


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

Kristen K. Beck¹  | Michael-Shawn Fletcher¹ | Giri Kattel^{2,3} | Linda A. Barry⁴ | Patricia S. Gadd⁴ | Henk Heijnis⁴ | Geraldine E. Jacobsen⁴ | Krystyna M. Saunders⁴

¹School of Geography, University of Melbourne, Parkville, Vic., Australia

²Department of Infrastructure Engineering, University of Melbourne, Parkville, Vic., Australia

³Nanjing Institute of Geography and Limnology Chinese Academy of Sciences (NIGLAS), Nanjing, China

⁴Australian Nuclear Science and Technology Organisation, Lucas Heights, NSW, Australia

Correspondence

Kristen K. Beck, School of Geography, University of Melbourne, Parkville, Vic., Australia.

Email: beckk@student.unimelb.edu.au

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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 a.s.l. 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 kyr. The significant negative lagged relationship between pollen AR and $\delta^{15}\text{N}$ 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, cladocerans, climate change, Late Quaternary, long-term fire, nutrient dynamics, Tasmania, terrestrial-aquatic ecosystems

1 | INTRODUCTION

Aquatic ecosystems are known to respond both “directly” and “indirectly” to climatic change (Ball et al., 2010; Battarbee, 2000). “Direct” aquatic ecosystem responses to climate change are principally influenced by changes in temperature and lake level on aquatic environments (Gell, Tibby, Fluin, Leahy, & Reid, 2005; Schindler, 1997; Smol & Cumming, 2000), 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 (Augustinus, Bleakley, Deng, Shane, & Cochran, 2008; Huvane & Whitehead, 1996; Korsman & Segerstrom, 1998; Lancashire, Flenley, & Harper, 2002; Wang, Yang, Anderson, & Dong, 2016). Despite the importance of climate in driving terrestrial ecosystem dynamics, and the clear relationship between terrestrial and aquatic ecosystems (Augustinus et al., 2008; Engstrom, Fritz, Almendinger, & Juggins, 2000; Huvane & Whitehead, 1996; Korsman & Segerstrom, 1998), most research into long-term aquatic ecosystem change focuses 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, 1997, 2001), salinity/lake depth (Gasse, Barker, Gell, Fritz, & Charlie, 1997; Gell, Mills, & Grundell, 2012; Saunders, McMinn, & Roberts, 2007; Smol & Cumming, 2000) and water chemistry (Schindler, 2001). Direct responses result in aquatic ecosystem changes that are either synchronous with (Prebble, Sim, Finn, & Fink, 2005), or independent of (Tibby, Penny, Leahy, & Kershaw, 2012), changes in the terrestrial environment. In contrast, indirect aquatic ecosystem responses to climate that are mediated through the terrestrial environment are characterized by a lagged response of the aquatic environment to terrestrial change (Fritz, Engstrom, & Juggins, 2004; Heggen, Birks, & Anderson, 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 (Pienitz, Smol, & MacDonald, 1999; Whitehead, Charles, Jackson, Smol, & Engstrom, 1989), mixing/turbidity (Augustinus, Cochran, Kattel, & D’Costa, 2012; Lotter, 2001) and the trophic status of water bodies (Engstrom et al., 2000; Fritz & Anderson, 2013; Heggen et al., 2010).

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 (Bowman, Maclean, & Crowden, 1986; Brown, Crowden, & Jarman, 1982; Jarman, Crowden, & Brown, 1982). As a result, waterbodies in this landscape are uniformly dystrophic, with nutrient inputs largely derived from the acid peat soils (Tyler, 1974, 1992; Vanhoutte, Verleyen, Vyverman, Chepurnov, & Sabbe, 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 (Fox-Hughes, Harris, Lee, Grose, & Bindoff, 2014; Mariani & Fletcher, 2016; McWethy et al., 2013).

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 hypothesize 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 hypothesize 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 $\delta^{13}\text{C}$) and nitrogen (elemental and $\delta^{15}\text{N}$) 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 kyr (Beck, Fletcher, Gadd, Heijnis, & Jacobsen, 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.

2 | 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 (McGlone, 1989; Veblen & Ashton, 1982), with more than 30% of Tasmanian subalpine rain forest lost to fire over the last two centuries (Holz, Wood, Veblen, & Bowman, 2015).

