

# Assessing anthropogenic climate change and land use impacts on lake ecosystems in Hawke's Bay, Aotearoa- New Zealand

By

Samantha McAulay

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## Abstract

Lakes across Aotearoa-New Zealand carry strong cultural, ecological, and economic value but are currently threatened by anthropogenic climate change and land-use pressures (MfE, 2021). Anthropogenic climate change is having rapid effects on lacustrine environment, with temperatures expected to increase 1-2°C over the next century (MFE 2020, ). The last 1,000 years of climate history has however experienced weather conditions similar to those predicted during the Medieval Climate Anomaly, (MCA) which may provide a useful analogue of ecosystem structures. Aotearoa-New Zealand also has a unique history of land use due to the relatively recent migration of humans experiencing three major land-use changes: Pre-human impact environment ( $\leq 1250$  CE), subsistence agriculture ( $\sim 1250$ -1820 CE) and intensification of agriculture ( $\sim \geq 1820$  CE). With these distinct phases it allows for the identification of how ecosystems adapt to varying degrees of catchment pressures.

This study focuses on Kaweka Lake in the Hawke's Bay region of the north island, Aotearoa-New Zealand. The two aims of this thesis are to identify evidence of the anthropogenic climate change within an lake of Aotearoa-New Zealand, how ecosystems change in response to previous climate shifts, with providing possible analogues for predicted future conditions, as well as catchment pressures on biodiversity. These aims were achieved by using a multi-proxy approach of the pre- and post-human environment of Lake Kaweka utilizing paleolimnological and environmental reconstruction methods of using fossilised chironomid head capsules, palynology, eDNA and hyperspectral scanning.

The pre-human environment was characterised by a closed catchment of tall trees with an ecosystem which was the steadiest observed, producing an environment with naturally high levels of nutrients and algae growth, likely driven by high rates of natural erosion of the region. The beginning of subsistence agriculture is identified by the introduction of charcoal

in the record and rapid decline of tall trees, which is replaced by shrubs and grasses, particularly *Pteridium esculentum*. There is also a change of the primary production within the lake to be primarily dominated by macrophytes as indicated by the increase abundance of *Naonella kimihia*. (Boothroyd, 2012). The intensification era is defined by the decline of indigenous fauna and introduction of exotics, specifically *Pinus* and where biodiversity experiences the most instability with a transition to more environmentally tolerant species. Temperature reconstruction shows evidence of anthropogenic climate change as well as the MWA, which may provide an analogue for an ecosystem which may be more resilient to future warming under anthropogenic climate change. However, this may be affected by the culminated effects of historic and current land use practices.

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<b><u>Contribution</u></b>	<b><u>Researcher</u></b>
Research	Samantha McAulay
Writing	Samantha McAulay
Editing	Samantha McAulay, Dr. Andrew Rees, Dr. Susie Woods
Data collection	Lakes380
Hyperspectral scanning	GNS
Pollen analysis	GNS- Xun Li
Chronology	Lakes380
eDNA laboratory work	Cawthron Institute- Dr. Susie Woods, Georgia Thomson-Laing, Jacob Thomson-Laing, Samantha McAulay
Chironomid preparation	Samantha McAulay
Chironomid identification	Dr. Andrew Rees
Data analysis	Samantha McAulay, Dr. Andrew Rees

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## Chapter 1: Introduction

### Motivation, rationale, and research aims

Lakes in Aotearoa-New Zealand are taonga, possessing strong cultural, ecological, and economic value. However, these delicate ecosystems are threatened by anthropogenic climate change and land-use changes causing pressures on various lake processes and biodiversity (MfE, 2021). Anthropogenic climate change, driven by increased atmospheric carbon dioxide, has led to unpredictable and severe weather patterns and increasing temperatures, both of which negatively impact lacustrine ecosystems and processes (Hamilton *et al.* 2013). The impacts of anthropogenic climate change on ecosystems are also compounded by land-use changes. The history of land use changes within Aotearoa-New Zealand is unique due to the relatively recent arrival of humans to the archipelago approximately 700 years ago (Anderson, 1991; Glade, 2002; Woodward *et al.*, 2014). Since the first migrations occurred, estimated through the use of environmental proxies and oral histories, there have been three distinct land-use phases: the arrival of the early ancestors of Māori (~A.D. 1250), the arrival of Europeans (~A.D. 1820) and the intensification of agriculture (~A.D. 1920). The distinction of these phases allows for the identification of possible environmental impacts and how ecosystems can adapt to varying degrees of catchment pressures.

Sediments within a lake are constantly being deposited, preserving indicators of previous lake health as well as catchment properties and local climate, equivalent to centuries of monitoring. These indicators include a variety of ancient eDNA targets archived in the sediments, as well as plant and invertebrate macrofossils, which provide a continuous and detailed understanding of environmental perturbations and the corresponding ecosystem responses.

The aims of this study will be to assess changes within Kaweka Lake, Hawke's Bay, encompassing the last 1,000 years to assess how climate and land-use changes may have impacted the ecosystem's biological integrity. This study focuses on the last 1,000 years as it encompasses the Medieval Climate Anomaly (MCA), when temperatures were approximately 0.5°C warmer in Aotearoa-New Zealand (Cook *et al.* 2002; Burrows & Greenland, 1979; van den Bos *et al.* 2018) potentially serving as a useful analogue for future warming under anthropogenic climate change (Woodward & Shulmeister 2006). All three phases of human settlement in Aotearoa-New Zealand, as well as some of the pre-human era, are contained within this time constraint, permitting comparative analyses of land-use impacts.

This study focuses on one of the Kaweka Lakes in the Hawke's Bay region of the North Island. It is a lake of good ecological health with a long history of human settlement within the region. Hawke's Bay is also a sensitive Kidson climate region that responds to trough, zonal, and blocking regimes (Kidson, 2000); see section 2.5.2 for more details of the study site. Improving our knowledge on how both previous climate shifts and the magnitude of different anthropogenic impacts on lacustrine environments affect lake health is critical in protecting the environment and setting management targets into the future (Barouillet *et al.*, 2022; Domaizon *et al.*, 2017; Woodward & Shulmeister 2006).

## 1.1 Aims

### 1.1.1 Is there evidence of anthropogenic climate change in a lake of good ecological condition in Aotearoa-New Zealand?

To address this aim, I will reconstruct the last 1,000 years of climate history at Kaweka Lake, located in Hawke's Bay. The last 1,000 years of climate history in Aotearoa-New Zealand encompasses the Medieval Climate Anomaly (MCA), when temperatures were about 0.5°C warmer than 1950 (Cook *et al.* 2002; Burrows & Greenland, 1979; Lüning *et al.*, 2019; van den Bos *et al.* 2018). Consequently, the MCA could serve as a useful analogue for future warming predicted under anthropogenic climate change. Understanding how species richness and abundances respond to previous climate events allows for insight into how current ecosystems will change, directing various management practices to protect the environment and increase resilience of particular species which may be expected to decline (Capo *et al.*, 2022; Barouillet *et al.*, 2022).

### 1.1.2 How does ecosystem diversity change in response to climate and catchment pressures?

To address this aim, I will be identifying DNA-derived communities and following species diversity fluctuations over the period of 1,000 years in Kaweka Lake. The last 1,000 years of human history in Aotearoa-New Zealand encompasses the pre-human era which allows for the understanding of natural variability as well as subsequent human migrations and population expansions through into present times (Anderson, 1991; Wilson, 2005). Freshwater ecosystems are intrinsically linked to both climate and land-use changes and can become compromised by over-exploitation, and pollution, altering important ecosystem services like filtration capacity and groundwater flow regulation (Dale, 1997; Pielke 2005; Teuling *et al.*, 2019). These catchment changes can lead to ecological impacts on biodiversity inhibiting ecosystem function and resulting in mass extinction (Dirmeyer *et al.*, 2010; Lv *et al.*, 2023; Prevedello *et al.* 2019).

## Chapter 2: Literature Review

### 2.1 Lakes as archives of environmental history

By definition, lakes are bodies of standing water surrounded by land. Most lake water is supplied by a surrounding watershed/catchment that is often large, relative to the lake's size (Cohen, 2003). Lakes are vital to the cultural and environmental identity of Aotearoa-New Zealand with around 3,820 lakes larger than one hectare and 775 lakes having a margin of at least 0.5 km long, taking up approximately 1.3% of the total available land cover (excluding offshore islands) (LAWA, 2021). Few countries of comparable size have the same diversity of lake origins. Aotearoa-New Zealand has a complex biogeographical history culminating in mountainous, glacial, volcanic, landslide, dune/coastal and human-made lakes (Nathan, 2007) with each of these lake types providing a magnitude of essential ecosystem services. These services play a global role in atmospheric and landscape carbon cycling by storing and processing organic and inorganic carbon (Tranvick *et al.*, 2009). Regional-scale lake services include climate regulation through the exchange of heat and water via evaporation into the atmosphere, as well as impacting regional water cycles with the replenishment of groundwater supplies, flood mitigation and nutrient transport (Kundzewicz, 2008). Lakes are disproportionately rich in biodiversity relative to size because they provide a variety of habitats for plant and invertebrate species and migration stops and breeding grounds for many bird and fish species (Pearman *et al.*, 2022). Lakes also support a variety of human aesthetic and recreational needs, increasing overall well-being and quality of life (Gascon *et al.*, 2015). Aquatic ecosystems are also taonga for Māori, often woven into whakapapa and iwi identity, underpinning the connection to the natural world or more practically serving as a place that sustains mahinga kai. (LAWA, 2021).

Lakes are extremely sensitive to slight changes in the environment, acting as sentinels on the landscape creating historical archives of the surrounding catchment (Cohen, 2003). The term archive refers to both the historical record, contents and how or where these records are stored: the container (Figure 1). All lakes experience both intrinsic and extrinsic forcing variables which create the subsequent history of the lake. These different variables can include climate, volcanic and tectonic activity, animal and plant biota and human activities, all which are highly interactive (Cohen, 2003). These variable records are stored in three different types of container archives. The water itself is an archive, particularly in lakes with long resident times, which can date back multiple millennia (Cohen, 2003). A more durable archive is the geomorphology of the lake basin, specifically, the lake's shape and shoreline as these features can persist long after the lake has disappeared (Cohen, 2003). However, the most important archive for paleolimnology is the accumulated sediments. These sediments provide the most durable container as they persist for the lake's entire lifecycle and can remain long after the lake or the geomorphology is destroyed (Cohen, 2003). Content archives are the sediment inputs of the lake's records, stored in the accumulated sediments. It is these content archives which hold value for investigating past environmental conditions and can include a variety of sediment types including terrigenous, chemical, biogenic, volcanic, and cosmogenic particles, and fossils that originate outside of the lake, such as pollen, or within the lake, like chironomids, or aerosol and water-borne pollutants (Cohen, 2003). Because of this, lakes can act as early indicators of a changing climate and time capsules of land-use changes (Dieffenbacher-Krall et al. 2008; Thompson et al. 2005; Rogora et al. 2018; Walker, 1987; Woodward & Shulmeister, 2006).



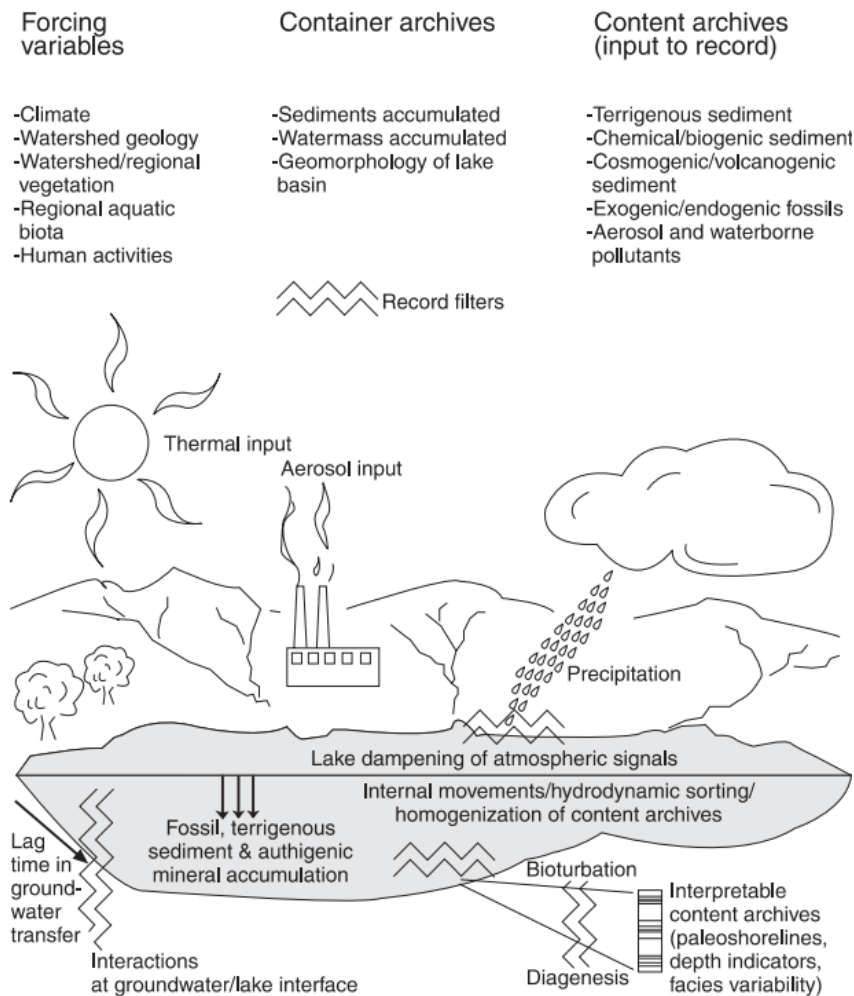


Figure 4: A simplified model of the important controlling factors of the formation of the sedimentary archives within lakes. Forcing variables are external factors that manage the creation, characteristics, and persistence of the lake. Container archives house the indicators of external environmental changes and conditions. Content archives are the physical records that paleolimnological history uses in environmental reconstruction. Zigzag lines indicate major points of record filtering. (Retrieved from Cohen, 2001).

## 2.2 Use of Paleolimnology

Paleolimnology and environmental reconstructions are tools which can inform future conservation management directions by quantifying how current lake ecosystems and catchment use compare to a pre-human environment (Cohen, 2003; Beermann et al. 2018; Il'yashuk & Il'yashuk, 2002; Mrozińska & Bąkowska, 2020). Lake sediments are often deposited over time and preserve the indicators of lake biodiversity and catchment changes over millennia. Examining these sediments has the potential to offer detailed documentation

of a lake's history, providing insights into the relationships of the possible drivers of change (both natural and anthropogenic) and the indicators of a lake's ecosystem responses.

### 2.3 Indicators of lake ecosystem diversity and land use changes

To identify baseline conditions, paleolimnology largely depends on the ability to separate past human land uses from natural forces within the lake. Ways to identify anthropogenic impacts on the environment using lake sediments included in this study involve sampling pollen grains and plant macrofossils, charcoal, chlorophyll- $\alpha$  content, eDNA and chironomid remains.

#### 2.3.1. Pollen and charcoal

Pollen grains and spores are typically dispersed in an environment through wind, rain and animals, and accumulate within lake sediments. Therefore, the overall assemblages of pollen sampled from sediments is often reflective of the of the surrounding catchment vegetation, with certain specific indicator taxa being representative of human influences as well as mean annual temperatures, growing season length, rainfall, and drought (Newnham *et al.*, 2013; van den Bos *et al.*, 2018). Pollen records can also highlight past vegetation dynamics which can be related to a variety of influences from changes in Earth's orbit to finer scales of climate drivers like ENSO (El Niño-Southern Oscillation) and the SAM (Southern Annular Mode) (Lorrey & Bostock 2017). As Aotearoa-New Zealand is an isolated island country, there are multiple plant species which indicate the arrival of humans and from where those populations originated. Introduced species which indicate European arrival, for example, include *Pinus* and *Salix* species (Berg, 2007). Macrophytes with large amounts of lignin are silicified, preserving in lake sediments and are used as indicators of water chemistry, particularly

nutrient levels, sedimentation and salinity; these taxa also aid in developing the chronology of the lake.

Wherever there is plant material, there will often be fire, and charcoal is found in Aotearoa-New Zealand lake sediments of all ages (Perry *et al.*, 2014). Throughout the Holocene and along with modern observations, natural forest fires often only occurred on ridge tops or individual trees from lightning strikes, but forest fires were extremely rare, as weather systems carrying lightning tended to be associated with wet fronts. Volcanism is also a potential fire source, but eruptions causing fires during the Holocene were rare and localised (Ogden, Basher & McGlone, 1998; Perry *et al.*, 2014). From the soil charcoal surveyed, approximately 12% of the land area in Aotearoa-New Zealand was exposed to prehuman fires, notably some wetland systems in Northland and southwestern regions of the South Island; however, these events were rare (1-2 events/ millennia) and with the exception of a few, ecologically insignificant (Ogden, Basher & McGlone, 1998; Perry *et al.*, 2014; McWethy *et al.*, 2010). Where fire is neither frequent nor predictable, species are less likely to have evolved specific adaptations either in the form of recovery or tolerance. Aotearoa-New Zealand has a few plant species which have a rapid response to fires; however a number respond rapidly to any form of disturbance including bracken fern/ rārahu (*Pteridium esculentum*), mānuka (*Leptospermum scoparium*), kānuka (*Kunzea ericoides*) and tutu (*Coriaria*) (Ogden, Basher & McGlone, 1998; Perry *et al.*, 2014). The lack of fire adaptations in the landscape and long successional recovery periods of forests gives the view that, prior to human arrival, the forests of Aotearoa-New Zealand rarely burned. Approximately 700 years ago, an increase in magnitude and frequency of charcoal in stratigraphic records coincides with occurrences of indicator pollen taxa and is thus considered strong evidence for an anthropogenic influence on the environment, particularly as forest burnings were historically the chosen method of

land clearance of early settlers (Ogden, Basher & McGlone, 1998; Perry *et al.*, 2014; Wilson, 2005).

