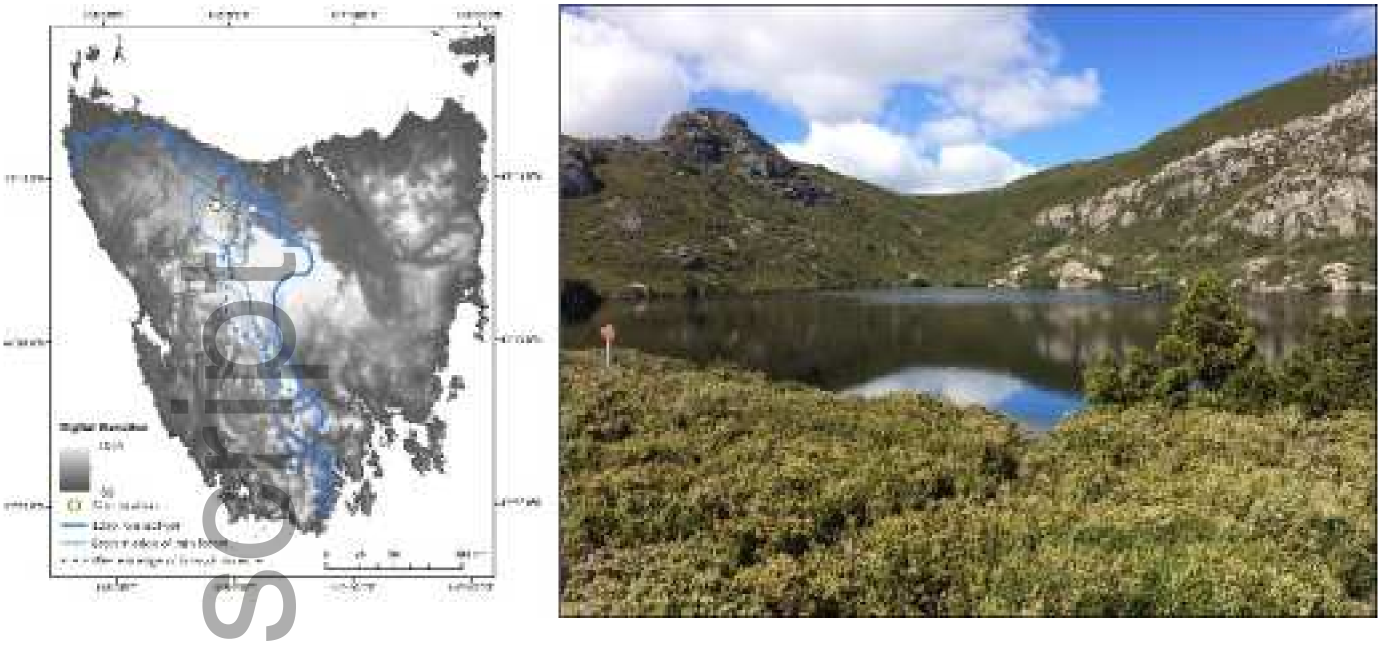
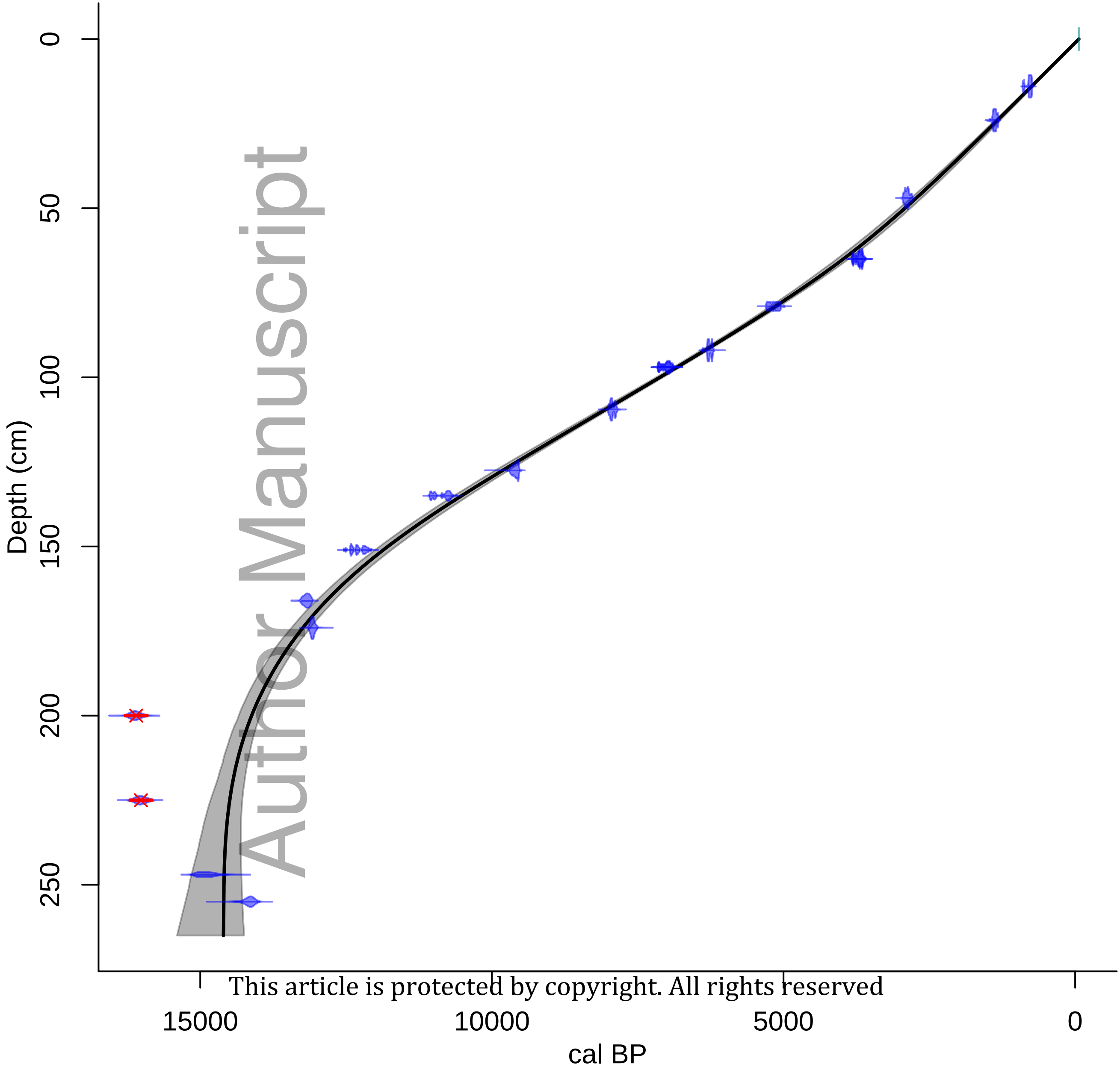