2.1 | 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; Kamenik,

Szeroczyńska, & Schmidt, 2007; Kattel & Augustinus, 2010; Kattel, Gell, Perga, & Jeppesen, 2015; Lotter, Birks, Hofmann, & Marchetto, 1998). 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) (Augustinus et al., 2012; Geddes, 1988; Green, 1976; Kattel & Augustinus, 2010; 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; Kattel & Augustinus, 2010; Lotter, Birks, Eicher, & Hofmann, 2000). *Bosmina meridionalis*, a pelagic cladoceran, is endemic to Australia and New Zealand and is an indicator of relatively clear water and oligotrophic conditions (Geddes, 1988; Green, 1976). *Chydorus sphaericus* is a eurytopic taxa, found in both littoral and pelagic habitats, showing responses to nutrient enriched environments (Frey, 1980; Kattel & Augustinus, 2010; Lotter et al., 1998).

2.2 | Site description

Paddy's Lake (41°27'04" S, 145°57'41" E) is a cirque lake situated at ca. 1065 m a.s.l. 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 (Pemberton & McKibben, 2004; Seymour & Calver, 1995). Average monthly temperature ranges from ~4.6–14°C, with an annual average of ~12.3°C (Beck et al., 2017, Bureau of Meteorology, 2016a,b). The local vegetation

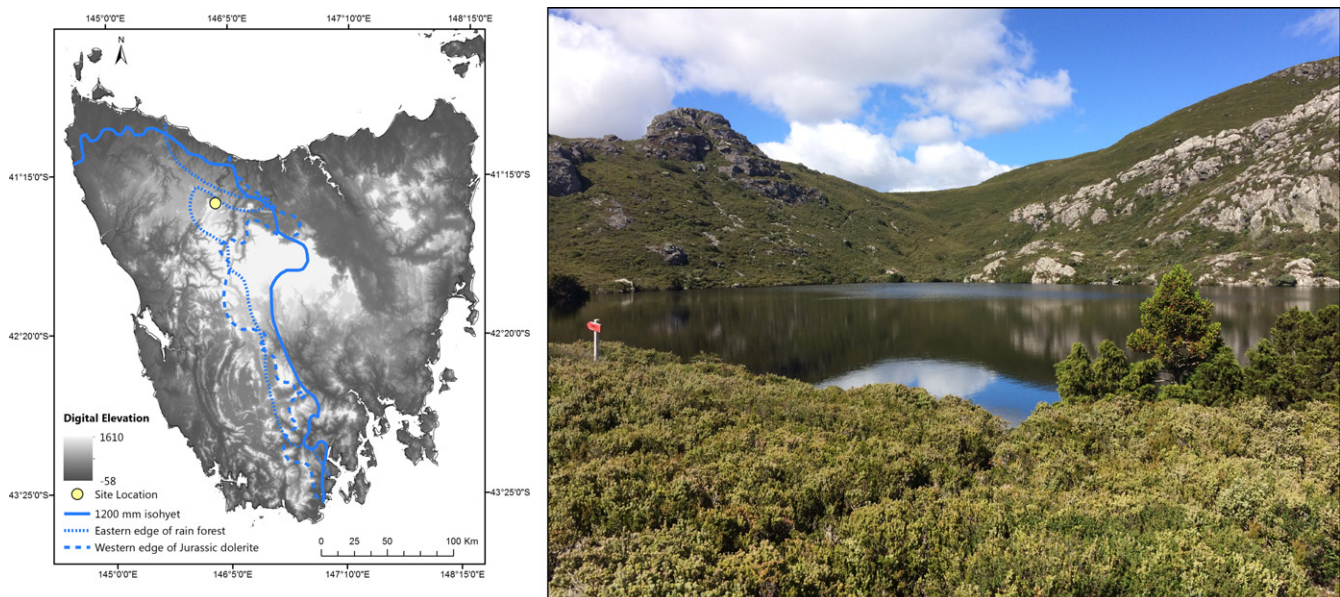


FIGURE 1 Digital elevation map of Tasmania and location of Paddy's Lake (yellow dot), on the left, featuring Tyler's Line (Tyler, 1992) determined by precipitation (solid blue line), rain forest boundary (dotted blue line) and the dolerite edge (blue dashed line). On the right, a photograph of Paddy's Lake [Colour figure can be viewed at wileyonlinelibrary.com]

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 (Fletcher & Thomas, 2010; Jackson, 1968).

3 | MATERIALS AND METHODS

3.1 | 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 S1 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).

3.2 | Cladoceran analysis

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

3.3 | Geochemistry

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

3.4 | 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 (Matthias & Giesecke, 2014; Sugita, Hicks, & Sormunen, 2010). Background charcoal (particles $\text{cm}^{-2} \text{yr}^{-1}$) 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.

3.5 | Numerical analyses

3.5.1 | Detrended correspondence analysis and cluster analysis

Detrended correspondence 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).