Invertebrates' response to fire tends to be greatly variable and difficult to detect. However, one generally consistent response pattern to fire is the immediate decrease of invertebrate taxa abundance (Araneda *et al.*, 2012; Driessen & Kirkpatrick, 2017; McWethy *et al.*, 2010). This decrease may be associated with the post-fire composition of vegetation and structure which can increase water temperature due to the opening of the canopy, change the water chemistry, and increased sedimentation rates. Fire can cause immediate changes in water chemistry from both the by-product of the heat and smoke and ash inputs. These inputs decrease the levels of dissolved oxygen, as well as increase water pH and inorganic nitrogen and phosphorus (Smith *et al.*, 2011). These changes in water chemistry and temperature are often temporary, but may have impacts on species abundances, particularly sensitive taxa. A study by Delettre (1994) on the impact of fires on terrestrial chironomid communities found that after an initial decline in abundance, the second year post-fire observed increased species richness and abundance, before markedly decreasing again the following year. This suggests larvae briefly benefitted from ephemeral in-wash of post-fire nutrients.

### 2.3.2 Chlorophyll- $\alpha$ from hyperspectral scanning

Spectroscopic methods utilise the reflectance in the visual to near visual light range, measuring the spectral data directly from the fresh sediment cores (Butz *et al.*, 2015). When compared to a spectral index of reflectance spectra, quantitative data concerning chlorophyll  $\alpha$ , bacteriopheophytin  $\alpha$ , lutein, chlorins and organic carbon can be estimated, all of which relate to environmental changes surrounding the lake (Butz *et al.*, 2015). Chlorophyll  $\alpha$  and lutein are produced by plants with bacteriopheophytin  $\alpha$  being produced by bacteria. The

concentration of these chemicals in a sediment core fluctuates with algal concentrations and oxygen levels within the environment, increasing under anoxic conditions which can result in a decline in biodiversity (Butz *et al.*, 2015). In particular, the Relative Absorption Band Depth (RABD) 660 to 670 measured by hyperspectral scanning is correlated to the amount of chlorophyll- $\alpha$  and degradation products archived in sediment cores (Rein & Sirocko, 2002).

The microbiome of lake sediments is just one aspect of taxa which can represent benthic community health. eDNA (environmental DNA) metabarcoding of this microbiome can identify benthic communities' health and trends (Capo *et al.*, 2022; Domaizon *et al.*, 2017; Pearman *et al.*, 2022). These trends can then be related to anthropogenic impacts as well as changes in the environment, including nutrient availability and water chemistry (Cohen, 2005). DNA-based methods allow for the study of intra-specific diversity and ecosystem functions of past lacustrine environments. DNA reflects information about the organisms which have lived both in the sediments and the water column. Sediment can store the DNA of biological communities for millennia; however, the extent to which the DNA is preserved is determined by multiple factors. Anoxic conditions, a low-stable temperature and stable stratification appear to be some of the most crucial factors promoting DNA preservation in lacustrine sediments (Martinez *et al.*, 2014). Other factors influencing degradation speed include: mineralogical composition, organic matter load, and DNase activity. Another technical factor is the choice of gene region used to target specific groups of species. Mitochondrial cytochrome c oxidase 1 (CO1) is the 648-bp (base pair) segment known as the universal code as it can identify most of the kingdoms, but is primarily used for animal. As the CO1 segment is less reliable in capturing DNA from fungi and bacteria, 16S and 18S ribosomal RNA (rRNA) genes are preferred. Nevertheless, as the studies into sedimentary DNA grow,

successful results can be obtained from systems which are fully oxygenated and from lakes in temperate and arid environmental conditions.

Many of the organisms which can be recorded in the sedimentary eDNA record can tell a variety of things about the state of a lake's health and natural fluxes of nutrient levels and stratification (Barouillet *et al.*, 2022; Capo *et al.*, 2017; Domaizon *et al.*, 2017). Lake eukaryotic microalgae have several dominant groups (chlorophytes, diatoms, chrysophytes, cryptophytes, and dinoflagellates) which can indicate different environmental conditions. Eukaryotic microalgae are phylogenetically diverse, each having different requirements of nutrient levels, pH levels, light and temperature requirements to thrive (Barouillet *et al.*, 2022). Bacteria and archaea, which are found in most aquatic environments are also able to be identified in the sediment record with diversity and abundances tightly linked to environmental conditions, including light, oxygen, nutrients and organic matter. Understanding these groups are important, as they contribute to ecosystem productivity by being primary producers and are a part of the process of recycling organic matter into the trophic network (Barouillet *et al.*, 2022). Changes of cyanobacteria can indicate anthropogenic stress on a lake as they respond positively to increased nutrient enrichment and warmer temperatures. However, due to the lack of long-term data of natural cyanobacterial community's, pre-human disturbances and interannual variability are not fully known (Barouillet *et al.*, 2022).

### 2.3.3 Chironomidae

Although time-consuming, due to from identification and need of taxonomic expertise chironomids are among the best indicators of overall lake health and summer temperatures (Coa *et al.*, 2019; Dieffenbacher-Krall *et al.* 2008; Eggermont & Heiri, 2012; Nazarova *et al.*, 2008; Walker, 1987; Wang *et al.*, 2008 Woodward & Schulmeister 2006). Chironomidae

(Order: Diptera) are non-biting midges that spend much of their life as aquatic with a lifecycle that can range from less than a week to over a year depending on the species, season and environmental conditions. Chironomidae have wormlike bodies between 1-20 mm with distinct head capsules that are preserved by lake sediments (Figure 2).



Figure 5: (left to right) Chironomid midge larvae Orthocladiinae and Chironomidae. Both subfamilies are native to New Zealand and commonly found in lakes. (Retrieved from <https://www.landcareresearch.co.nz/>).

It is estimated there are well over 10,000 species within the Chironomidae family worldwide and this family is frequently the most abundant group in any given freshwater environment, often making up at least 50% of the macroinvertebrate species present. This high diversity can be attributed to the antiquity of the species and relatively low mobility leading to high levels of isolation and evolutionary plasticity (Armitage *et al.* 2012). Chironomids are geographically ubiquitous, free-living, holometabolous (winged adults distinct from aquatic juveniles) insects (exceeded by only a few mites, lice and springtails) and are found in a variety of environments within every zoogeographic region. These environments cover a gradient of temperatures, pH levels, salinity, lake depth and oxygen availability, including elevations up to 5,600 m a.s.l in the Himalayan Mountain range, where temperatures get to -16°C and to depths of over 1,000 m in the sediments of Lake Baikal, the world's deepest freshwater lake (Beermann *et al.* 2018). This diversity enables certain species to be extremely tolerant of different environmental conditions, surviving in situations so polluted no other insect can

endure (Beermann *et al.* 2018). These polluted environments include stagnant farm ditches affected by agricultural and horticultural runoff high in nitrogen and phosphorous (Wilson & McGill, 1977) as well as rivers impacted by high levels of heavy metal inputs including copper (Cu), zinc (Zn), chromium (Cr), nickel (Ni) and lead (Pb) common in urban environments and mining runoff (Deliberalli *et al.* 2018; Larocque *et al.* 2001).

Chironomids have four life stages: egg, larvae, pupa, and adult, with a majority of the lifecycle spent in the larval stage and most of that being in the fourth instar (Figure 3). Larval chironomids go through four instars each undergoing ecdysis (the process of shedding the outer cuticle). The first two instars do not preserve particularly well and lack observable diagnostic features. While the soft parts of all the instars tend to decay, the chitinous head capsule of the third and fourth instars can be well-preserved in lake sediments, making chironomids a useful indicator for environmental reconstructions (Porinchu & MacDonald, 2003).

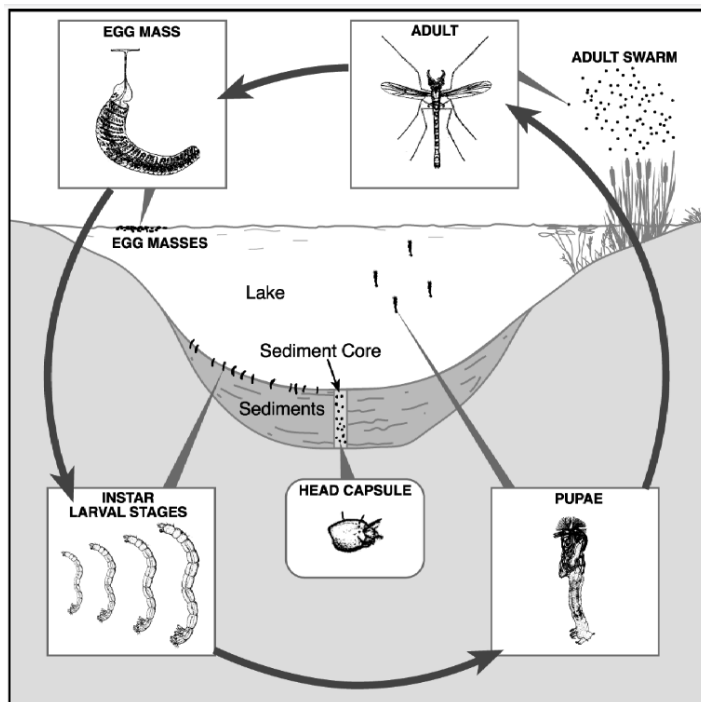


Figure 3: Typical lifecycle of Chironomidae. Retrieved from Porinchu & MacDonald, 2003).



The earliest fossils of chironomids have been dated to the Jurassic period of the Mesozoic (Il'yashuk & Il'yashuk, 2002). However, remains typically only become abundant in lake sediments through the late or post-glacial periods since the last glaciation 21,000 years ago (Il'yashuk & Il'yashuk, 2002).

The Chironomidae's ability to exist in a large range of environments has been achieved by relatively slight morphological, behavioural, or physiological adaptations (Armitage *et al.* 2012). These adaptations include different functional feeding groups, modes, and behaviours. A morphological adaption as a result of a chemical modification is displayed by the genus *Chironomus* through a change in colouration. *Chironomus* adapted its colour by appearing bright red due to a haemoglobin analogue which increased its ability to capture oxygen in depleted environments (Poznańska *et al.* 2017) (Figure 4).



Figure 4: Image of a *Chironomus*, demonstrating the red colouring due to a haemoglobin analogue. (Retrieved from <https://www.landcareresearch.co.nz/>).

Behavioural adaptations due to reduced water levels can include horizontal migration to reach more damp areas or burying deeper into the moist substratum (Poznańska *et al.* 2017).

Physiological adaptations in dry conditions can also involve modifying lifecycles by accelerating their development into adults to increase the chances of successful breeding (Poznańska *et al.* 2017).

Chironomid subfamily distributions are closely related to maximum lake depth and mean summer temperatures at a range of spatial and taxonomic levels (Dieffenbacher-Krall *et al.* 2008; Eggermont & Heiri, 2012; Larocque *et al.* 2001; Walker *et al.* 1991) (Figure 5). Trends observed globally of chironomid distributions are similar to those seen within Aotearoa-New Zealand (Woodward & Shulmeister, 2006) with three subfamilies, which are widely distributed comprising the majority of the taxa observed in lake sediments: *Chironomidae*, *Tanypodinae* and *Orthoclaadiinae*. Other subfamilies which are also widely distributed but less common in Aotearoa-New Zealand include: *Diamesinae* and *Podominae* (Eggermont & Heiri, 2012). The diversity and abundances of many of these subfamilies are linked to temperature along both latitudinal and elevational gradients. *Diamesinae*, *Podominae* and *Orthoclaadiinae* are more common in cool or cold-water environments, whereas the other groups, particularly *Chironomidae* and *Tanypodinae*, are often found at higher abundances in intermediate to high temperatures, with studies into the distribution of subfossil remains confirming these trends (Eggermont & Heiri, 2012).

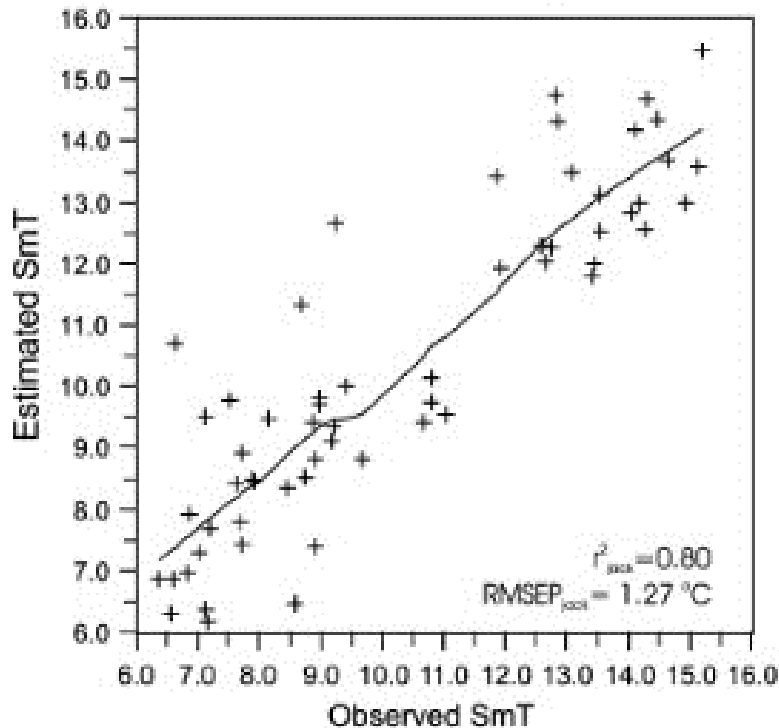


Figure 5: Observed vs. estimated mean summer temperatures ( $^{\circ}\text{C}$ ) using subfossil Chironomids from 60 sites across Southern Alps, Aotearoa- New Zealand. Retrieved from Dieffenbacher-Krall, Vandergoes and Denton, 2007.

These correlations, as well as chironomid species richness and the biological knowledge of individual taxa and ecological optima, has led to the group being used as a biological and climate monitoring tool in a variety of palaeoecological studies (Beermann *et al.*, 2018; Eggermont & Heiri, 2012; Larocque-Tobler *et al.*, 2010; Il'yashuk & Il'yashuk, 2002; Mrozińska & Bąkowska, 2020; Wagner *et al.*, 2009; Walker *et al.*, 1991; Woodward & Schulmeister, 2006-2007) (Figure 5). These palaeoecological studies include quantitative and qualitative calibration models which allow for the reconstruction of various environmental characteristics and parameter changes based on species assemblages.

Numerous climatic processes, both direct and indirect, influence chironomid species' presence, abundance, and distribution (Walker, 1987). Higher temperatures provide longer growing seasons, which facilitate greater biological productivity as well as increase the chemical weathering rates, which yield higher nutrient levels. Catchment vegetation can

influence the nutrient fluxes within a catchment which also indirectly influences chironomid fauna (Deliberalli *et al.* 2018; Mrozińska & Bąkowska, 2020; Walker, 1987), with direct impacts of temperature driving species distribution to align with environmental tolerances (Armitage *et al.* 2012; Beermann *et al.* 2018). Climatic effects can also exacerbate landscape impacts, leading to anthropogenic-driven eutrophication which chironomid assemblages can dramatically respond to, with drops in oxygen and light levels reducing species abundance and diversity. Increased nutrient loading in lakes is influenced by urban and agricultural land use and can dramatically increase the productivity of lakes and create anaerobic conditions (MfE, 2022). In addition to these, allochthonous inputs resulting from human behaviour, such as sewage and fertilizer run-off, compound de-oxygenation of aquatic systems (Walker, 1987). The head capsule subfossils of chironomids, thus can provide a record of past eutrophication events, which has led to this group of invertebrates being frequently used in ecological and environmental monitoring as a tool to investigate land-use changes and impacts as well as a proxy for climate change (Armitage *et al.*, 2012; Dieffenbacher-Krall *et al.*, 2008; Larocque *et al.*, 2001; Walker, 1987).

## 2.4 Climate of Aotearoa, New Zealand

### 2.4.1 Historic climatic patterns

The Holocene is the current geological epoch beginning approximately 11,650 cal years before present, starting after the transition from the last major glacial epoch. The Holocene is an interglacial period, characterised by a relatively stable, warm climate (Jones & Mann 2004). However, despite a relatively stable climate, there have been a variety of episodes in Aotearoa-New Zealand falling outside of mean Holocene climate (Gellatly *et al.*, 1988), for instance rapid expansion of glaciers in three phases between 12 and 9 ka BP. These phases occurred around 11,900, 10,900-10,250 and 9500 BP suggesting a cooler climate occurring

with temperatures that were 2-3 °C lower than present and markedly drier conditions (Gellatly *et al.*, 1988). This decline in precipitation is consistent with a southward shift of the south-westerly wind belt, causing the westerly winds over the country to decline (van den Bos *et al.*, 2018).

After these glacial expansions, the climate between 9 and 5 ka BP became markedly wetter and milder due to temperatures rising rapidly (Gellatly *et al.*, 1988). This warming is observed throughout Australasia and suggests this period was one of maximum warmth generally referred to as the Holocene Thermal Maximum (HTM), as a result of a subtropical front (van den Bos *et al.*, 2018) with temperatures approximately 1-1.5°C above present day (Lorrey & Bostock 2017). This phase is an important benchmark for testing climate models, as it represents the most recent example of major natural climate change. For climate models to produce trustworthy predictions into the future, they must also accurately reconstruct past climates.