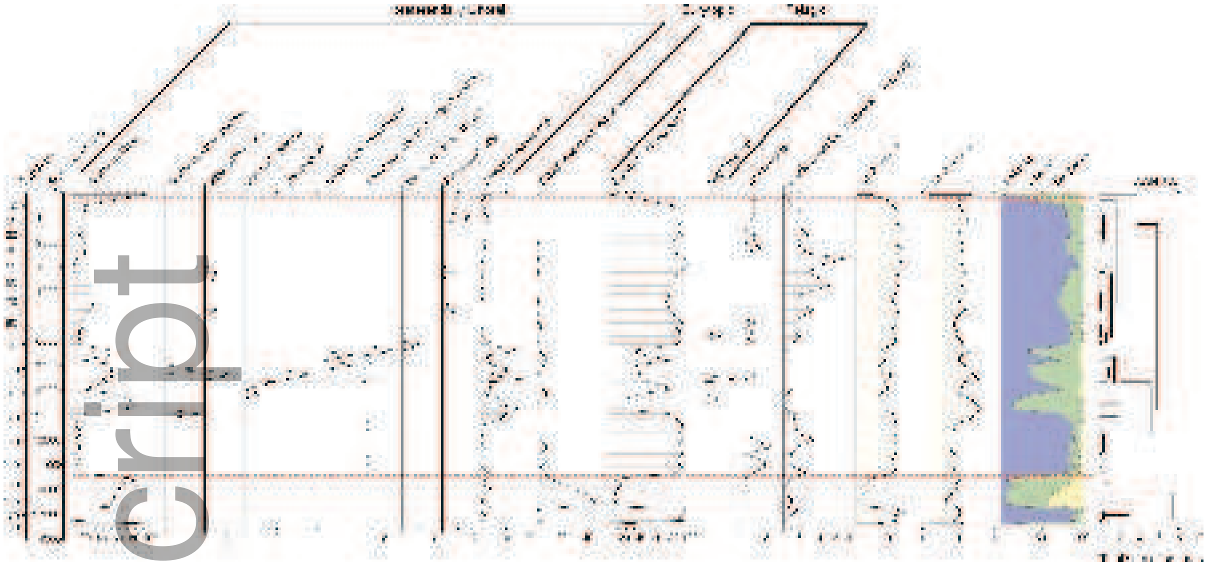