3.5.2 | 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 $\delta^{15}\text{N}$, 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, Telford, & Birks, 2013; Seddon, Froyd, Witkowski, & Willis, 2014). Data were 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, Stanley, & Podobnik, 2011). Cross correlation was run with four lags of 400 years in R.

4 | RESULTS

4.1 | Chronology

Radiocarbon results are accessible in S1 of the Supporting Information, with full details in Beck et al. (2017). An age-offset estimate of 223.5 years 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).

4.2 | Cladoceran analysis

A total of 13 cladoceran taxa were identified throughout the Paddy's Lake record (Figure 5). Cladoceran diversity was very low; however, not abnormal for a Tasmanian alpine lake (A. Kotov & R. Shiel, personal communication). Seven significant CONISS zones were produced and Table 1 lists the taxonomic trends in each zone.

4.3 | Geochemistry

All C%, N%, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results are the mean of replicate analyses, the standard deviation of the replicates are $\leq \pm 0.3$ for all $\delta^{13}\text{C}$ and $\leq \pm 0.4$ for all $\delta^{15}\text{N}$ results. These organic geochemical indicators show a distinct shift at ca. 13.4 ka (Figure 3). 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 $\delta^{13}\text{C}$ occur prior to ca. 13.4 ka (maximum = -23.5‰) then decline to persistently low values. High $\delta^{15}\text{N}$ values ($\sim 2\text{‰}$) occur prior to ca. 13.4 ka, then decline at ca. 13 ka and ca. 12 ka. $\delta^{15}\text{N}$ values peak at ca. 8.5 ka ($\sim 2.2\text{‰}$) and ca. 6 ka ($\sim 2.3\text{‰}$), a rise at ca. 2.5 ka is followed by stable values until present (Figures 3a and 4f). 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 (Figures 3h and 4a).

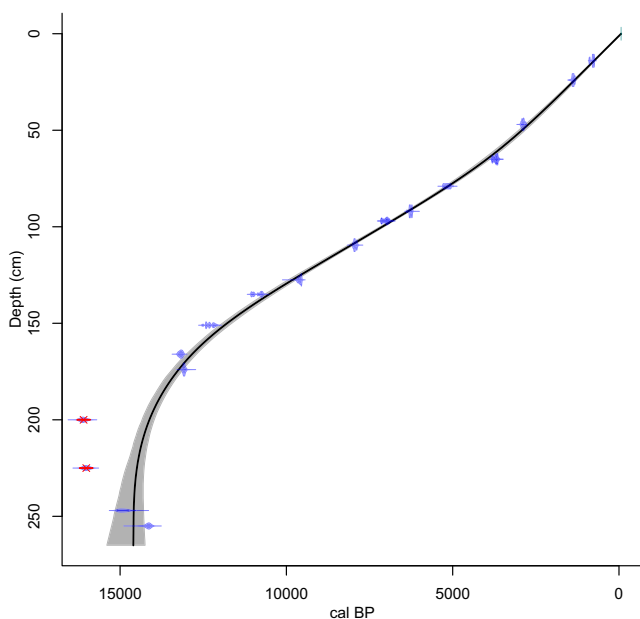


FIGURE 2 Age-depth model of Paddy's Lake, Tasmania with a smooth spline model (factor = 0.50; goodness-of-fit of 83.38) calibrated using SHCal13 (Hogg et al., 2013). Outlier dates are marked in red (Beck et al., 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

4.4 | 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 3g,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 4h). 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.

4.5 | Numerical analyses

4.5.1 | Detrended correspondence analysis

Trends in the cladoceran DCA axis 1 scores (explained variance = 25.1%) follow changes in the pelagic taxa *Bosmina meridionalis* (Figures 4e and 5). 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 S2 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 (Figure 4d).

4.5.2 | Cross correlation

Pollen AR has a positive correlation with $\delta^{15}\text{N}$ (–1600 to 400 year lag). A negative response in $\delta^{15}\text{N}$ 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 year lag). The oligotrophic:eutrophic cladoceran ratio show a positive correlation with $\delta^{15}\text{N}$ (400 to 1200 year lag) (Figure 6).