Several major ice volume fluctuations occurred throughout the mid-Holocene between 5 ka-1 ka BP likely driven by a more prominent blocking over zonal regime (Lorrey & Bostock, 2017). The climate variations of Aotearoa-New Zealand through the last 2,000 years can be grouped into four multidecadal timescales. The first intervals (approximately 2,000 years ago to 450 CE) is represented by frequent blocking with moderate-to-cool temperatures, whereas the second interval (~450 - 750 CE) is characterised by a more variable hydroclimate and warmer temperatures. The third interval (~ 750 – 1500 CE) possesses variable water balance and surface temperatures, implying more frequent blocking regimes, with the phase between 900 and 1500 AD often referred to as the Medieval Climate Anomaly (MCA), with temperatures 1°C warmer than present (Cook *et al.*, 2002; Lorrey & Bostock, 2017; Lüning *et*

*al.*, 2019). The MCA ending around 1500 CE is two centuries later than other Northern Hemisphere regions, like across Europe, which suggests possible interhemispheric climate lag mechanisms (Lüning *et al.*, 2019). The final interval (1500 CE into the onset of the 20<sup>th</sup> century) was likely influenced by greater trough and zonal regimes, typified by the more frequent wet and cold conditions. These periods of climatic differences were major regional events, and the patterns are similar to those observed in the Northern Hemisphere throughout the European Alps (Gellatly *et al.*, 1988) with evidence suggesting that a Little Ice Age (LIA) between 1450 and 1850 CE was about 1.0°C lower than present, for which there is some evidence in Aotearoa-New Zealand (Cook *et al.*, 2002; Lorrey & Bostock, 2017).

#### 2.4.2 Current climatic patterns

Aotearoa-New Zealand is located in the southwest of the Pacific Ocean between 34 and 47°S, which lies largely within the prevailing Southern Hemisphere circulation belt (westerlies) while also intercepting the subtropical convergence zone, characteristic of the mid-latitude Southern Hemisphere (Newnham *et al.*, 2013). These westerlies interact with the mountainous topography of the country resulting in localised and regional-scale climate variations, particularly concerning precipitation (Lorrey *et al.*, 2007). As an isolated island country, surrounded by the ocean, the regional weather and climate variations of Aotearoa-New Zealand are prone to influences from moisture-laden, humid maritime airmasses, high-pressure systems from sub-tropical zones as well as low-pressure systems from the sub-Antarctic Southern Oceans (Lorrey *et al.*, 2007). Anti-cyclones/ridges, fronts, and depressions/troughs from within the westerly flow predominantly govern the regional weather cycles of Aotearoa-New Zealand (Newnham *et al.*, 2013).

The mountain ranges that trend southwest to northwest over the North and South Islands dictates the regional precipitation regimes. These mountain ranges create a strong west-east

gradient of both precipitation and air temperatures (Figure 6) with the seasonal- and decadal-scale variability being largely dictated by these interactions between the westerly winds, topography, and global weather phenomena (Lorrey *et al.*, 2007).

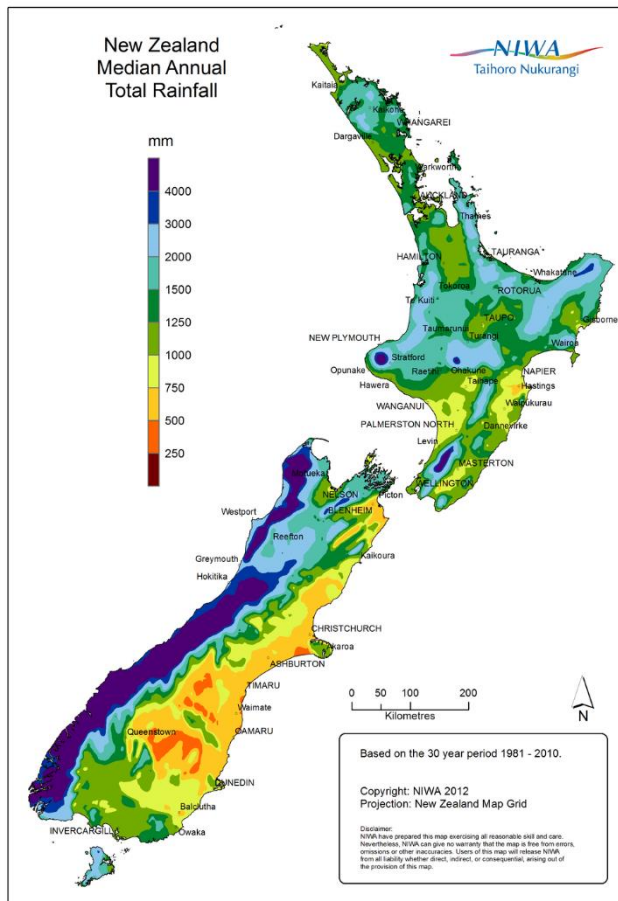


Figure 6: Map of the median annual rainfall based over a 30-year period (1981-2010) of Aotearoa-New Zealand. (Retrieved from NIWA <https://niwa.co.nz/climate/national-and-regional-climate-maps/national/>).

The climate of Aotearoa-New Zealand also includes teleconnections to various global weather phenomena including the El Niño-Southern Oscillation (ENSO), the Inter-decadal Pacific Oscillation (IPO) and the Southern Annular Mode (SAM) (Lorrey *et al.*, 2007). ENSO is a recurring climate pattern which dominates the seasonal to inter-annual climate throughout the Pacific region. The climate pattern involves changes in water temperatures within the Pacific Ocean occurring over periods of time ranging from 3 to 7 years. Surface water temperatures across the ocean oscillate in a warming and cooling pattern ranging between

1°C to 3°C, directly affecting precipitation and easterly trade winds (Lorrey *et al.*, 2007). The IPO is a major source of decadal variability in the southwest Pacific, which manifests ENSO-like climatic features characterised by similar sea-surface temperatures and atmospheric pressure anomalies (Jiang *et al.*, 2013).

SAM is a ring-shaped climate pattern in the middle to high latitudes of the southern hemisphere which extends from the South Pole to the latitudes of Aotearoa-New Zealand. SAM describes a north-south movement of strong westerly winds which blow nearly continuously within the mid-high latitudes of the Southern Hemisphere. The changing positions and strengths of the westerly winds of SAM control precipitation, wind, temperature, and overall storminess of the country (Jiang *et al.*, 2013). The interactions of these global weather phenomena create a largely temperate climate across Aotearoa-New Zealand. While the far north can experience more subtropical influences, often during the summer, and the inland alpine ranges across the South Island can reach below 0°C in winter, most of the country lies close to the coast, creating, on average, moderate rainfall, abundant sunshine, and mild temperatures, varying between 10 and 14°C annually (Wratt *et al.*, 2015). These general climate features create six Kidson climate zones in Aotearoa-New Zealand characterised by a set of 12 daily weather types derived from a 40-year dataset (Kidson, 2000) (Figure 7).

These 12 daily weather types fall into the three major weather regimes; low pressure systems (troughs) which cross the entire country, high pressure systems from the north with a west-east flow into the south (zonal patterns) and blocking patterns with high pressure systems in the south. Blocking patterns occur when high pressure systems sit across the south of the islands, often resulting in sunny, dry weather that is more common through the summer and autumn months. This regime is associated with above normal temperatures, with



precipitation over the southwest of the country being less than that which occurs over the northeast. Zonal patterns are categorised by more west-east wind flows which bring normal levels of precipitation in the northeast and milder conditions in the south, common in spring. Lastly is the trough regime, often correlated with winter conditions as it is associated with below average air pressure, increasing storminess, as well as cooler temperatures over the west and above average precipitation across the country.

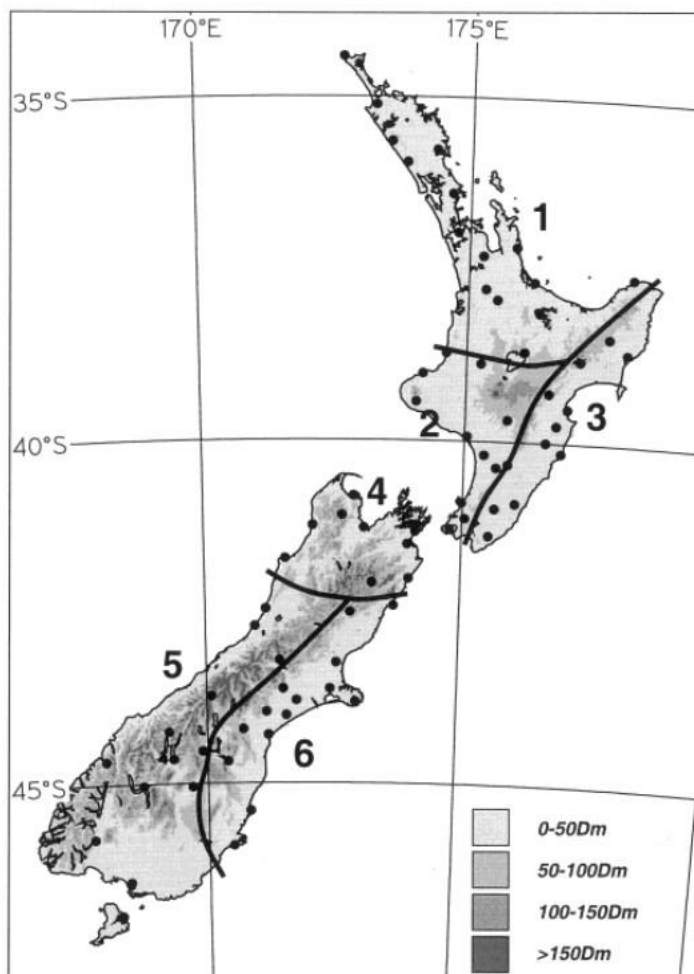


Figure 7: Map of Aotearoa- New Zealand's with lines representing the different Kidson climate regions (modified from Kidson, 2000). Black dots represent the locations of the 74 rainfall stations used to define the six homogenous regions labelled 1-6 which is superimposed onto a map showing the surface elevation in 500m (50Dm) contours.

Kaweka Lake is located in the Eastern North Island zone which is greatly influenced by the ESNO patterns. This region is characterised by near-average precipitation in trough conditions, below-average precipitation in zonal conditions and above-average precipitation during blocking conditions. However, Aotearoa-New Zealand has been experiencing higher-

than-average temperatures with more erratic precipitation events, which have persisted since 1950 CE and are atypical for the last 10,000 years which may influence how these regions are defined in the future (MfE, 2020).

## 2.5 Anthropogenic climate change and land-use pressures

Climate change is a natural process that has previously been influenced by ocean currents, Earth's orbital changes and volcanic eruptions. However, this process is currently being modulated by anthropogenic influences, which have resulted in observable warming since at least the 1970s (MfE, 2020-2022; Pachauri & Reisinger, 2007; Rosenzweig *et al.*, 2008). Warming is a response to human emissions changing the composition of the global atmosphere by altering greenhouse gas (GHG) concentrations, primarily carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O) and water vapour (H<sub>2</sub>O). The cause of these gas concentrations increasing is due to a variety of human activities including transport, electricity production as well as industrial and agricultural practices, with a global increase of these GHG concentrations of 70% since pre-industrial times (Rosenzweig *et al.*, 2008). These GHGs can persist in the atmosphere for hundreds of years after being released, influencing both present and future climate shifts. These GHGs are radiatively active, absorbing long-wavelength radiation and trapping heat which would have otherwise been escaped into space. Observational responses to anthropogenic climate change are found across a wide range of systems, primarily biological and hydrological systems with significant changes relating to warming conditions. These changes, which can impact the freshwater systems include an increase in primary production from longer growing seasons leading to lower oxygen and nutrient levels and increasing the risk of algal and toxic cyanobacterial blooms (Rosenzweig *et al.*, 2008), saltwater incursion from rising sea levels, as well as periods of inundation and drought due to changes in the time, frequency and intensity of storms (MfE, 2020).

### 2.5.1 Land-use pressure influencing local climate

Alongside the influences GHGs have on climate, land-use effects may be as least as important when concerning altering regional weather patterns (Dirmeyer *et al.*, 2010; Prevedello *et al.* 2019). Land use refers to the management practices which humans implement on a site (e.g. agriculture, urbanisation) whereas land cover is a descriptor of the vegetation at the site (e.g. native forest, pasture) (Dale, 1997). Where the Earth's climate can affect the terrestrial ecosystem's structure and function, the process can also work in reverse with changes in landcover and land use influencing the climate through both biophysical and biogeochemical processes which can confound the effects of anthropogenic climate change (Dale, 1997; Dirmeyer *et al.*, 2010; Lv *et al.*, 2023; Prevedello *et al.* 2019).

The biophysical processes of Earth's atmosphere respond to changes of energy, water, land and the proportion and movements of water and ice. Any changes of these surface fluxes can strongly influence atmospheric circulation patterns and thermodynamics (Foley *et al.*, 2003). These changes can include an increase of ocean temperatures during an ENSO, a collapse of a large ice sheet, or the replacement of native forest cover with pasture. Firstly, these changes can modify surface albedo, changing the energy balance and surface temperature. This can in turn impede how surface temperature stabilises and cools itself by shifting the balance between sensible and latent heat loss, with changes of the vegetation height and density influencing surface energy fluxes by altering how air mixes close to the ground. Rough surfaces like forests mix air more efficiently, enhancing surface cooling (Foley *et al.*, 2003) (Figure 8). This localised climate shift can affect species' fitness as they respond to the changes in temperature. Insects are highly responsive to temperature as they are ectotherms, elevating their metabolic and reproductive rates in response to warming until their thermal limit is reached. Higher metabolic rates can lead to increase stress on the insects which can

impede abundance and diversity (McGlynn *et al.*, 2019). A temperature shift can also restrict the species' habitat range, increasing intra-species competition for resources and creating novel predator/ prey relationships.

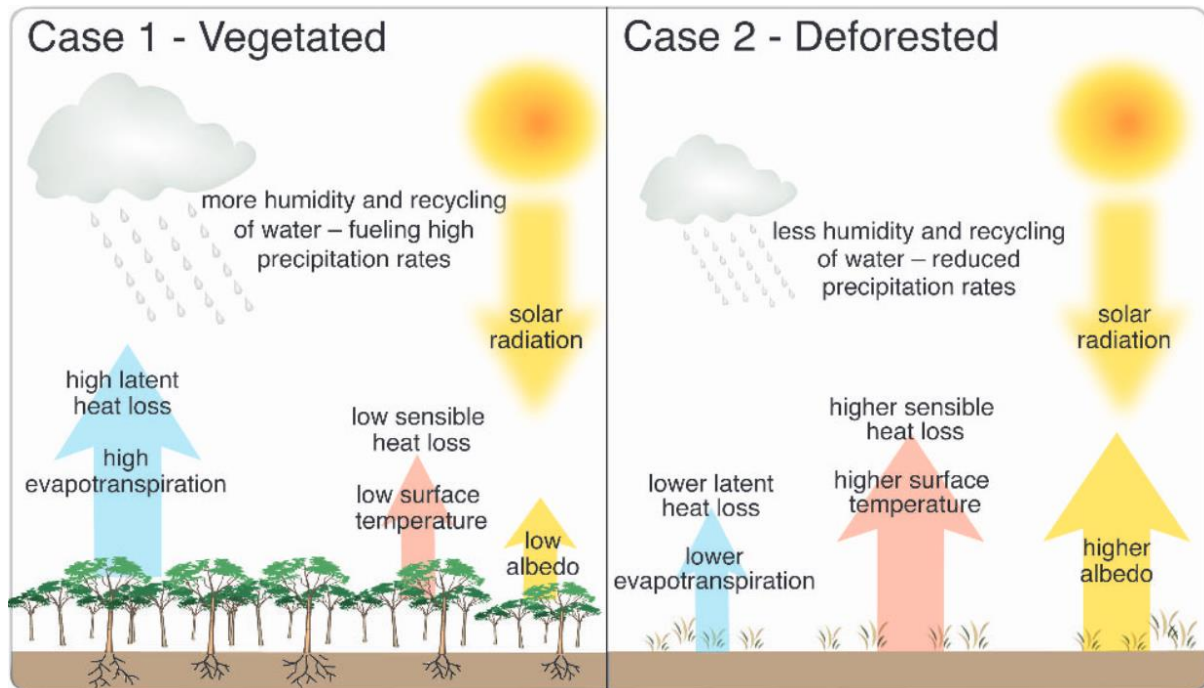


Figure 8: Diagram depicting relationship between forest cover and the climatic variables albedo, surface temperature and evapotranspiration. Left: A natural tropical forest cover showing low albedo due to the forest canopy which provides energy for plants to photosynthesize and transpire, which leads to high latent heat loss which cools surface temperature. Right: A deforested site with bare soil resulting in higher albedo, reducing the amount of energy which can be absorbed at the surface. This leads to a serve reduction of latent heat loss and higher surface temperatures with no means of removing the excess energy through transpiration (Retrieved from Foley *et al.*, 2003).

Aside from the atmospheric fluxes associated with landcover changes, ecological and environmental impacts can occur as a result of a changing landscape (Dirmeyer *et al.*, 2010; Dale, 1997; Foley *et al.*, 2003). These can be observed in fluctuations in local transpiration rates as a result of an altered albedo creating fewer cloud formations and more erratic precipitation. Locally, Hawke's Bay is expected to have less winter rainfall over the next 50 years; however, due to seasonal variation, precipitation is expected to increase in the summer. A change in seasonal precipitation can affect invertebrates as it can change seasonal-driven behaviours, such as reproduction. Changing precipitation patterns also affect

how nutrients move through the system altering the carbon cycle influencing mineralisation and sediment burial as well as food availability (Borrelli *et al.*, 2013).

#### 2.5.2 Land use pressure on freshwater ecosystems health

The effects of human-induced land-use changes within Aotearoa-New Zealand are unique due to the relevantly recent human history on the islands, which has had abrupt and profound impacts (Woodward *et al.*, 2014). Aotearoa-New Zealand was among the last major landmasses to be colonised by humans with three distinct land-use periods (Glade, 2002). These phases include the arrival of the early ancestors of Māori (~A.D. 1300), the arrival of Europeans (~A.D. 1820) and the intensification of agriculture (~A.D. 1920). These late arrivals led to abrupt changes in land use and allow Aotearoa-New Zealand to be an excellent case study of the possible effects humans have on the environment (Woodward *et al.*, 2014).