a
0.8
0.4
0
-0.4
δ15N vs. Pollen AR
more available 14N with
increased productivity
-1600
-800
0
800
1600
b
0.8
0.4
0
-0.4
Pollen DCA axis 2 vs. Cladoceran DCA axis 1
shift in vegetation before
shift in cladoceran composition
-1600
-800
0
800
1600
c
0.8
0.4
0
-0.4
δ15N vs. oligotrophic:eutrophic ratio
increasing oligotrophy with
less available 14N
-1600
-800
0
800
1600
Lag years

Figure 6:

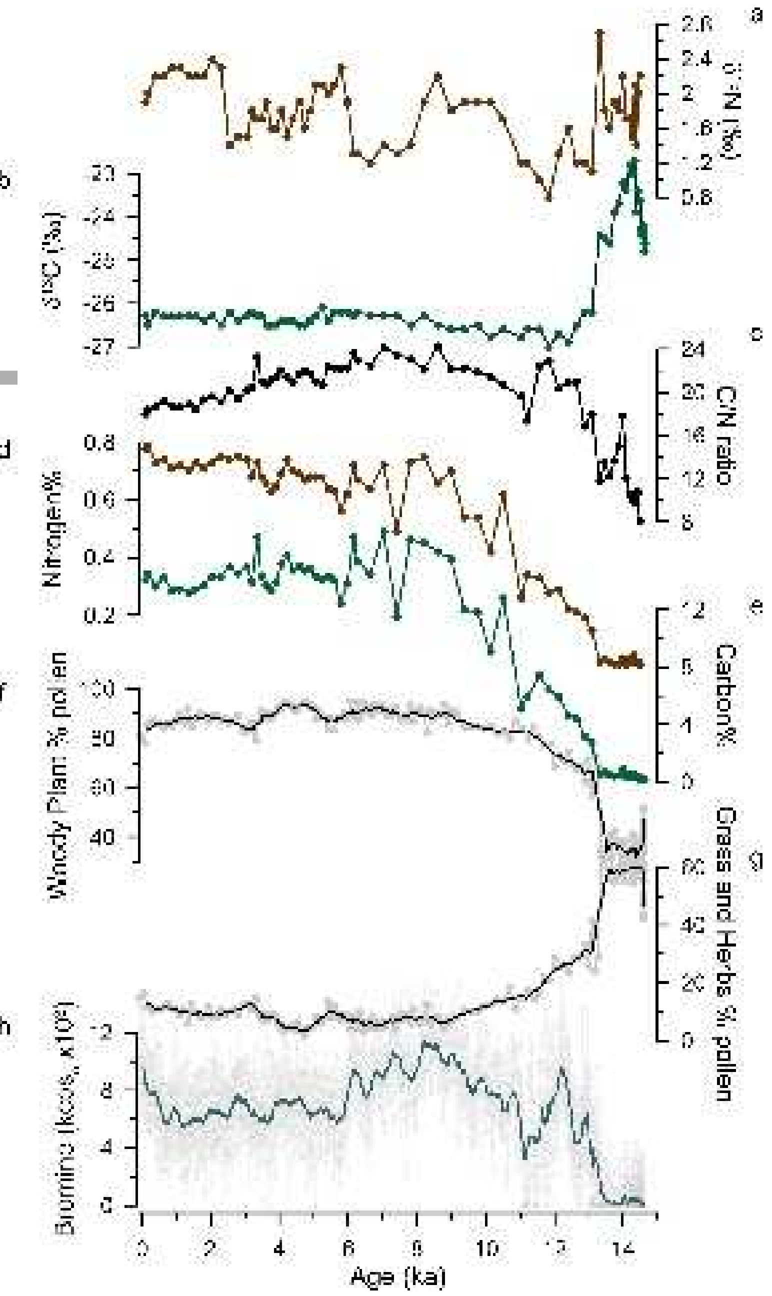


jbi_13144_f1.tif