5 | DISCUSSION

5.1 | Vegetation change and lake nutrient dynamics

We observe a significant negative lagged relationship between pollen AR and the $\delta^{15}\text{N}$ content of organic matter within Paddy's Lake throughout the last ca. 13.4 kyr (Figure 6a). Linear relationships between pollen ARs and plant biomass has been shown in temperate systems in the Northern Hemisphere (Matthias & Giesecke, 2014; Sugita et al., 2010), 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$. Once vegetation productivity decreases (reduced pollen AR), available ^{14}N decreases and aquatic organisms are forced to use ^{15}N —classic Rayleigh Distillation

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	<i>Alona guttata</i>	89.3	—	—
			<i>Bosmina meridionalis</i>	9.7	—	—
			<i>Chydorus sphaericus</i>	1.0	—	—
2	13.3–12.8	174.5–165.5	<i>Alona guttata</i>	8.2	10.7	6.7
			<i>Bosmina meridionalis</i>	88.8	92.4	82.5
			<i>Chydorus sphaericus</i>	1.9	3.9	0.0
			<i>Simocephalus</i> spp.	1.0	2.9	0.0
3	12.7–11.6	163.5–147.5	<i>Alona guttata</i>	57.6	81.4	39.8
			<i>Bosmina meridionalis</i>	9.9	16.5	4.3
			<i>Chydorus sphaericus</i>	30.6	46.6	10.8
			<i>Simocephalus</i> spp.	1.9	4.8	0.0
4	11.3–8.9	114.5–118.5	<i>Alona guttata</i>	10.6	17.0	5.6
			<i>Alona quadrangularis</i>	0.1	1.0	0.0
			<i>Bosmina meridionalis</i>	83.0	90.4	72.0
			<i>Chydorus sphaericus</i>	3.1	7.7	0.0
			<i>Diaphanosoma</i> cf. <i>unguiculatum</i>	0.2	1.0	0.0
			<i>Simocephalus</i> spp.	2.2	10.0	0.0
			Unknown	0.8	2.6	0.0
5	8.7–6.4	116.5–92.5	<i>Alona guttata</i>	49.4	80.0	15.3
			<i>Alona quadrangularis</i>	0.1	1.0	0.0
			Small <i>Alona</i> sp.	0.2	2.4	0.0
			<i>Alonella excisa</i>	0.2	2.0	0.0
			<i>Alonella</i> sp.	0.2	2.4	0.0
			<i>Biapertura intermedia</i>	0.1	1.0	0.0
			<i>Bosmina meridionalis</i>	38.9	76.9	13.6
			<i>Chydorus sphaericus</i>	3.0	7.9	0.0
			<i>Daphnia</i> spp.	0.2	1.9	0.0
			<i>Diaphanosoma</i> cf. <i>unguiculatum</i>	0.4	3.0	0.0
			<i>Simocephalus</i> spp.	7.3	17.3	1.0
			Unknown	<0.1	1.2	0.0
6	6.2–0.3	90–6.5	<i>Alona guttata</i>	17.7	51.0	4.4
			Small <i>Alona</i> sp.	0.1	1.0	0.0
			<i>Bosmina meridionalis</i>	80.3	94.7	45.9
			<i>Chydorus sphaericus</i>	0.8	3.5	0.0
			<i>Daphnia</i> spp.	<0.1	1.0	0.0
			<i>Pleuroxus</i> spp.	0.1	2.0	0.0
			<i>Simocephalus</i> spp.	0.9	3.7	0.0
			Unknown	0.4	1.7	0.0
7	<0.1	2.5	<i>Alona guttata</i>	92.6	—	—
			<i>Bosmina meridionalis</i>	1.9	—	—
			<i>Chydorus sphaericus</i>	1.9	—	—
			<i>Simocephalus</i> spp.	3.7	—	—