Māori arrival from southeast Polynesia saw the introduction of subsistence horticulture as well as the beginning of dominant forest type changes. Vegetation changes which resulted from forest burnings, made land available for building settlements (pā), created pathways for migration, and cleared sites for cultivation, especially for bracken fern (*Pteridium esculentum*), a primary source of carbohydrates (Wilson, 2005). This introduction of forest burnings impacted the environment by removing patches of old growth forests which had rarely been disturbed at such levels resulting in higher sensible heat loss with lower rates of transpiration at local levels (Wilmshurst, 2007).

The beginning of European settlement created the next identifiable land-use changes beginning in approximately 1820. These changes included large-scale deforestation practices of forests and wetlands to allow for the establishment of low-density agriculture, primarily of sheep and cattle, which has since become the country's economic backbone (McGlone, 2009).

European migration also brought with it the introduction of a wide range of plant species. Exotic plant species indicative of European land clearance for agriculture includes an increase of grasses (Poaceae), willow (*Salix*) and gorse (*Ulex europaeus*) many of which have since become invasive species (Wilmshurst, 2007). Another significant plant indicator of this time is the introduction of pine (*Pinus*), originally used for shelter belts and woodlots (Berg, 2007).

The third land-use phase occurred throughout the early 20<sup>th</sup> century, primarily beginning in the 1920s due to the increasing accessibility of superphosphate fertiliser, a growing international market and the start of organised agricultural research. Technological innovations also increased productivity, particularly aerial topdressing (MfE, 2020). This allowed for applications of grass seed and fertilisers, as well as herbicides and pesticides at greater rates. Over a ten-year period between 1950-1960, the sheep numbers alone grew by 40% (Macleod & Moller, 2006), and by 2020, roughly 40% of Aotearoa-New Zealand had been converted into agricultural land (MfE, 2021). The intensity of land-use changes has greatly impacted the country's freshwater environment with models estimating that of the 3,820 lakes in Aotearoa-New Zealand, 46% were estimated to have poor to very poor water quality between 2016 and 2020 in terms of nutrient enrichment (MfE, 2022).

Changes of land use within a catchment can have a variety of effects on the local hydrological cycle and ecosystem health, greatly impacting the species within these environments and possibly overriding the effects of anthropogenic climate change (Dale, 1997; Dirmeyer *et al.*, 2010; Lv *et al.*, 2023; Prevedello *et al.* 2019). Within Aotearoa-New Zealand the effects of a changing landscape are observable in a variety of different factors, especially when concerning agricultural management practices. These terrestrial changes, which can impact freshwater, can be seen through accelerated soil degradation and erosion. Erosional

processes naturally occur through wind, rain, and freeze-thaw temperature fluxes and are an important component of the carbon cycle as well as a key mechanism for distributing nutrients across landscapes and into freshwater environments (Dirmeyer *et al.*, 2010). Aotearoa-New Zealand has naturally high levels of erosion mainly due to the weak and highly erodible rocks paired with high precipitation rates; however, erosion is occurring at an accelerated rate due to anthropogenic influences. Most human-induced soil erosion is caused by pastoral farming, and forestry when plantations are felled, with an estimated 192 million tonnes of eroded soil entering freshwater systems each year (MfE, 2021). Of the soil which is eroded, 44% comes from exotic grass cover, including pastoral farmland (MfE, 2021). Soil inputs from agricultural lands are often high in nutrients from the addition of fertilisers on the land which greatly influences the degree of algal blooms throughout catchments (Borrelli *et al.*, 2013). Soil that has washed into freshwater can greatly degrade the environment by reducing the water-holding capacity and infilling stream/lake beds with extra sediments. Filling these lakebeds alters the environment in which invertebrates survive and reproduce. Extra sediments in the water can block respiratory organs and reduce visibility which can impede a species' ability to locate food, as well as limit sunlight in the system (Jones *et al.*, 2012).

## 2.6 Land-use change history of Aotearoa-New Zealand

Aotearoa-New Zealand was among the last major landmass to be colonised by humans with a long-running debate over the timing of the first settlement. Currently, the late settlement hypothesis (Anderson, 1991) is the preferred theory with the early ancestors of Māori arriving from tropical east Polynesia between c. 1250 and 1300 CE. These original settlers discovered the country on several deliberate voyages of exploration, navigating the Pacific Ocean with the use of prevailing winds, ocean currents and celestial navigation techniques (Wilson, 2005).

The navigator credited with first discovering Aotearoa-New Zealand in much of Māori folklore is Kupe, a legendary explorer from Hawaiki, featuring prominently in the mythology and oral histories of different iwi (Royal, 2005). It was once believed that these early explorers came to Aotearoa-New Zealand in a single great fleet of seven waka (canoes), although it is now accepted that many migrations occurred with at least 40 vessels during this time (Royal, 2005).

Early Māori history can be divided into the Archaic period (1300 – 1500 AD) and the Classic period (1500 – 1642 CE) (Anderson, 1991). The Archaic period was defined by the early settlers living a hunter/gatherer, nomadic lifestyle. Archaeological sites that aid in defining this era include the Wairua Bar (Te Pokohiwi) midden (Brooks *et al.*, 2011). Wairua Bar is a unique site in Aotearoa-New Zealand in terms of the preserved material's diversity, abundance and size. It contains some of the greatest displays of community and personal wealth as yet uncovered, with the strongest connection to Hawaiki (Brooks *et al.*, 2011). This is shown through stone adzes, fishing equipment, personal ornaments made of shell, bone, tooth and stone as well as a collection of small tools, needles, hammer stones, files and tattooing chisels (Brooks *et al.*, 2011). The midden's assemblage of different species' bones is diverse including many bird species (some of which are now extinct), particularly flightless groups such as the moa (Order: Dinornithiformes), sea mammals, fish, shellfish and the domestic dog species, kurī (*Canis lupus familiaris*) which arrived alongside Māori. Another animal brought over through the migration period was the rat species kiore (*Rattus exulans*) (Brooks *et al.*, 2011). Both dog and rat aided in the settlement of the country as a known source of food, skin/pelt, and companionship from the kurī. Pre-human Aotearoa-New Zealand was dominated by avian and reptilian fauna, many of which were not adapted to defend against mammalian predators resulting in the localised extinctions of many of these



species. This increase in localised extinctions, population pressures and tribal competition, in addition to a changing climate, theorised to be contemporaneous with the progression from the MCA into the LIA (Cook *et al.*, 2002), led to the transition into the Classic period. This time is defined by groups settling in one area with a greater reliance on subsistence agricultural practices with extensive gardens containing crops, creating a need for fortified pā (villages) with an emerging warrior culture and more elaborate art forms (Wilson, 2005).

Māori primarily used fire as a form of maintaining and clearing sites to allow for population growth and cultivation. It also encouraged the growth of bracken fern which was a key source of carbohydrates (Wilson, 2005). Bracken fern expansion is identifiable in pollen and charcoal records found in lake and wetland sediments and is often used as a tool for identifying possible environmental shifts where written history is difficult to find (McGlone *et al.*, 2005; Newnham *et al.*, 2013). This form of subsistence agriculture reduced Aotearoa-New Zealand's extensive % native forest and shrubland cover prior to human settlement from 80% to approximately 50% remaining by the 18<sup>th</sup> century (Wilson, 2005) (Figure 9). However, the dense bracken fern with its large network of rhizomes and wetlands emerging from opened canopies protected much of the lacustrine environments from being inundated by eroded soil (Wilmschurst, 2007).

Although the first European contact was with Abel Tasmin, a Dutch explorer in 1642, the first European landing on the islands wasn't until 1796 with the British explorer James Cook (Ministry for Culture and Heritage 2020). Over the next 60 years, contact grew with more Europeans arriving in the country to begin a thriving sealing and whaling market, along with Christian missionaries (Ministry for Culture and Heritage, 2020). European settlement in

Aotearoa-New Zealand increased through the 19th century with a draw of cheap land and gold deposits discovered in the mid-century (Ministry for Culture and Heritage, 2020).

European population growth brought with it more changes to the remaining land cover and animal diversity. With the increase in population and the forming of an Acclimatisation Society came new animals, plants, parasites and diseases (Wilmshurst, 2007). The remaining pockets of forests and scrublands were burnt, drained, and logged to allow for new farmland. With European settlement, a further 36% of the forest was felled to allow for more intensive farming practices and town developments to where today only 24% of land cover is native species (Wilmshurst, 2007) (Figure 9).

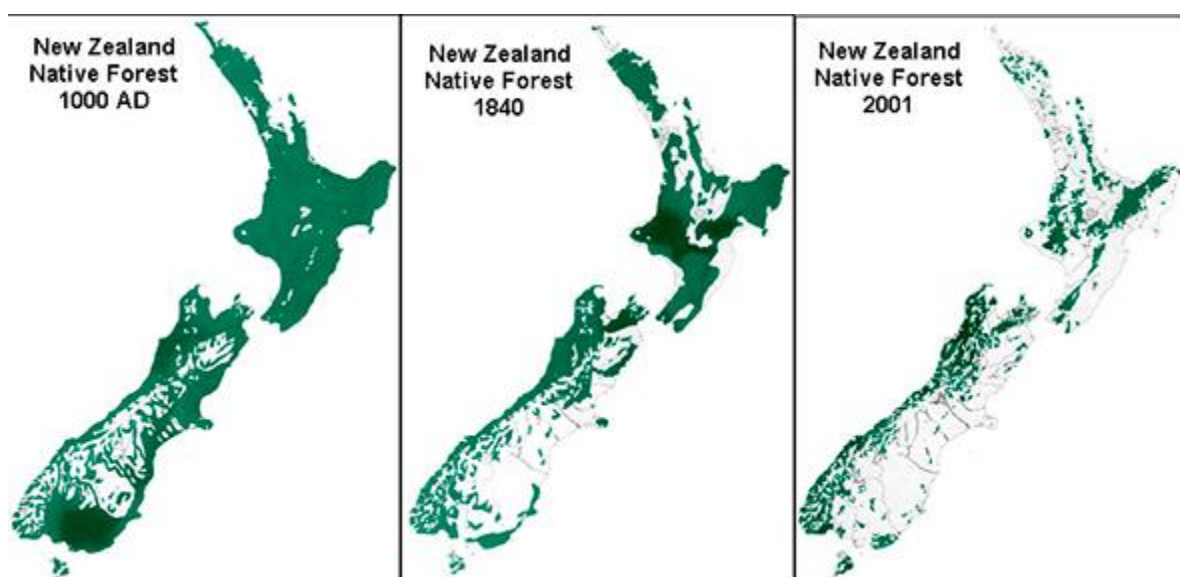


Figure 9: Three maps of forest cover changes over Aotearoa, New Zealand. First map showing Aotearoa New Zealand native forest extent prior to human arrival. Second map Aotearoa New Zealand showing native forest in 1840, after Māori settlement, prior to European. Third map showing Aotearoa New Zealand native forest in 2001. (Retrieved from <https://envirohistorynz.com/2009/11/21/237/forestcover/>).

Much of this land development occurred in lowland areas where up to 90% was destroyed with the remaining forests being highly fragmented. Wetlands, grass and shrublands were also decimated from the original expanses, dropping to 10% after being drained or modified (McGlone, 2009). Increased introduction of many plants and animal species, both purposeful and accidental, also had detrimental impacts on the environment and landscape. Of the 54

introduced mammal species, 31 dominate the present landscape including rats, mustelids, and many ungulate species including cows, goats and pigs (MfE, 2007). Of the 25,000 introduced plant species, 2,000 are established in the wild and have since been classified as ecological weeds. These mammal introductions into the environment decimated the indigenous communities, increasing competition for resources with exotic species often outcompeting the natives, while also increasing nutrient inputs, soil compaction and erosion, all altering the natural carbon and water cycle (MfE, 2007).

As of 2021 50% of land in Aotearoa-New Zealand is dedicated to agriculture and forestry, with exotic grass cover taking up a large portion of that at 40%, exotic forestry using 8% and cropping and horticulture using 2%. The remaining half is comprised of 1% urban and 49% native forest cover (MfE, 2021). These land use changes are also captured in paleolimnological studies, potentially obscuring the possible effects of anthropogenic climate change.

Based on the available literature and historical accounts of the timing of land use changes, the three land-use phases within Lake Kaweka are defined as:

**Pre-human:** pre-1250

**Subsistence agriculture:** 1250 to 1850,

**Intensification:** 1850 to present.

### Chapter 3: Methodology

Historical baselines are often used as conceptual baselines for lake ecosystem and diversity assessments and climate reconstructions (Battarbee, 1999; Bennion *et al.*, 2011; Cohen, 2003) with the assessments of land-use changes, potentially providing greater information of the observed historical lake ecosystem changes. Therefore, reconstructing the past environment of Lake Kaweka will allow for the assessment of possible anthropogenic impacts against the natural baseline conditions to produce information, which is critical in informing future mitigation strategies. This thesis will use a multi-proxy paleo-based approach to reconstruct the past environment of Lake Kaweka. The use of multiple proxies enables correlation of the evidence when concerning historical land uses and ecosystem and environmental changes as a consensus between a wide variety of proxies enables stronger arguments. Specifically, this thesis will identify if anthropogenic climate change is impacting lakes of good ecological conditions in Aotearoa-New Zealand. To investigate previous climate conditions, a midge-based temperature reconstruction model will be used, based on fossilised chironomid head capsules with radio-carbon dating to provide age constraints.

To fulfil research aim 2 and identify how lake ecosystem diversity respond to climate shifts and different levels of catchment pressure, palynology will be used to recreate catchment land use phases. Ecosystem responses will be characterised by Digital Droplet Polymerase Chain Reaction, hyperspectral imaging as well as chironomid head capsule identification, before analysis of the data which was conducted under the guidance of Andrew Rees.

### 3.1 Site description

My study will focus on the western lake of the two Kaweka lakes in Hawke's Bay east of Mt Kuripapango (Figure 10). These lakes are also known as Kuripapango Lakes, or the Twin Lakes, located in Kaweka Forest Park. The lakes were formed from a large slip off Mt Kuripapango thousands of years ago which dammed two streams. Kaweka Lake (west), the study lake, is the larger of the two (8 hectares), with a depth of 18 m, situated at an altitude of 677 m (Lakes380, 2021).

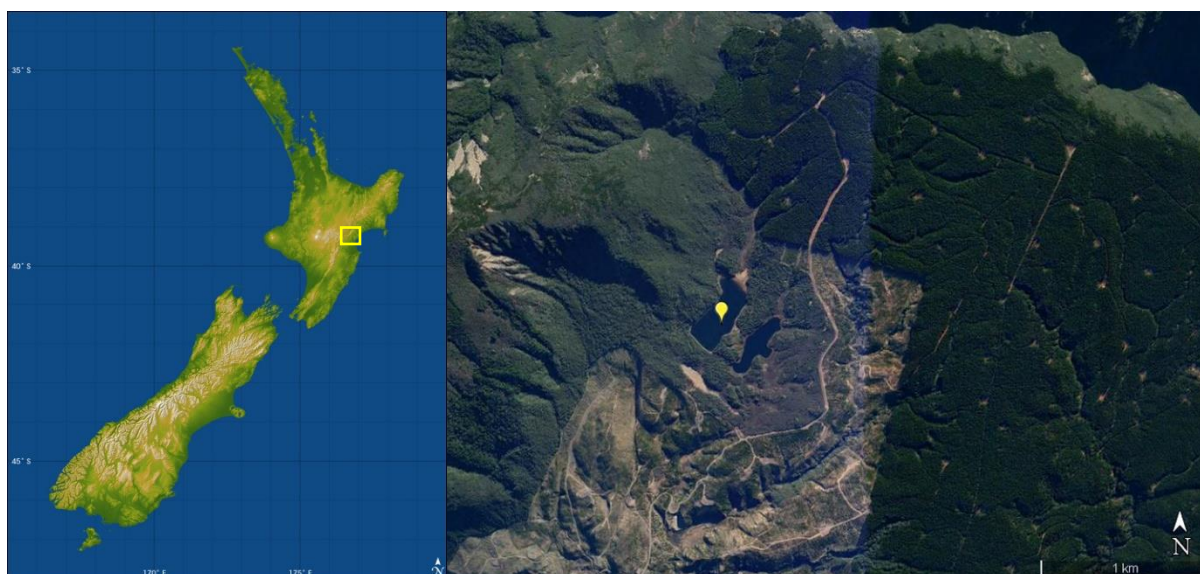
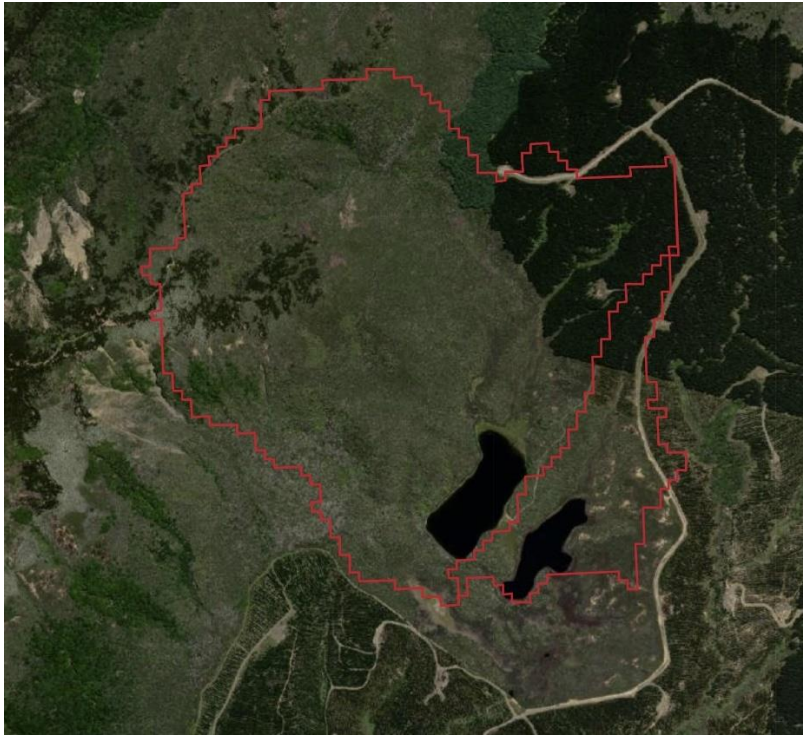


Figure 10: Map of the Kaweka Lakes location. The study lake is the larger western lake marked by the yellow pin.