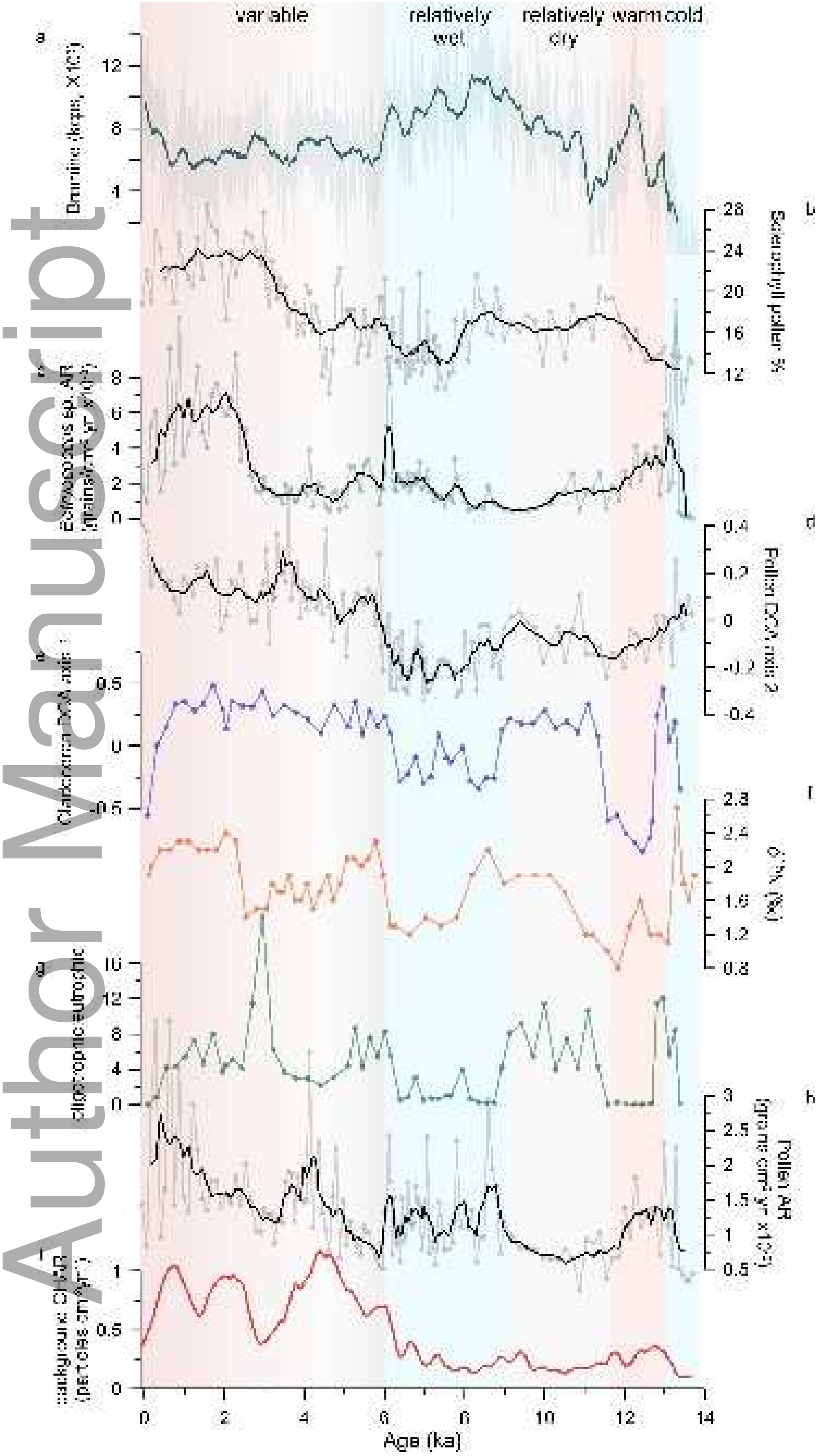

0
50
100
150
200
250
Depth (cm)
15000
10000
5000
0
cal BP



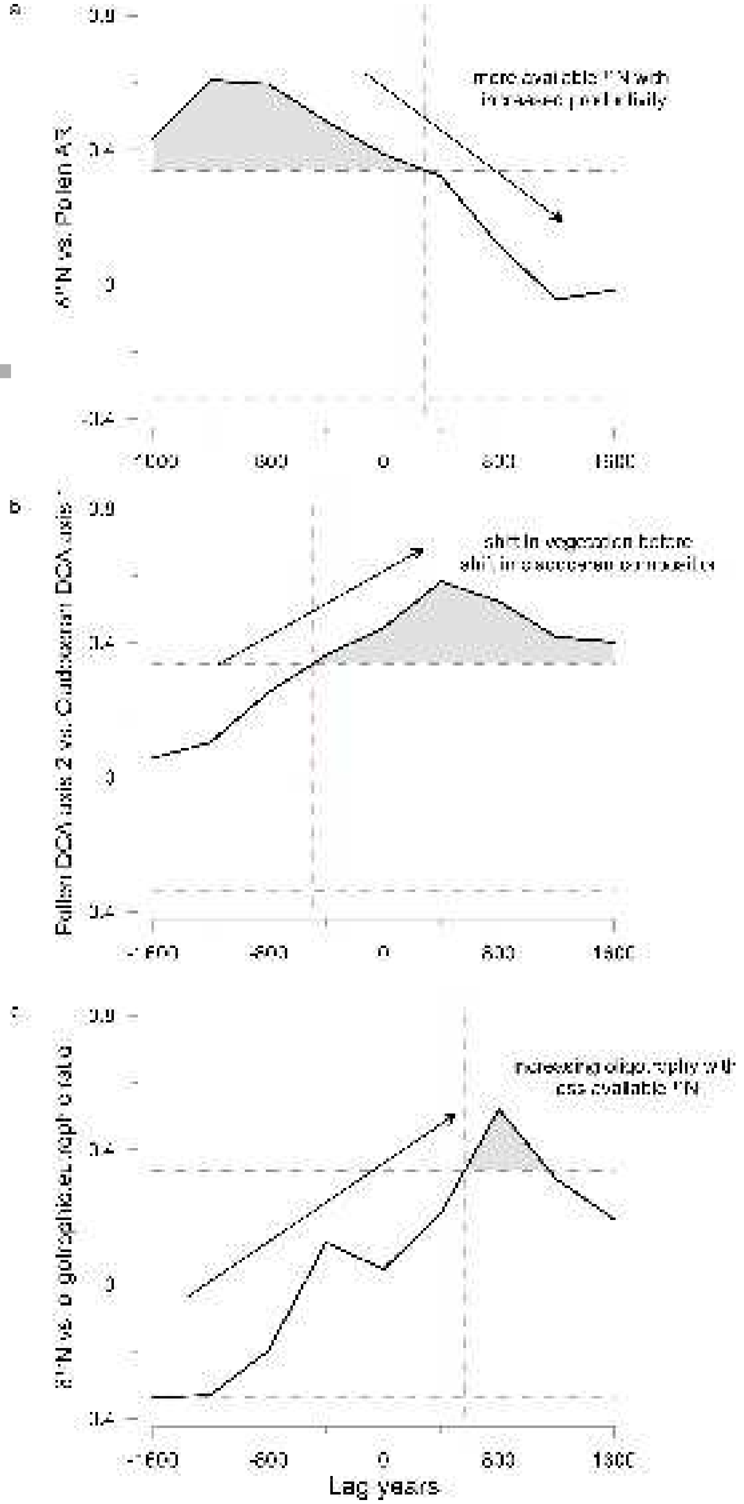
jbi_13144_f3.tif



jbi_13144_f4.tif



jbi_13144_f5.tif



jbi_13144_f6.tif