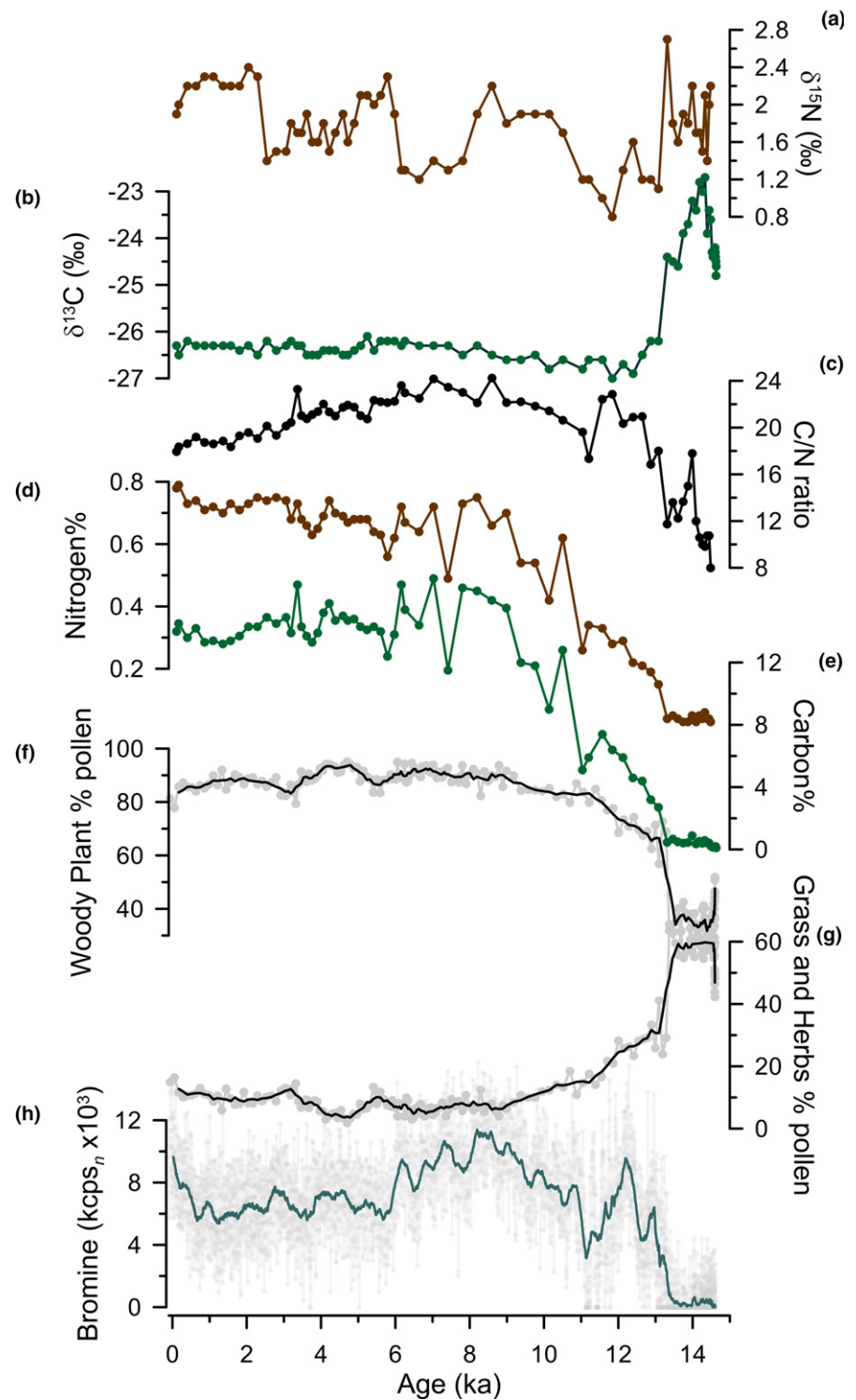


FIGURE 3 Summary figure of Paddy's Lake vegetation types and nutrient indicators. (a) $\delta^{15}\text{N}$ (‰); (b) $\delta^{13}\text{C}$ (‰); (c) C/N ratio; (d) sediment Nitrogen percentage; (e) sediment Carbon percentage; (f) percent woody plant pollen (grey) with a weighted average (black, window width = 5); (g) percent grass and herb pollen (grey) with a weighted average (black, window width = 5); and (h) Bromine ($\text{kcps}_n \times 10^3$) (grey) and weighted average (dark green, window width = 61) (Beck et al., 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

(Talbot, 2001; Talbot & Johannessen, 1992)—resulting in an increase in organic matter $\delta^{15}\text{N}$ values.

While the negative lagged relationship between pollen AR and $\delta^{15}\text{N}$ is significant over the entire ca. 13.4 kyr sequence, we observe an apparent decoupling of these variables after ca. 3.4 ka. This decoupling is manifest as persistently high $\delta^{15}\text{N}$ values (Figure 4f) despite an increase in pollen AR (Figure 4h). We note that this decoupling is coeval with the establishment of both sclerophyll-

dominant vegetation around the lake (Figure 4b) and a marked increase in the colonial algae *Botryococcus* spp. (Figure 4c). *Botryococcus* spp., likely *Botryococcus braunii* (Kützing), [$\delta^{15}\text{N}$ signature of 4–7‰ (Heyng et al., 2012)] is an algae common in oligotrophic waters that prefers shallow littoral environments (Aaronson, Berner, Gold, & Kushner, 1983; Clausen, 1999). We interpret this shift as reflecting increased nutrient consumption by *Botryococcus* spp. that depleted ^{14}N stocks within the lake. The shift towards sclerophyll-