The dominant forest type in the Kaweka Lake catchment is māhoe (*Melicytus ramiflorus*), kōhūhū (*Pittosporum tenuifolium*) and mānuka, with a portion of exotic forestry (*Pinus radiata*) being cultivated on the north-eastern reaches of the study lake's catchment (Figure 11) growing on a relatively steep, greywacke, scree terrain (Walls, 1998). The only road access is a gravel forestry track around the outside of the lake's catchment. The Iwi/representative group of the area are the Ahuriri hapū.



*Figure 11: Catchments of each of the lakes which make up Kaweka Lakes as indicated by the red line. Right lake= study lake.*

Rainfall in the Hawke's Bay region is highly variable and sporadic with over 2000 mm annually falling over Kaweka Forest Park, while coastal areas of the region can receive less than 800 mm as well as large and sudden temperature variations (Chappell, 2014). Northerly winds in the region are commonly associated with storms resulting from slow-moving depressions/ fronts. These orographic effects in the region are important with thunderstorms being common (Burrows & Greenland, 1979). Historically the region shows periods, approximately 1450, 1650 and 1800-1850 AD of greater storminess, evidenced through severe forest damage and greater erosion, with flood sizes since 1860 AD being greater than the preceding 200 years. These events, however, cannot be unequivocally separated from fires set by early settlers or tectonic disturbances that occurred during similar timeframes (Burrows & Greenland, 1979).

Hawke's Bay is a relatively sunny region of the country with most districts having over 2,000 sunshine hours per year with average summer temperatures between 20-25°C and January

being the warmest month (Figure 11) Precipitation over the Kaweka Ranges remains relatively consistent throughout the year; however, July is the month which receives the most rain, as well as the lowest temperatures (Figure 12). The high-country zones of Hawke’s Bay are open and exposed, therefore experiences gales frequently, with snow during the winter season influenced by cold, southerly winds (Chappell, 2014).

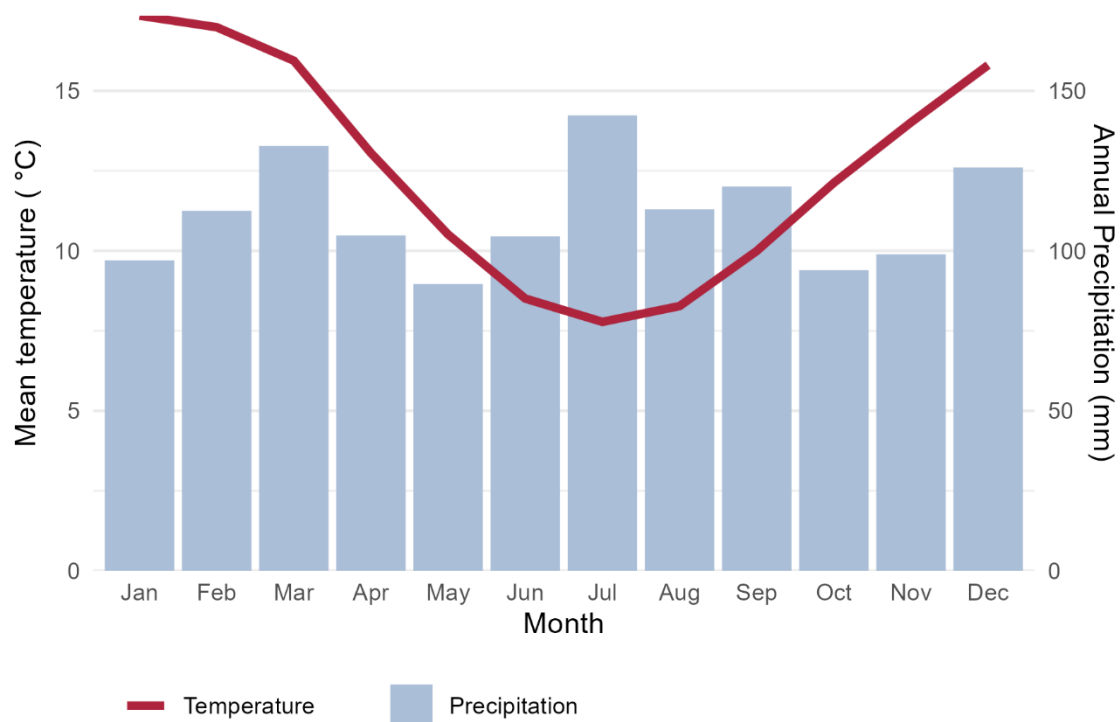


Figure 12: Monthly overview of the mean temperatures (°C) and annual precipitation (mm) from Kaweka Forest climate station (agent number: 2970) between 1975-2005. Data accessed from: <https://cliflo.niwa.co.nz/>.

### 3.1.1 Trophic level of Kaweka lake

Based on a one-off water chemistry sample and a bacterial index developed and undertaken by the Lakes380 team, the trophic level of Kaweka Lake 1 is mesotrophic (Pearman et al 2022). These lakes are categorised by intermediate levels of production with moderate amounts of nutrient input and alkalinity. Mesotrophic lakes often have clear waters allowing for a variety of aquatic plant growth and macroinvertebrate species (Pearman et al. 2022).

### 3.1.2 Site and regional history

Lake Kaweka is located within Kaweka Forest Park, managed by DOC (Department of Conservation). The lakes themselves have remained relatively undisturbed within the catchment until human settlement, with pine forestry affecting the catchment in more recent history,. Kaweka Forest Park's earliest settlements are on the western foothills, concentrated around Tūtaekurī River, approximately 10 km east of Kaweka Lake, as the river provided excellent transport routes for early settlers (DOC, 2005). The area was known for good food production, which led to subsistence farming on the foothills with multiple burnings to encourage plant growth. The northern reaches of the remaining forest were also prominent places for Māori, with two natural hot springs: the Mangatutu and Mangatainoka. The upper reaches of the Mohaka River, which is fed from these springs, was a renowned eeling ground for many tribes, even those as far away as Taupō (100 km northeast) (DOC, 2005).

European arrival introduced large-scale land-use changes, primarily through farming of merino sheep across the ranges by the late 1800s (DOC, 2005). This led to expansive fires throughout the ranges with one musterer writing "we were given a box of matches as we mustered and told to burn off where we could" (DOC, 2005). The first permanent transportation route through the region was via Kuripapango, in the southern reaches of the forest. This began as a packhorse track before being developed into a road in 1881. This increased human pressure on the landscape as it became an important stopping place for both packhorse trains and bullock wagons, becoming a holiday retreat with two hotels offering activities including tennis, trout fishing, pheasant shooting and pig hunting. However, the completion of an alternative railway route in 1905, and a fire destroying one of the hotels quickly ended development in the area (DOC, 2005).



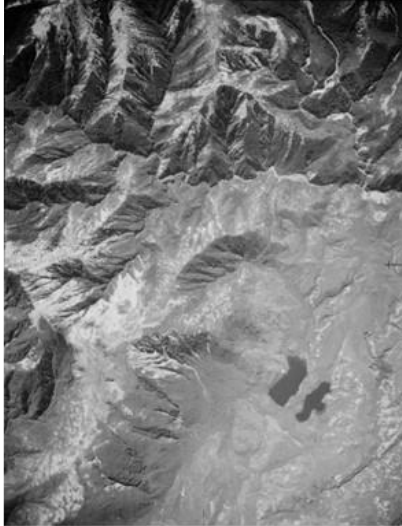
Erosion was rife throughout the forest as a result of the continual history of burning, trampling and grazing (DOC, 2005). This erosion stripped the fertility from the soil, leaving it exposed to being blown or washed away. This made the farming of the area unsustainable and by 1900 sheep were mustered with only the wild and stray sheep remaining on the southern reaches of the Kaweka ranges. This left the hills exposed, with only poor soils for regeneration, as well as continual pressures from other introduced mammals including rabbits, deer, and possums (DOC, 2005).

Currently, the forest has regenerative species including mānuka/kānuka with podocarp/broadleaf forest established in the lowlands and red and mountain beech (*Nothofagus fusca*/*N. cliffortioides*) in the higher altitudes (DOC, 2005). A few rare plant species persisted throughout the continual disturbances including *Dactylanthus* and mistletoe along with some sub-alpine shrubs, tussocks, herbs and flowers.

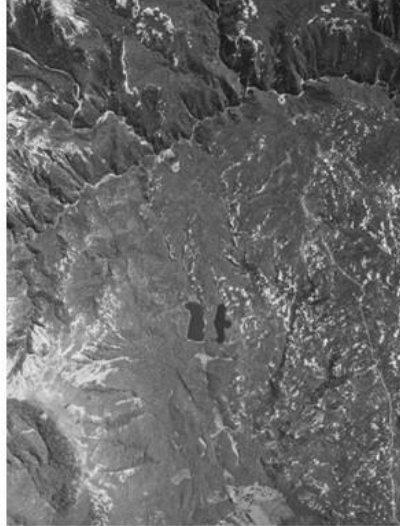
The construction of walking tracks throughout the forest began in the 1960s with much of the ranges becoming a State Forest with extensive commercial pine forestry in 1964 (DOC, 2005). Historical photographs show pine forestry beginning in the Kaweka lakes catchment around February 1971 (Figure 13.1).

Current management is focusing on the removal of *Pinus contorta*, which was initially planted in 1954 to aid in controlling erosion but is now displacing many endemic species (Figure 13.2). Pests continued to be controlled, particularly invasive mammalian species, with a focus on deer and possums. These species compact soil and disrupt forest regeneration as well as enhance erosion. Other management projects include the upkeep of the infrastructure, walking tracks and historical sites, ecosystem protection, and education (DOC, 2005).

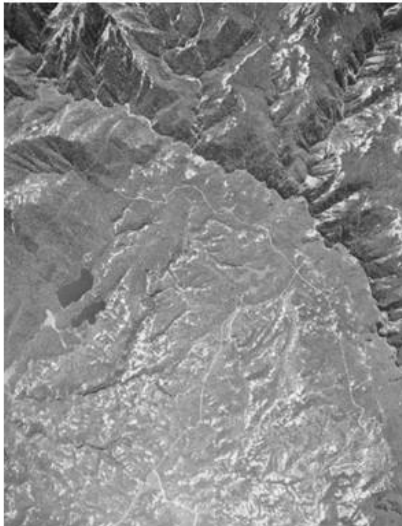
a: 1955



b: 1966



c: 1969



d: 1971



e: 1980



f: 1991



*Figure 13.1: Historic aerial photographs of Kaweka Lakes. (Left to right: a) Earliest photo of Kaweka Lakes, 1955; b) January 1966; c) March 1969; d) February 1971; e) October 1980; f) October 1991). (Retrieved from <https://retrolens.co.nz/>).*



*Figure 13.2: Current satellite image of Kaweka Lakes. Retrieved from google maps.*

## 3.2 Field sampling

### 3.2.1 Core sampling

Collection of the sediment cores were undertaken by the team at Lakes380. Sediment core barrels were cleaned with sodium hypochlorite 2% (bleach) before coring. Cores were extracted on 4 September 2020 at a depth of 18 m using an UWITEC gravity corer with a 90-mm diameter, 2-m long polyvinyl chloride barrel (Mondsee, Austria). UWITEC corers are hand-operated, transportable, and easily deployable for the effective collection of sediment from a lakebed (Figure 14)

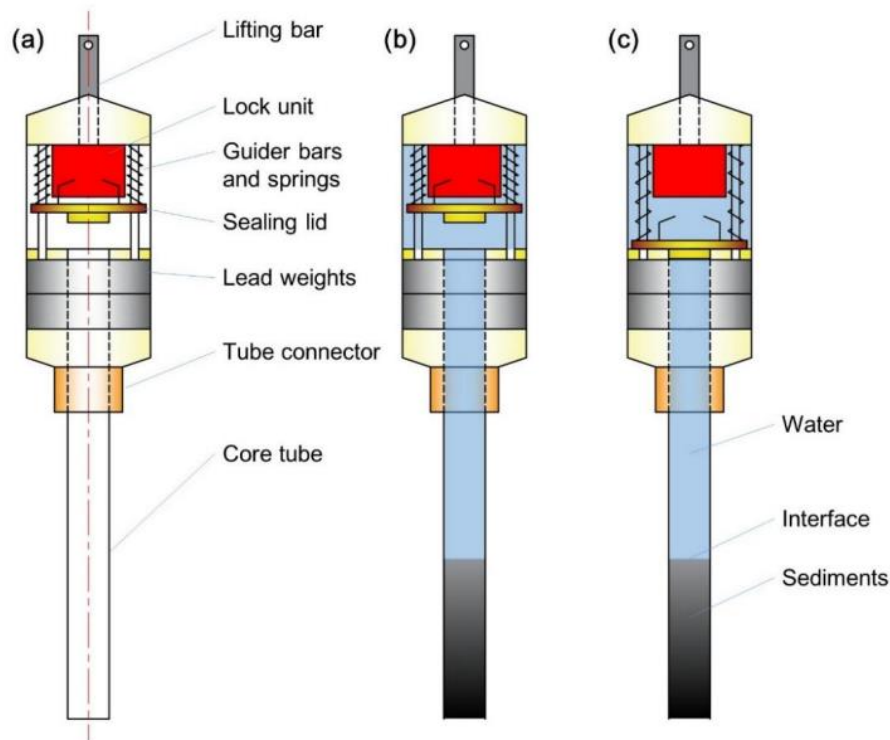


Figure 14: (a) Principal structure of a gravity corer, (b) corer while penetrating in working state and (c) corer in working state while lifting with core (Gong *et al.*, 2019).

Collection took place in the centre of the lake, the likely area of maximum deposition. Once the core was brought to the surface, florist foam was packed into the core tube to prevent movement of sediment. Once settled, cores were transversely cut in half (1-m) lengths for transportation (Figure 15). Cores remained refrigerated throughout transit to GNS Science where they were then split, described, and imaged.





*Figure 15: Image of the core collected from Lake Kaweka after splitting.*

### 3.3 Laboratory Analysis

#### 3.3.1 Subsampling

Subsampling was conducted by the team at Cawthron Institute. In a separate room from where the DNA work was undertaken, cores were split in half lengthways using a manual saw and a guillotine. Longitudinal sections were then photographed and described by sediment

type, colour and presence of organic material. To eliminate cross-contamination caused by splitting the cores, the top 2-3 mm of the half-core was carefully removed with a sterile spatula. A second DNA-free spatula was used to collect sub-samples (c. 0.5 g) from the centre of the half-cores at a variety of depths down the core. In general, these sub-samples were taken at 1 to 2-cm intervals in recent sediments and 4 to 5-cm intervals in older sediments resulting in 22 sediment subsamples. DNA sub-samples were kept in a dark freezer (-20°C) until DNA extraction.

Cores were also subsampled for pollen and chronological analyses ( $^{14}\text{C}$  and  $^{210}\text{Pb}$ ). The other half-core was used for the non-destructive analysis which include measurements with a hyperspectral imaging scanner (HIS) and an Itrax X-ray fluorescence core scanner (XRF).

### 3.3.2 DNA Analysis

With guidance from Cawthron I preformed the molecular analyses (DNA extraction, PCR or ddPCR set-up, template addition, PCR/ddPCR analysis) conducted in separate, sterile, dedicated laboratories following sequential workflow to ensure no cross-contamination. Ultra-violet sterilisation was used for at least 15 mins before and after in rooms dedicated to DNA extraction, PCR set-up, or template addition. PCR/ddPCR set-up and template addition were done in laminar flow cabinets with HEPA filtration. Aerosol barrier tips (Axygen, USA for PCR; epT.I.P.S., Eppendorf, Hamburg, Germany for ddPCR) were used throughout.

### 3.3.3 Bacteria eDNA, amplification and bioinformatics

Using the DNeasy PowerSoil Kit (Qiagen, Germany), DNA was extracted from 22 samples of approximately 0.25 g of sediment following the manufacturer's instructions and using a QIAcube sample preparation robot (Qiagen) . A blank extraction control was included to ensure there was no contamination from the extraction kits.

The V3-V4 region of the bacterial 16S rRNA gene was amplified with a polymerase chain reaction (PCR) using the bacteria-specific primers 341F as described in Pearman et al. (2020); 5'-CCT ACG GGN GGC WGC AG-3' and 805R: 5'-GAC TAC HVG GGT ATC TAA TCC-3' (Klindworth *et al.*, 2013). Illumina™ were also included as overhang adapters to allow for dual indexing as described in Kozich et al. (2013). Library preparation and PCR reactions were done following Pearman et al. (2020). The sequencing was conducted on an Illumina Miseq platform at the Auckland Genomics Facility with the raw sequence reads being deposited in the National Center for Biotechnology Information.

Following Pearman et al. (2020), bioinformatics and QC of the sequencing data were done using cutadapt (Martin, 2011) and DADA2 (Callahan *et al.*, 2016). The amplicon sequence variants were taxonomically identified using the rdp classifier (Wang *et al.*, 2007) against the SILVA 138 reference database (Pruesse *et al.*, 2007).

#### 3.3.4 Environmental DNA extraction for eukaryotic taxa (18S rRNA and mitochondrial cytochrome oxidase I genes)

Up to 3 g of sediment samples were extracted using a combination of an alkaline lysis method with ethanol precipitation before using the DNeasy PowerSoil™ kit (Qiagen, USA), as described in Thomson-Laing et al. (2022). The lysis steps included adding sodium hydroxide (6 mL, 0.33M) and Tris-EDTA (3 mL, pH 8) to the sediment samples held in 15-mL sterile tubes. The tubes were thoroughly mixed in a benchtop vortex (1 min) before incubation at 65°C for 50 min. Samples were then cooled at room temperature before going into a centrifuge at 3000 *xg* for 1 hr. A subsample (7.5 mL) of the supernatant was transferred into a 50-mL sterile tube with the lysis step being neutralized with the same volume of Tris HCl (7.5 mL, 1 M, pH 6.7). The precipitation step involved adding sodium acetate (1.5 mL, 3M, pH 5.2) and ethanol (30 mL, molecular grade 100%) to the same tube with samples being stored at -20°C (> 12 h).

Samples were then centrifuged at 3000 *xg*, for 1 hr before discarding the supernatant. These extraction steps were undertaken in batches of 22 including a blank control.

Following ethanol precipitation, the whole sediment pellet (up to 0.5 g) was transferred using a sterilised spatula into bead beating tubes from a DNeasy PowerSoil™ kit (Quiagen, USA). DNA was then extracted as described above for the bacterial eDNA.

### 3.3.5. PCR amplification and bioinformatics of the 18S rRNA and mitochondrial cytochrome oxidase I genes

The DNA was amplified by primers for the 18S ribosomal RNA gene; 5'-AGG GCA AKY CTG GTG CCA GC-3' and 5'-GRC GGT ATC TRA TCG YCT T-3'; (Zhan *et al.*, 2013) and the mitochondrial cytochrome oxidase I (COI) primers using 5'-GGW ACW GGW TGA ACW GTW TAY CCY CC-3' and 5'-TAN ACY TCN GGR TGN CCR AAR AAY CA-3' (Leray *et al.*, 2013). Illumina™ overhang adaptors were attached to the taxa specific primers to allow for dual-indexing (Kozich *et al.*, 2013). PCR reactions were undertaken in triplicate 20-μL volumes and contained 10 μL of MiFi 2 × PCR mastermix, 2 μM of each primer (final conc.) and 5 μL of template DNA. All PCRs had an initial denaturation step of 55 °C for 5 min and a final extension time of 5 min at 7 °C. Negative controls for both the PCR and extraction were included. SequelPrep normalization plates (ThermoFisher Scientific, USA), were used to clean and normalize pooled triplicate PCR products. An Illumina Miseq™ platform at the Auckland Genomics Facility was used for sequencing. Sequence library preparation was undertaken according to the Illumina 16S metagenomics library prep manual ([https://support.illumina.com/documents/documentation/chemistry\\_documentation/16s/16s-metagenomic-library-prep-guide-15044223-b.pdf](https://support.illumina.com/documents/documentation/chemistry_documentation/16s/16s-metagenomic-library-prep-guide-15044223-b.pdf)) with the exception that after the indexing PCR, 5 μL of each sample (including water samples acting as sequencing blank) were pooled and a single clean-up was undertaken. Quality control on the library pool was assessed



using a bioanalyzer before dilution (to 4 nM), denaturation, and a further dilution to 7  $\mu$ M with a 15% PhiX spike took place.

Bioinformatic and taxonomic assigned of the 18S rRNA and COI genes was undertaken as described in Pearman et al. (2022.)

### 3.4 Chironomid sampling

#### 3.4.1 Sample preparation and sorting

Chironomid head capsules were obtained from 1.5 cm<sup>3</sup> of sediment from the core at depths generally matching eDNA samples. Sediment was deflocculated with 10% KOH at 70°C for 20 min before being sieved through 95- $\mu$ m meshes (Walker *et al.*, 1991).

Samples were then pipetted into a grooved Perspex (Bogorov) sorter. This sorted was placed under a MOTIC Stereo Microscope SMZ-171. All head capsules and head capsule fragments identified were picked out from the residue using fine Dumont Tweezers, style 55. All head capsules from each sample were placed onto a separate microscope slide and mounted with Entellan. A minimum of 50 whole head capsules per slide was targeted, with sample sizes between 100-150 considered to give more reliable results (Heiri and Lotter, 2001; Quinlan and Smol, 2001; Wang et al, 2008).

#### 3.4.2 Identification

Identification was undertaken by Andrew Rees using a compound microscope (400x magnification). Chironomid head capsules were identified through a variety of guides and keys to obtain the highest taxonomic level possible (e.g., Cranston, 1982; Oliver and Roussel, 1983; Wiederholm, 1983; Schmid, 1993; Rieradevall and Brooks, 2001; Brooks *et al.*, 2007; Dieffenbacher-Krall *et al.*, 2008; Andersen *et al.*, 2013; Larocque- Tobler, 2014). Key characteristics are: shape, ventromental plates, number and shape of teeth on the mentum,

and, where present, mandibles. Remains with less than 50% of the head capsule present are not counted.

### 3.5 Land use reconstruction

#### 3.5.1 Chronology

The chronology was created using numerical age constraints as derived from  $^{14}\text{C}$  dating combined with Bayesian age-depth modelling (Figure 16); the chronology was provided by Lakes380. From the split core surface, terrestrial leaf macrofossils were extracted by hand-picking in-situ before being cleaned and pre-treated using a standard acid–alkali–acid procedure to remove carbonates, fulvic compounds and humic compounds. These pre-treated macrofossils were converted to  $\text{CO}_2$  following methods from Turnbull *et al.*, (2014) by combustion, graphitised and measured by accelerator mass spectrometry. The SHCal20 calibration curve (Hogg *et al.*, 2020) was used to convert the conventional radiocarbon ages to calendar years, with those that returned modern ages being calibrated with the BHDCGO curve (Turnbull *et al.*, 2014).

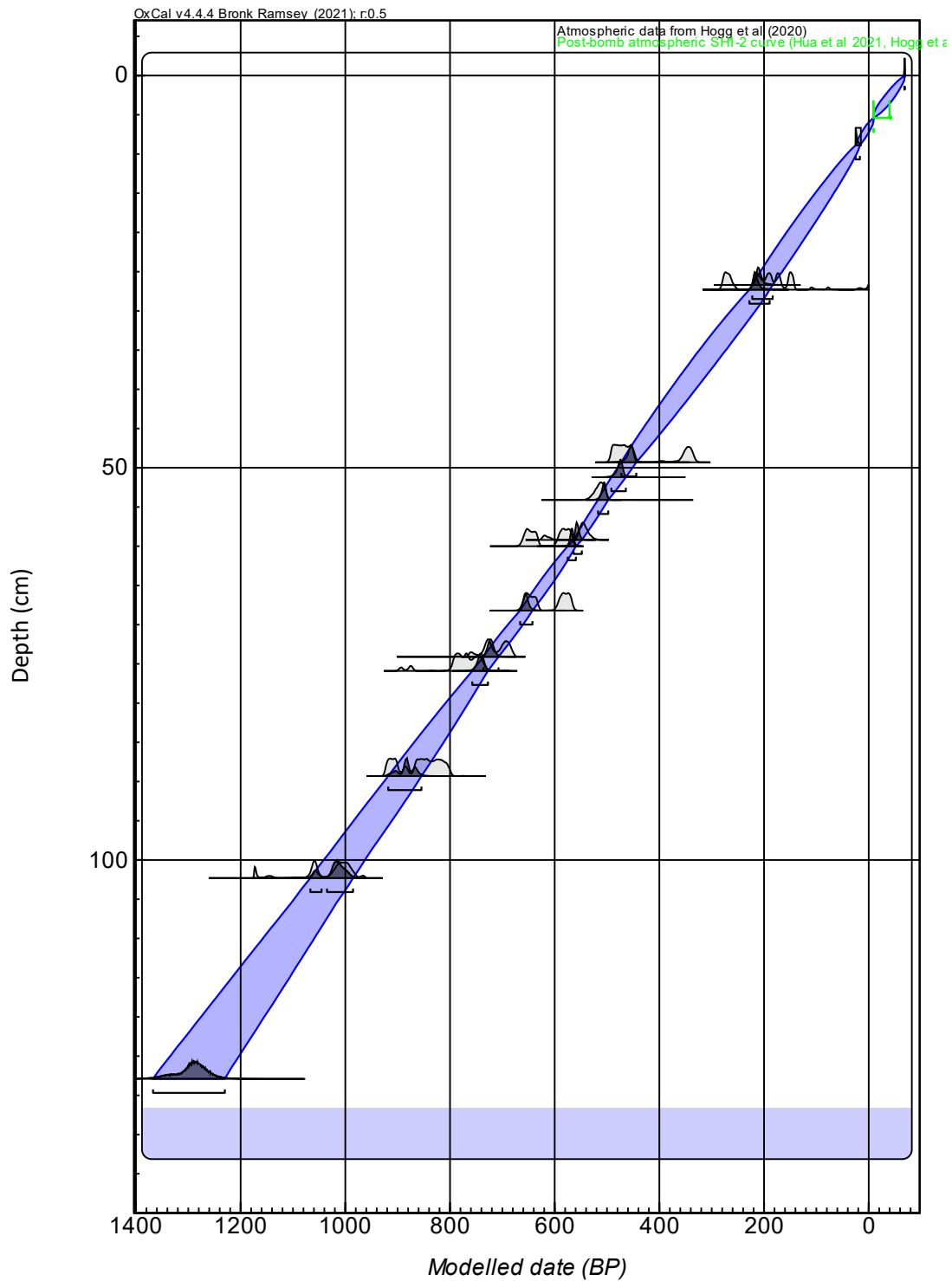


Figure 16: OxCal age model of Lake Kaweka sediment down core.

From the split core surface, terrestrial leaf macrofossils were extracted by hand-picking in-situ before being cleaned and pre-treated using a standard acid–alkali–acid procedure to remove carbonates, fulvic compounds and humic compounds. These pre-treated macrofossils

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Age-depth modelling was performed using the Bayesian framework in OXCAL 4.4 (Bronk Ramsey, 2009a) with the P\_Sequence prior model with a variable event thickness (Bronk Ramsey, 2008; Bonk Ramsey & Lee, 2013).

### 3.5.2 Pollen

The pollen stratigraphy was conducted and provided by Xun Li (GNS). To extract pollen from the core, 0.25 cm<sup>3</sup> of sediment was used at variable sampling intervals between 1-2 and 3-4 cm from the upper 65 cm of the core and at 10 cm intervals from the lower section. Standard laboratory techniques from Faegri and Iversen (1989) were followed to extract pollen using 10% hot hydrochloric acid, acetolysis and 6-µm sieving. Exotic *Lycopodium* tablets were combined with each sample which allows for calculation of pollen concentrations. Pollen and spore identifications were conducted using standard texts (e.g., Pocknall, 1981; Large & Braggins, 1991; Moar, 1993) and New Zealand pollen reference collections.

Pollen data were summarised as relative frequencies of a minimum 150-grain pollen sum. This sum only includes dryland plants: trees, shrubs and herbaceous plants both native and non-native and bracken fern. Bracken fern (*Pteridium esculentum*) is included in this category as its growth morphology in a post-disturbed environment is closer in its functional morphology to a shrub rather than a fern, with a stand being ecologically equal to that of shrubland (McGlone *et al.*, 2005). Pollen from the other groups including aquatic, wetland,

fern, tree-fern and non-palynomorphs were excluded from the pollen sum; their percentages, however, were calculated as a proportion of the dryland pollen, plus the respective group.

Charcoal was measured by the number of fragments present and represented as concentration per cm<sup>3</sup>. Pollen data were used to delineate different occupation periods of Kaweka Lake's catchment. Across Aotearoa- New Zealand, *P. esculentum* is used as a chronological marker for the first presence of Māori activity and settlement on the landscape, as it is an indicator of landscape disturbances (particularly burning) and nutritional source (McGlone *et al.*, 2005; Newnham *et al.*, 2013; Wilson 2005). For European activity and settlement on the landscape, *Pinus* spp. And other non-native taxa are used as the chronological markers, as they were introduced by colonialists. These markers were used to indicate the three periods of human activity in this study: pre-human (76.5–142.5 cm), evidence of subsistence agriculture (26.5–67.5 cm), and agriculture intensification (0–17.5cm).

### 3.5.3 Hyperspectral imaging scanner

A Specimen sCMOS-CL-50-V10E-SCB camera was used to scan the core, acquired and performed by GNS following Butz *et al* (2015), To capture the measurements, a spectral resolution of 1.3 nm and a spatial resolution of 41 µm (pixel size) were used. To quantify the absorption features associated with the pigments in the surface sediments, multiple relative absorption band depths (RABD) indices have been developed (e.g., Rein & Sirocko, 2002; Butz *et al.*, 2015; Schneider *et al.*, 2018). For this study, analyses of the spectral data were done using the RABD<sub>660-670</sub> index, which is correlated to the sedimentary pigments of chlorophyll *a* and its degradation products (Rein & Sirocko, 2002).

These results were then converted to a spectral index (Butz et al. 2017) with a span of values between 1-2.5, the higher values being associated with more of these compounds. This index is representative of autochthonous chlorophyll *a* and an indicator of algal abundance (Butz et al., 2017; Schneider et al., 2018).

### 3.6 Data analysis

#### *Stratigraphic plot*

The biological community composition was visualised with stratigraphic plots of non-rare species that were clustered using CONISS; all of these plots were made with the rioja package (Juggins, 2022). While this is useful for seeing trends in the most abundant taxa, principal coordinate analysis (PCoA) was used to visualise entire community change across a land-use gradient (i.e., pre-human, subsistence agriculture, and intensification). The distance matrices for the PCoAs were developed from the Bray-Curtis distance measure (Minchi, 1987).

#### *Model development*

A chironomid transfer function was developed from the surface samples in van den Bos (2019) for summer temperature (SmT) using the rioja package in R (Juggins, 2007). A detrended correspondence analysis (DCA) was run to assess modern taxa response across the gradient captured by the training set, which indicated unimodal methods would best model species response. Although many models were considered, based on gradient length and performance, weighted averaging partial least squares (WA-PLS) techniques were employed. Models were cross validated with 1,000 permutations and assessed based on the performance of the root mean square error of prediction (RMSEP) average bias of jack-knifed predictions ( $\text{AveBias}_{\text{jack}}$ ), maximum bias of jack-knifed predictions ( $\text{MaxBias}_{\text{jack}}$ ) and jack-knifed coefficient of determination ( $r^2_{\text{jack}}$ ).

#### *Reconstruction diagnostics*

Multiple reconstruction diagnostics were run to evaluate the reliability of the chironomid-inferred temperatures (outlined in Birks, 1995). Goodness of fit (Birks *et al.*, 1990) was assessed by passively fitting the fossil samples to an ordination constraint to SmT, which was derived from the modern training set. To assess the quality of fit, the squared residual distance of the modern samples were compared from the constrained axis to the distance of the fossil samples. Fossil samples were considered to have “poor” or “very poor” fits if they were larger than the 90<sup>th</sup> and 95<sup>th</sup> percentile of the modern squared residual distances, respectively. Rare taxa were also calculated, defined by having a Hill’s 2 (Hills, 1973) of  $\leq 5$  in the modern training set; these taxa are likely to be poorly modelled. Finally, Birks *et al.* (1990)’s modern analogue technique was used to determine the amount of dissimilarity between the modern and fossil samples. Fossil samples with “good” or “close” fit had modern analogues defined by the 2<sup>nd</sup> and 5<sup>th</sup> percentiles of all chi-squared distances in the modern data.

#### *Rate of change analysis*

Rate of change analysis was conducted following methods in Mottl *et al.*, (2021). Briefly, distance matrices were calculated between stratigraphic samples of all indicators using the Bray-Curtis dissimilarity measure. These distances are analogous to  $\beta$  diversity; however, Mottl *et al.*, (2021)’s methodology incorporates uncertainty from the age-depth model. Rates of change were calculated from 400-yr moving windows with 5 bins per window. The methodology has the advantage of converting all proxies into a rate of change; the 95<sup>th</sup> percentile of each bin was then used to identify periods of rapid change common to all indicators.

## Chapter 4: Results

### 4.1 Pollen and charcoal

Pollen and charcoal results are consistent with the results found across Aotearoa- New Zealand. The natural (pre-human) era has two distinct clusters, one which is distinct from the other eras and the other with some overlap with subsistence agriculture (evidence of Māori) which may indicate two sub-communities. *Phyllocladus* and podocarps characterise the earliest sub-community, while *Pteridium esculentum* and *Coriaria* characterise the second. The European phase reflects an increase in wetland taxa and introduced species. The two main axes of the PCoA explain 61.9% of the variance of the assemblages (Figure 17.2).

#### Pre-human

A total of 114 taxa were identified from the pollen samples. Prior to human influence, species were stable with the majority of species present being tall trees. Approximately 85-95% of species were *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Fuscospora* spp. and *Podocarpus* spp., with the rest of the vegetation comprised of the small trees *Phyllocladus* and *Coprosma* spp. and the tree fern *Cyathea smithii* (Figure 17.1).