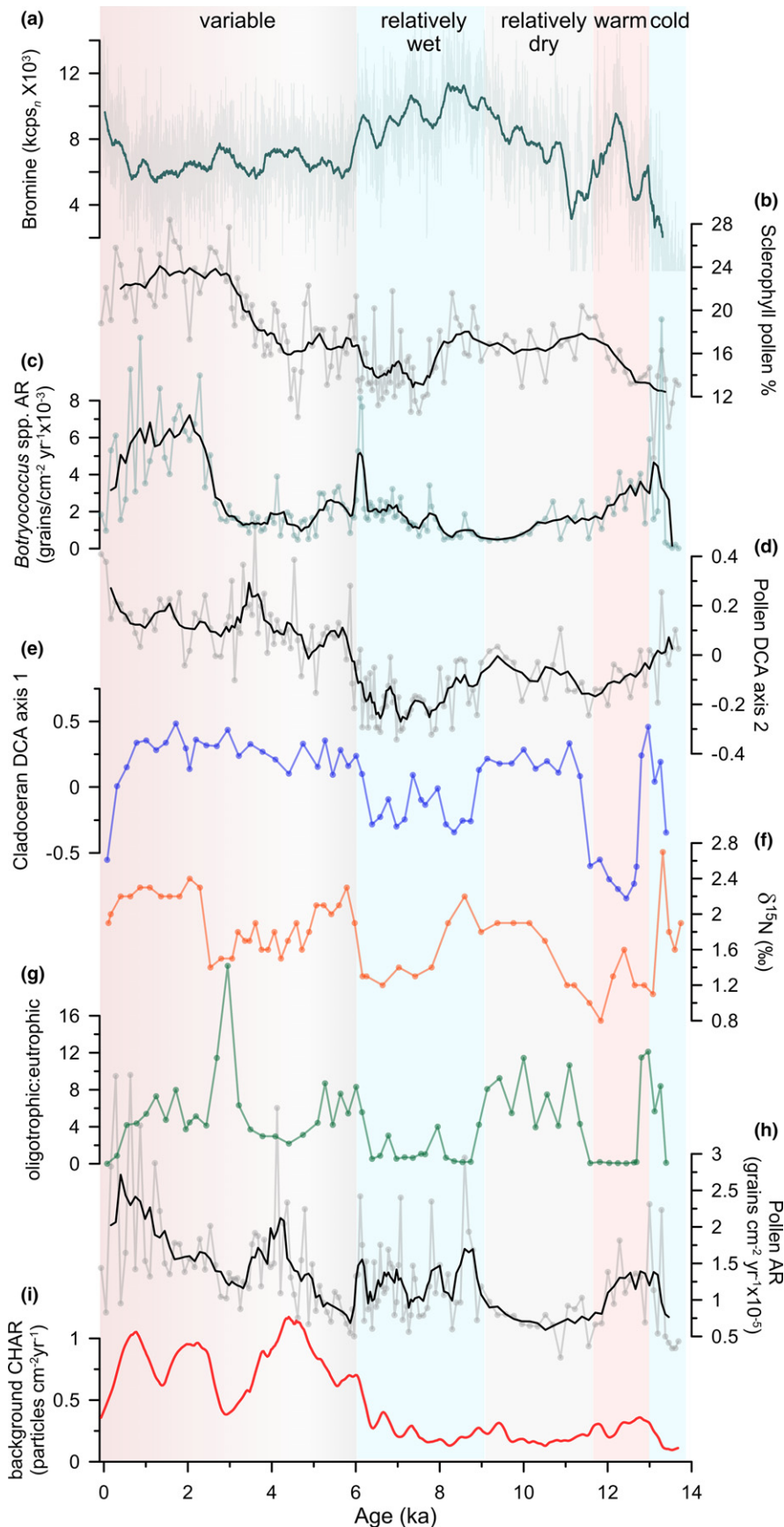


FIGURE 4 Summary figure of aquatic and terrestrial ecosystem changes at Paddy's Lake. (a) Bromine ($\text{kcpn} \times 10^3$) (grey) with a weighted average (dark green, window width = 61) (Beck et al., 2017); (b) percent sclerophyll pollen (grey) with a weighted average (black, window width = 3) (Beck et al., 2017); (c) *Botryococcus* spp. AR ($\text{grains}/\text{cm}^2 \text{yr}^{-1} \times 10^{-3}$) (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) $\delta^{15}\text{N}$ (‰) (orange); (g) oligotrophic: eutrophic cladoceran taxa ratio (green); (h) pollen AR ($\text{grains}/\text{cm}^2 \text{yr}^{-1} \times 10^{-5}$) (grey) with a weighted average (black, window width = 5); and (i) background charcoal particles/ $\text{cm}^2 \text{yr}^{-1}$ (red) (Beck et al., 2017). Shaded background colours indicate generic climate transitions [Colour figure can be viewed at wileyonlinelibrary.com]