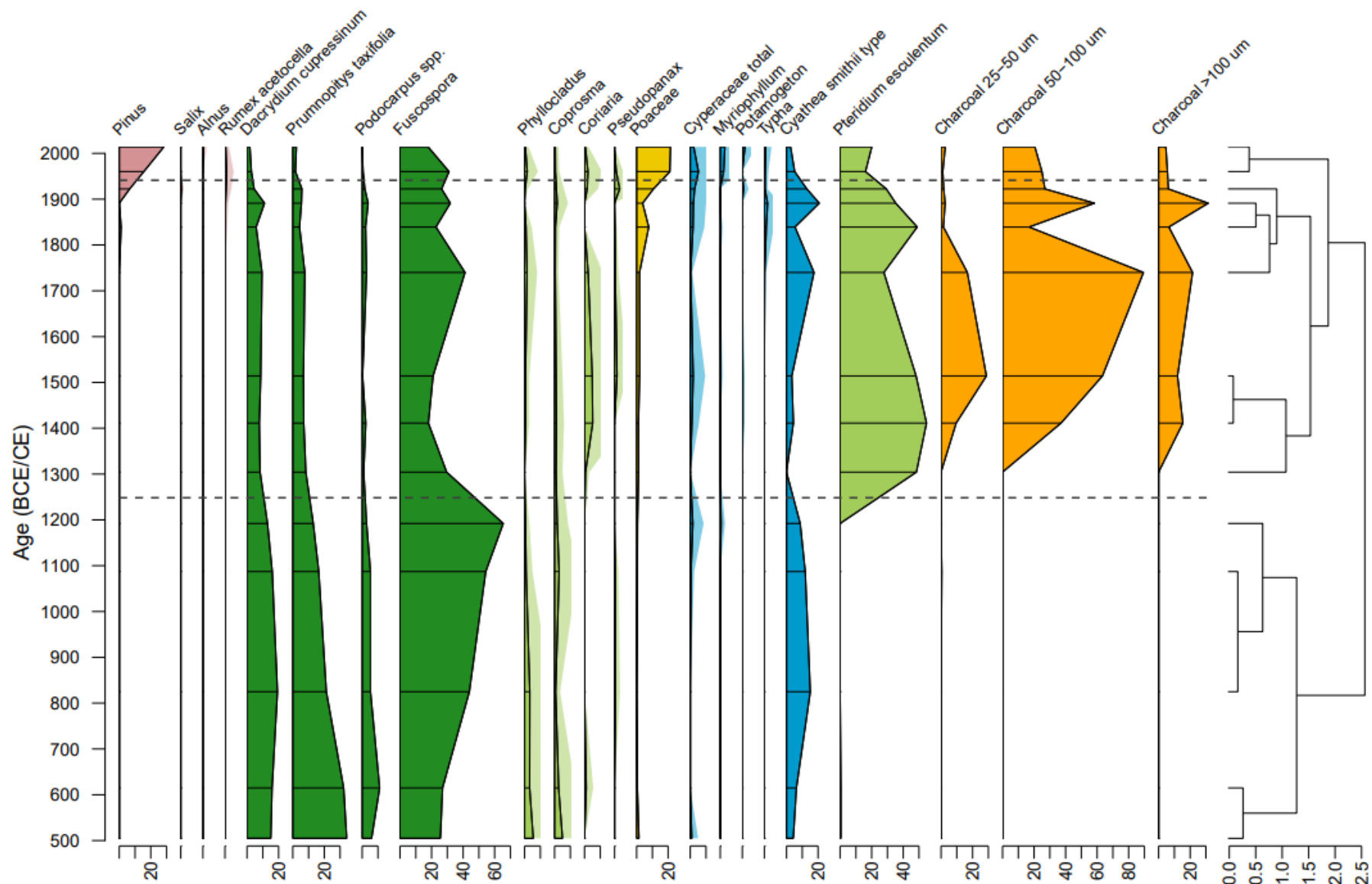


Figure 17.1: The y-axis depicts age, while the x-axis shows the abundance of different pollen taxa. Light pink = introduced species; dark green= tall trees; light green= small trees, shrubs and ferns; blue= wetland taxa; orange= charcoal concentrations. Dotted lines= indicate major changes in community structure identified by CONISS.

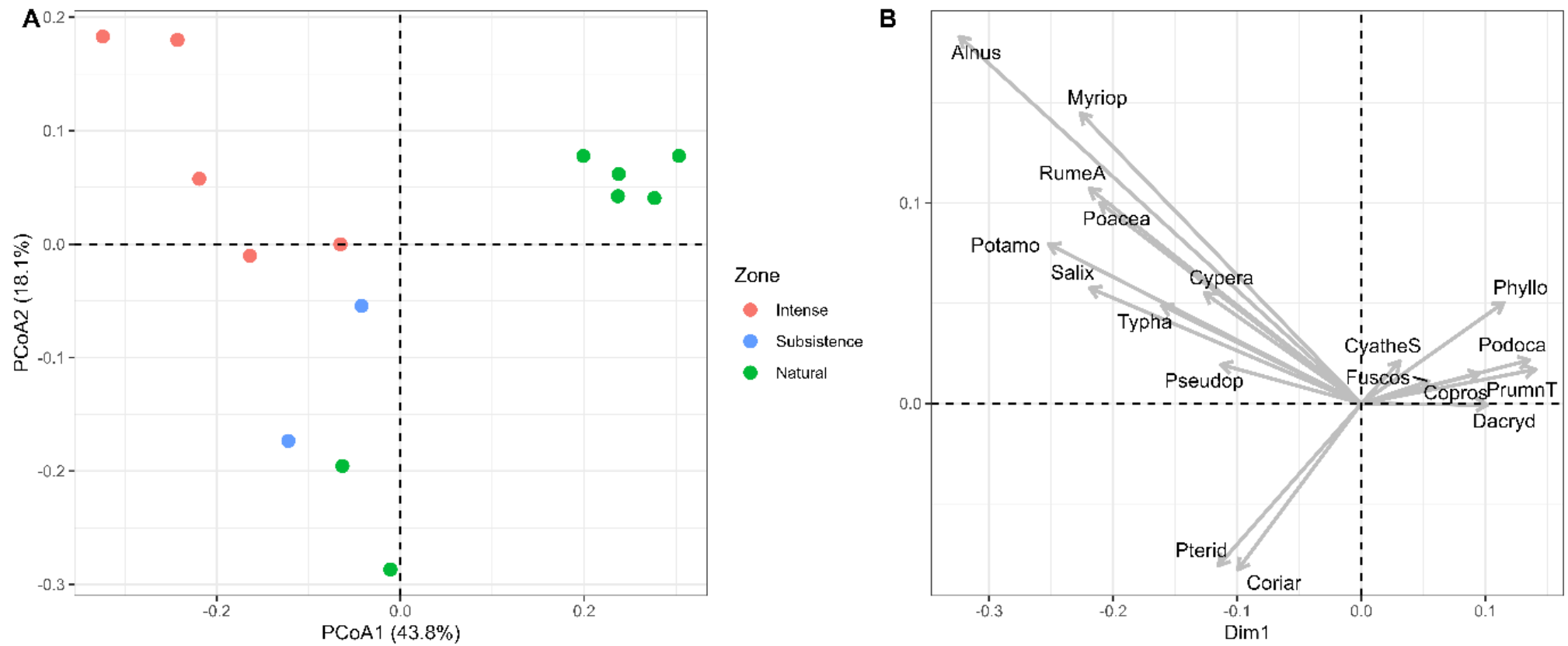


Figure 17.2: Principal coordinate analysis (PCoA) summarising the variation in the composition of the pollen community across the three eras of land use in Aotearoa-New Zealand.

### Subsistence agriculture

Representative of the arrival of humans onto the landscape, this period is characterised by several changes in the pollen spectra from a canopy dominated by tall trees to one characterised by small trees and shrubs. The abundances of the previously dominant *Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Podocarpus* spp experience a continual decline with *Fuscospora* spp. experiencing the greatest drop beginning ~1200 CE (95% CI: 1130-1270 CE), coinciding with the first recorded occurrences of *P. esculentum*, which dramatically spikes to contribute 60% of the total pollen record. This increase in *P. esculentum* slightly pre-empts the first large occurrence of charcoal, spiking to  $450 \times 100/\text{cm}^3$ . In addition, the abundance of tree ferns declined, and *Coriaria* appears for the first time.

### Intensification.

This time period is defined by the introduction of non-natives into the pollen record with a variety of *Pinus* spp. and Poaceae spp. which indicate the beginning of European influence on the environment. *Pinus* shows a continual increase accounting for 25% of the pollen record throughout the 20<sup>th</sup> century. The introduction of non-indigenous species into the pollen record co-occurs with the decline of *P. esculentum* which begins a decline in ~1850 (95% CI: 1830-1870 CE) to 20% by 2000CE as well as the continual decline of the native tall tree species. Charcoal is still present in the record although drops to a lower count of  $150 \times 100 \text{ cm}^3$ .

## 4.2 Chironomid

The two main axis of the PCoA explain 43.3% of the variance of the Chironomidae assemblages (Figure 18.2). The natural era is the most distinct, aside from one point of subsistence agriculture, which may be an indication of a sub-group. The intensification phase has the greatest variance, likely as a result of rare taxa like N4 (*Naonella*) and O19 (*Orthoclaadiinae* sp. 19). Of the 41 different species identified, the majority across all eras were warm tolerant species, defined by the environmental optima greater than 10°C. However, species types and abundances drastically fluctuated throughout the different eras.

### Pre-human

Prior to the arrival of humans to Aotearoa-New Zealand, the most abundant species was *Corynocera* which peaked at 50% abundance in ~ 1150 CE (95% CI: 1100-1200) (Figure 18.1). The pre-human period had the most occurrences of cold-adapted species, many of those being from the genus *Chironomus*, and this is the only time where *T. funebris* type B was observed.

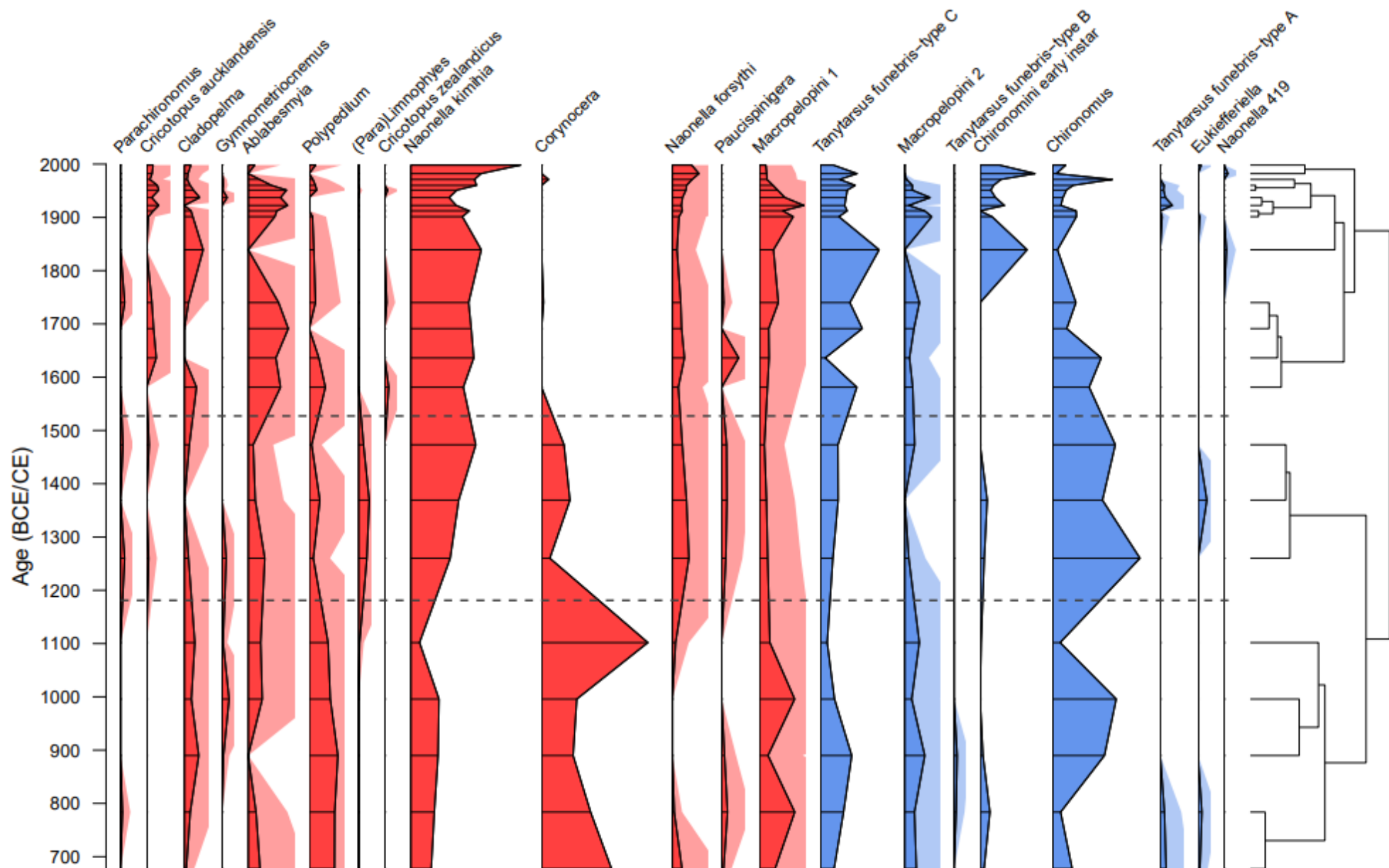


Figure 18.1: The y-axis depicts age, while the x-axis shows the abundance of different chironomid taxa. Red represents warm tolerant species; blue represents cool tolerant species. Dotted lines= major changes in community structure based on CONISS.

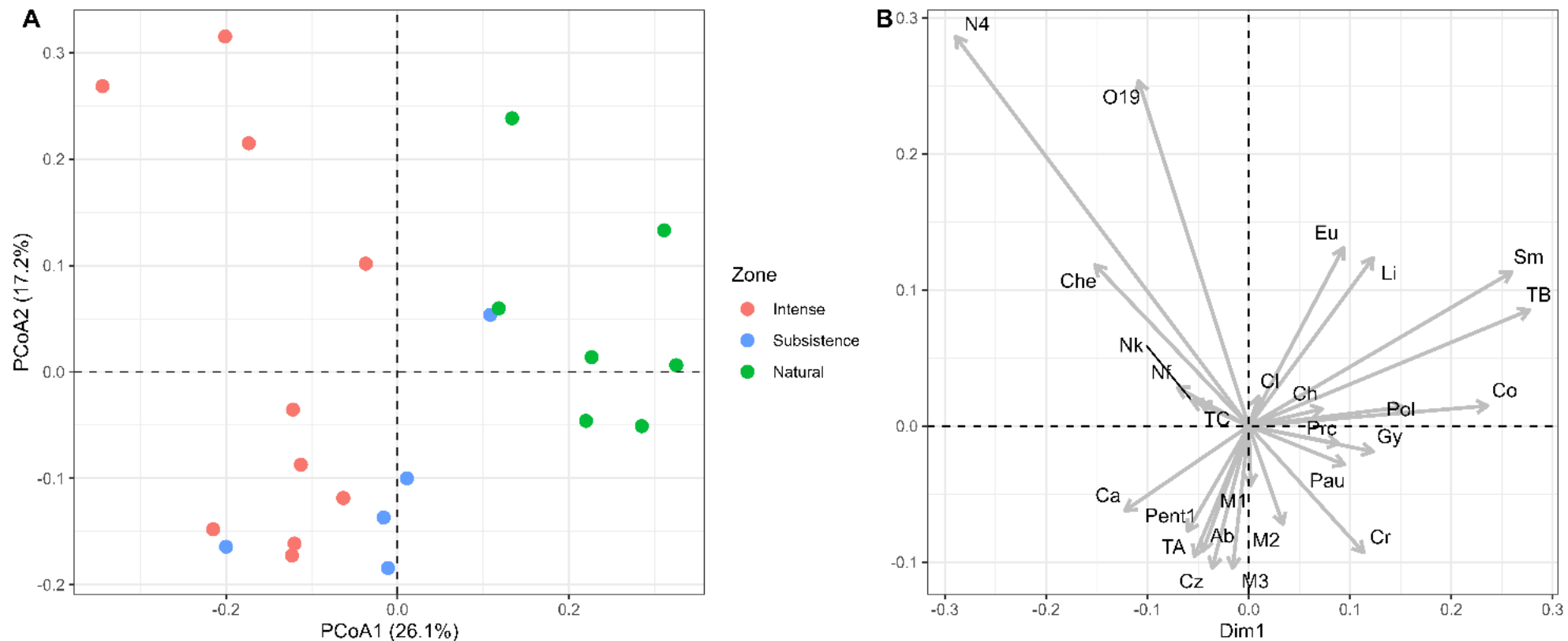


Figure 18.2: Principal coordinate analysis (PCoA) summarising the variation in the composition of the Chironomidae community across the three eras of land use in Aotearoa-New Zealand

### Subsistence agriculture

The beginning of subsistence agriculture corresponded to many species experiencing sharp declines in abundance, the most dramatic was *Corynocera* nearly completely disappearing from the record by approximately 1600 CE (95% CI: 1550-1650 CE). *Chironomus* also had a sharp initial decline at the beginning of this period but appears to have recovered by approximately 1300 CE. (95% CI: 1250-1350 CE). *N. kimihia*, *T. funebris* type C and *Macropelopini* also experienced initial declines at the beginning of this era but then stabilised. After moderate occurrences in the pre-human era, *N. frotyhi* grew to have a stable population, approximately 10% of the community present throughout the subsistence agriculture period. This was also the only time the species (Para) *Limnophyes* occurred.

### Intensification

While species diversity was not greatly impacted with the intensification of land use, counts were amongst the lowest for the record. Communities are also highly variable throughout this phase. However, after low occurrences of less than 5% in the earlier periods, *Chironomini* increase throughout this period to 20% reaching this peak by ~1970 CE (95% CI: 1950-1990) with *N. kimihia* being the most abundant species making up approximately 50% of the species present.

### 4.3 Sedimentary DNA

Amplicon sequence variants (ASVs) represent molecular species making it possible to distinguish variations in DNA sequences by a single nucleoid change. A total of 1,824 ASVs were recovered from Kaweka Lake using the CO1 gene, 3,739 when using the 18S rRNA gene and 16,464 when using the 16S rRNA.