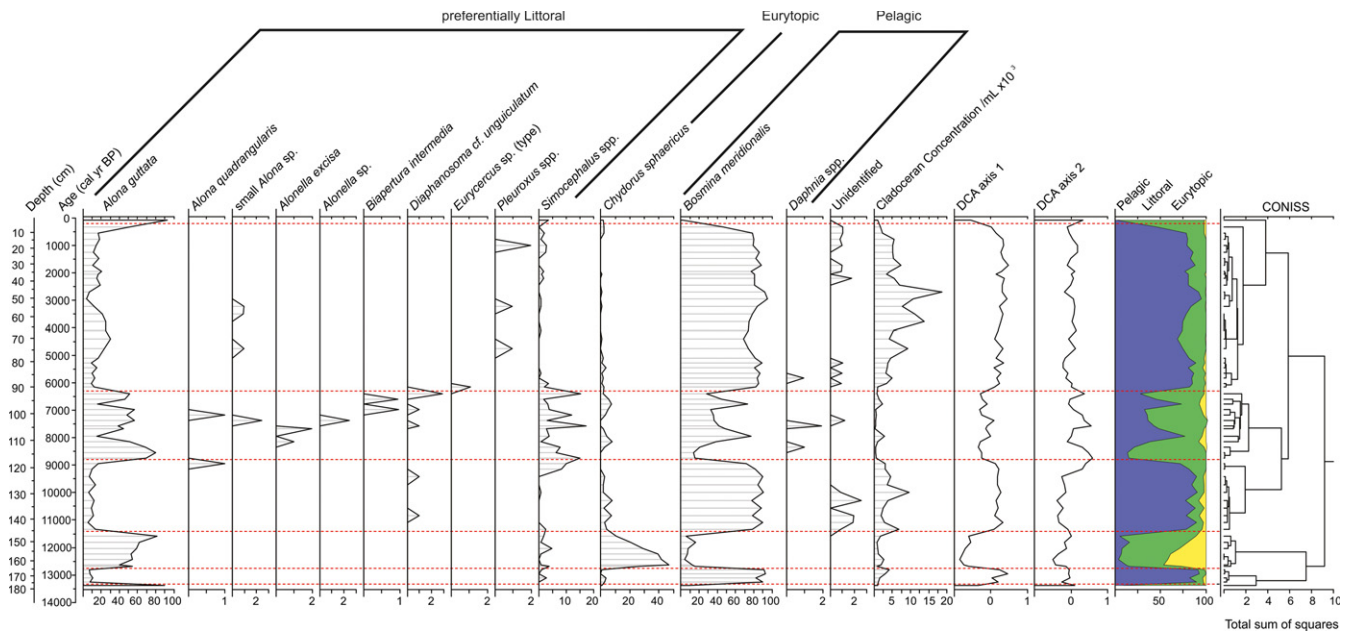


FIGURE 5 Stratigraphy of Paddy's Lake cladoceran taxa. Cladoceran species are presented as percentage composition and grouped by Pelagic (blue), Littoral (green) and Eurytopic (yellow) taxa. The DCA axis 1 (variance = 25.1%) and 2 (variance = 14.3%) scores estimate trends in the cladoceran percentage data. Red dashed lines indicate breaks in the seven significant CONISS zones [Colour figure can be viewed at wileyonlinelibrary.com]

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). Sclerophyll 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, Hua, & Bowman, 2011). It is possible, then, that the invasion of the catchment by sclerophyllous plant taxa lowered the nutrient status of the catchment organosols (C/N and Br; Figure 3c,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 $\delta^{15}\text{N}$ value of deposited organic matter.

5.2 | 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 kyr 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 (Beck

et al., 2017; Fletcher & Moreno, 2012; Fletcher et al., 2014; Macphail, 1979; Markgraf, Bradbury, & Busby, 1986; Stahle, Whitlock, & Haberle, 2016). 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.

While changes in hydroclimate could be expected to drive changes in lake level and a concomitant change in pelagic taxa (e.g. *B. meridionalis*) (Kattal & Augustinus, 2010; Korhola, Olander, & Blom, 2000), we find no consistency between regional hydroclimatic trends and changes in pelagic cladoceran taxa at Paddy's Lake (Figure 5). Critically, we do observe a significant lagged relationship between $\delta^{15}\text{N}$ and the oligotrophic:eutrophic cladoceran ratio through the last ca. 13.4 kyr (Figure 6c), 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" (Kattal & 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 (Kattal & Augustinus, 2010) (Figure 4e,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 (Beck et al., 2017; Fletcher & Moreno, 2012; Mariani et al., 2017; Stahle et al., 2016). These shifts in pollen AR and pollen DCA axis 2 are simultaneous with decreasing

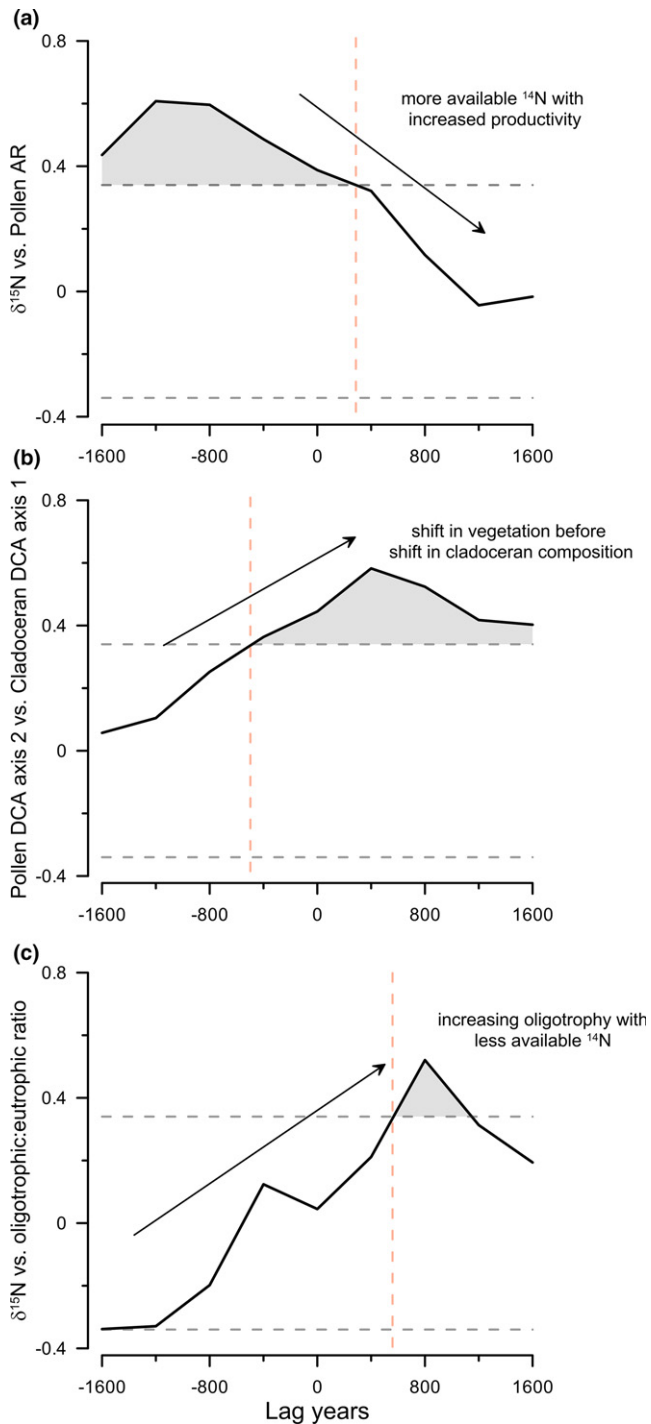


FIGURE 6 Cross correlation analysis of Paddy's Lake data with four lags of 400 year bins for: (a) $\delta^{15}\text{N}$ versus pollen AR; (b) pollen DCA axis 2 versus cladoceran DCA axis 1; and (c) $\delta^{15}\text{N}$ versus oligotrophic:eutrophic cladoceran ratio [Colour figure can be viewed at wileyonlinelibrary.com]

organic $\delta^{15}\text{N}$ values and an increase in the important occurrence of littoral cladocerans within the lake (Figure 5).

In contrast, "pelagic" cladocerans (e.g. *B. meridionalis*) at Paddy's Lake favour oligotrophic lake conditions (Geddes, 1988; Green, 1976) and increases in these taxa occur during phases of low relative

moisture, reduced regional forest cover, increased regional fire activity (Beck et al., 2017; Fletcher & Moreno, 2012; Mariani et al., 2017; Stahle et al., 2016), consistent with reduced terrestrial organic matter inputs (Br: Figure 4a) and $\delta^{15}\text{N}$ enrichment of organic matter within the lake: i.e. oligotrophic lake water (Figure 4f). Our results, then, reveal a shift towards more oligotrophic-tolerant cladoceran community (dominated by *B. meridionalis*) that precedes $\delta^{15}\text{N}$ enrichment of organic matter within the lake, reflecting (1) a shift towards 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 $\delta^{15}\text{N}$ 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 4), 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, 2001; Talbot & Johannessen, 1992)—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.

6 | 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 kyr 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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ORCID

Kristen K. Beck  <http://orcid.org/0000-0002-8257-9639>

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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.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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