#### 4.3.1 CO1

The two main axis of the PcoA explain 25% of the variance of the CO1 assemblages (Figure 19.2). The subsistence assemblages have two clusters, one with little variance creating a tight, separate cluster with a remainder which overlap with the pre-human cluster. The intensification phase is a distinct assemblage likely due to Tubifex which is positively correlated with Ochrophyta.

#### *Pre-human*

The lowest abundances of CO1 ASVs are observed prior to human settlement with only two groups occurring in high abundance (Figure 19.1). These groups are an unidentifiable eukaryote and Ochrophyta 1 (brown algae). Aside from a small recovery of Ochrophyta, ~ 950 CE (95% CI: 1050- 850 CE) was the only occurrence of this ASV.

#### *Subsistence agriculture*

At the beginning of subsistence agriculture era, there are new ASVs: Chlorophyta and Chlorophyta 1 and Ascomycota, all of which occur throughout the rest of the core. Mollusca abundance increases rapidly at the beginning of this phase, reaching a peak at approximately 60% in ~1400 CE (95% CI: 1350-1450) of ASVs present. Substance agriculture also saw the disappearance of Ochrophyta 1, which was replaced by a different group of Ochrophyte in the later era as well as the reoccurrence of unidentifiable eukaryotes from the pre-human era.



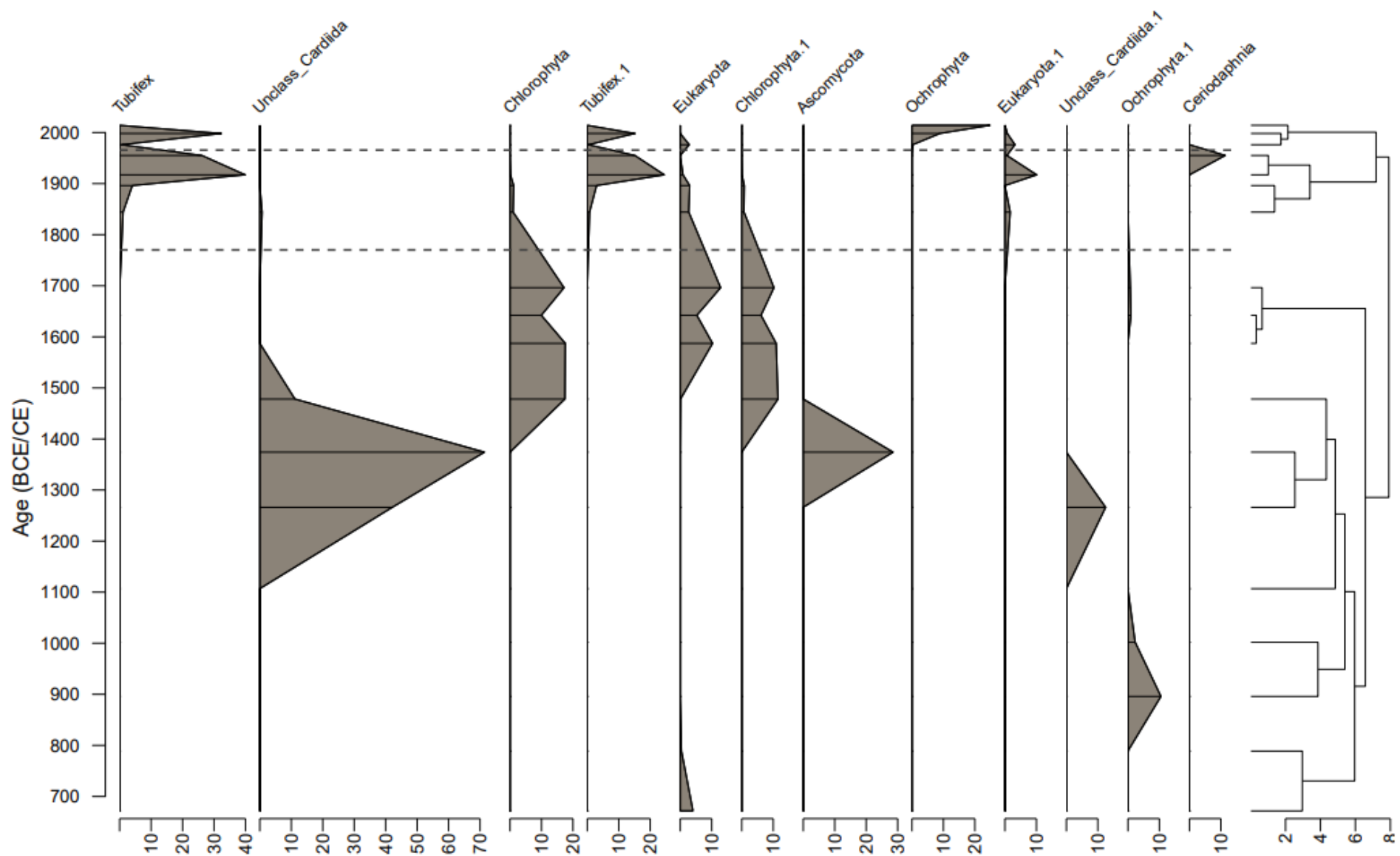


Figure 19.1: Principal coordinate analysis (PCoA) summarising the variation in the composition of the CO1 mitochondrial DNA community across the three eras of land use in Aotearoa-New Zealand.

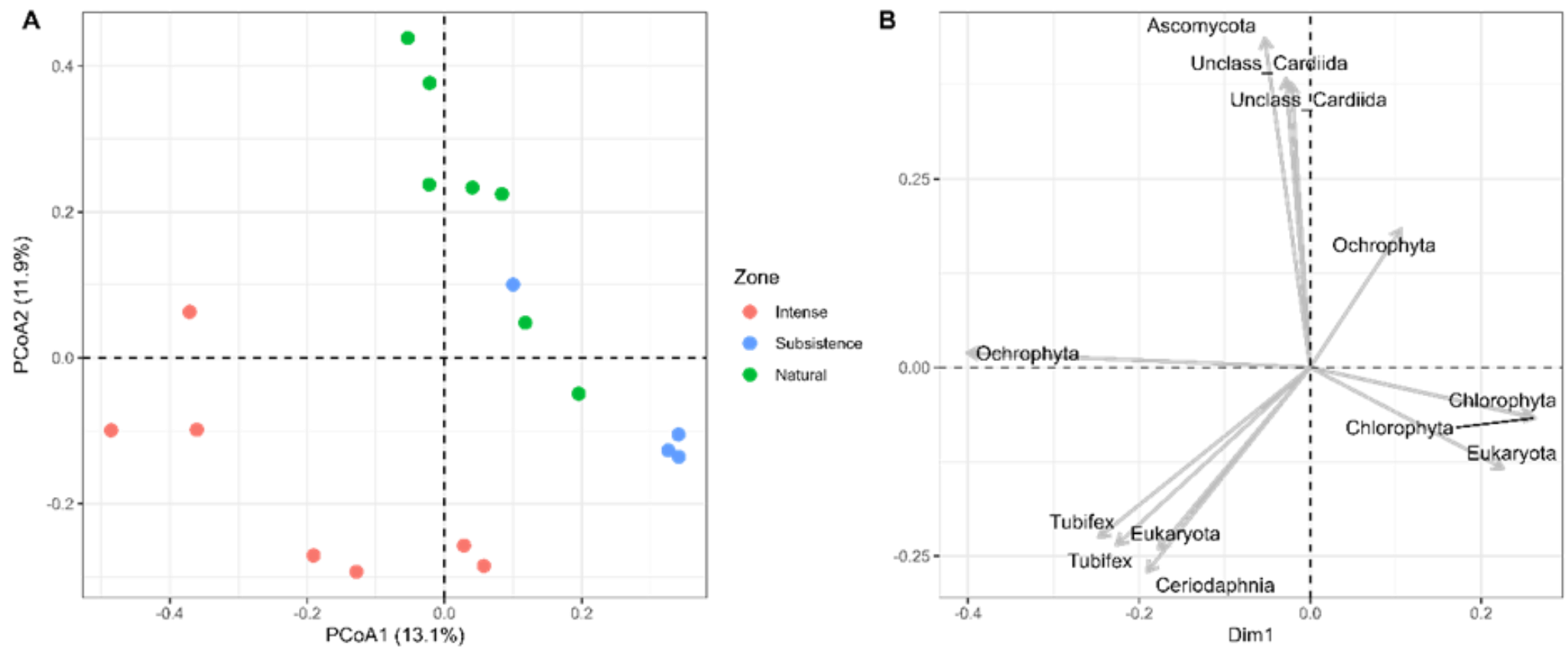


Figure 19.2: Principal coordinate analysis (PCoA) summarising the variation in the composition of the CO1 mitochondrial DNA community across the three eras of land use in Aotearoa-New Zealand

### *Intensification*

The intensification phase coincides with major variation within the data, with 11 common ASVs occurring within this era. Of these ASVs, three only occur within the last 150 years: Annelida, Annelida 1 and Ochrophyte. Although both Annelids experience rapid declines, when Annelida reaches its peak, it is the most abundant of the period, equating to up to 40% of overall ASV abundance.

### *4.3.2 18S*

The two main axis of the PCoA explain 32.6% of the variance of the 18S assemblages (Figure 19.2). None of the eras overlap but on subsistence sample clusters near the pre-human group and the intensification phase has two different clusters.

### *Pre-human*

The pre-human period has the lowest species diversity with five different common ASV types identified, none of which are unique to this era (Figure 20.1). *Potamogeton* reaches its maximum abundance of 40% at ~1100 CE (95% CI: 1030-1170 CE) just prior to subsistence agriculture.

### *Subsistence agriculture*

This period has the lowest overall abundance of species with only two common ASV groups reaching proportions over 10%, *Potamogeton* and Cryptomycotina. This is the only era in which Cryptomycotina occurs.

### *Intensification*

The intensification phase has the highest species diversity of common taxa, with all Cryptomycotina being recorded in high abundances. This era is the only one in which Labyrinthulaceae, *Tubifex* and *Prorodon* are recorded. The intensification period also contains the most variation within the entire dataset.

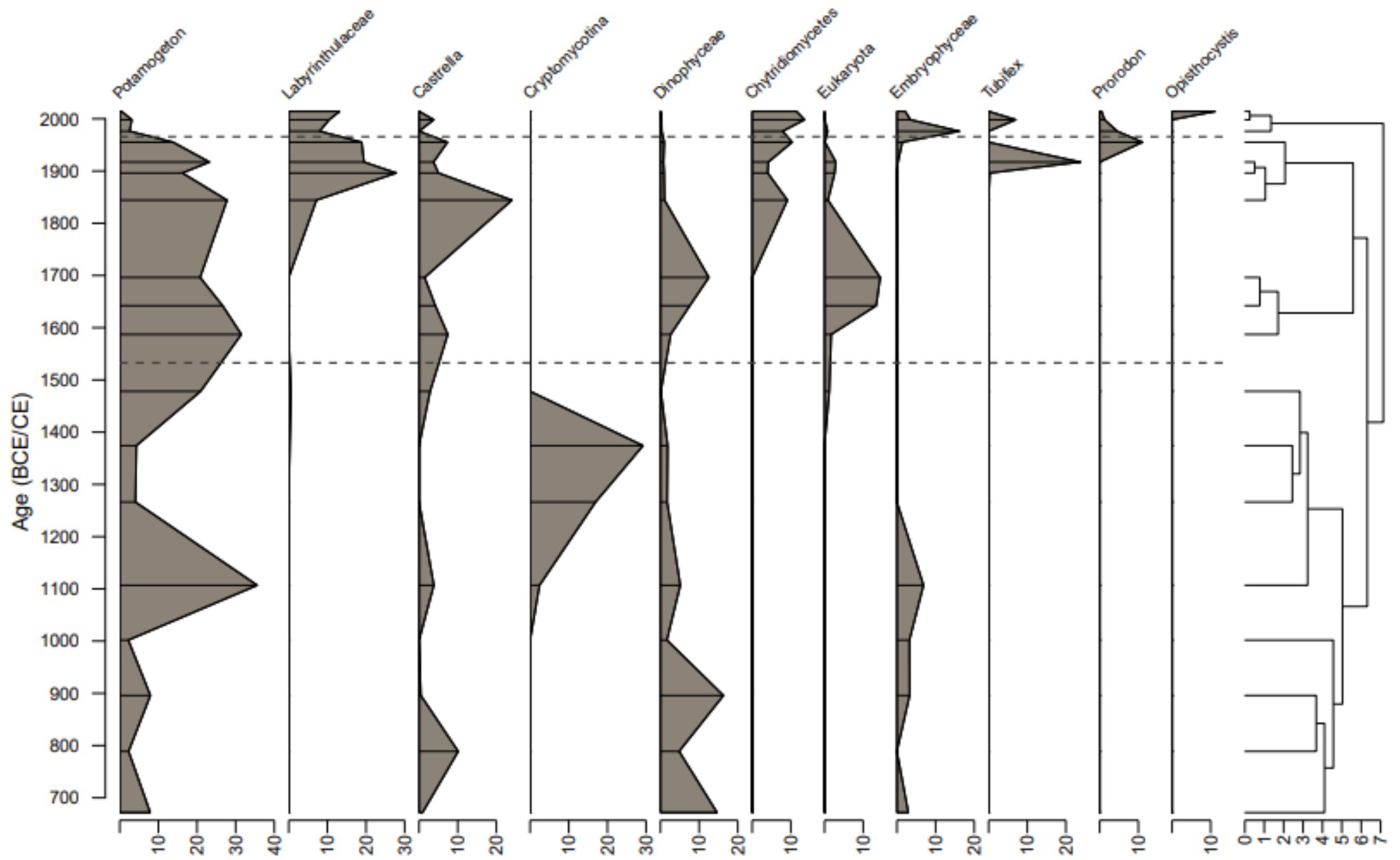


Figure 20.1: The y-axis depicts age, while the x-axis shows the abundance of different fungal species using the 18S gene. Dotted lines= indicate major changes in the community structure identified by CONISS

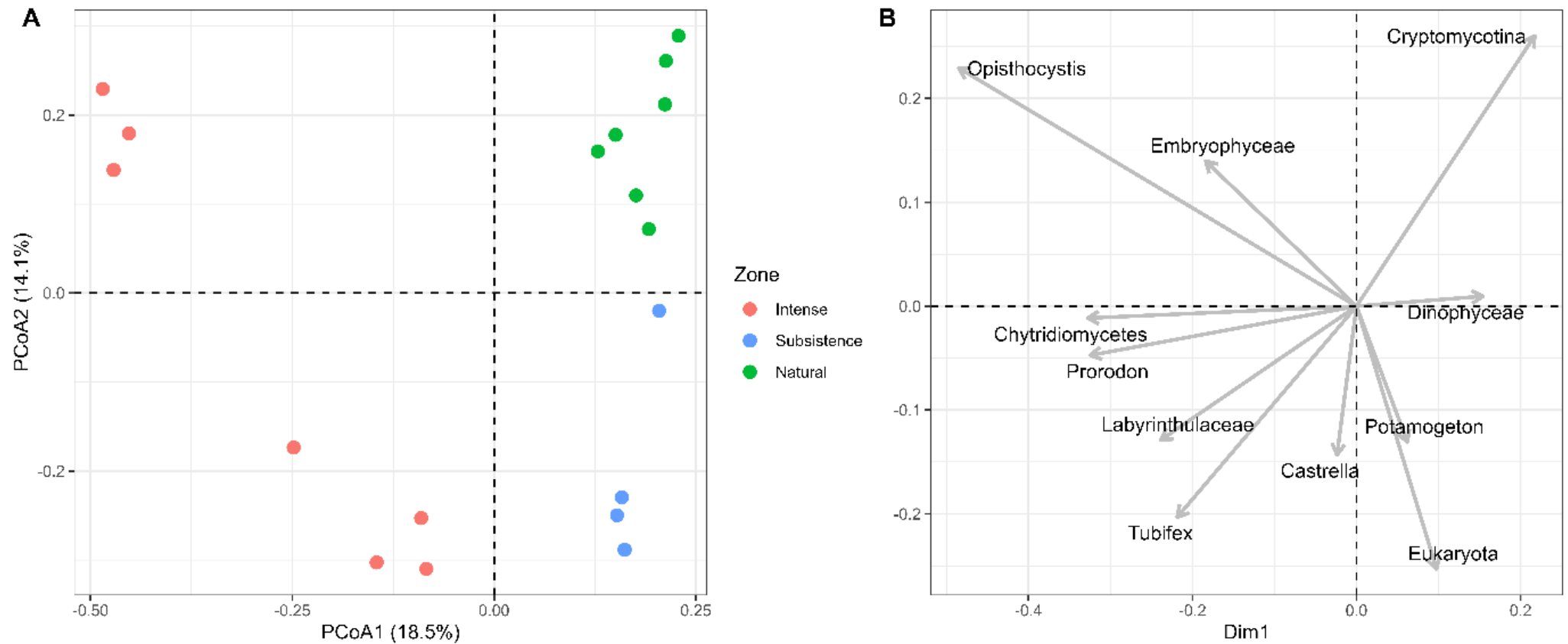


Figure 20.2: Principal coordinate analysis (PCoA) summarising the variation in the composition different fungal species using the 18S gene across the three eras of land use in Aotearoa-New Zealand.

#### 4.3.3 16S

The two main axis of the PCoA explain 45.8% of the variance of the 16S assemblages (Figure 21.2). None of the eras overlap with the intensification era, which has the most variation with two clusters being greatly different. The natural assemblage had the least variation, creating one tight cluster.

##### *Pre-human*

The pre-human era has the most consistent abundance of ASVs, with relatively high abundances of Caldatribacteriota, Chloroflexi and Chloroflexi 1. (Figure 21.1). However, many of them trended downwards at the transition to subsistence agriculture.

##### *Subsistence agriculture*

During the subsistence agriculture period, the downward trend of ASVs from the pre-human era continues with both Chloroflexi and Cladotribacteriota disappearing from the record. However, the end of this period is defined by sharp increases of all Acidobacterium and the only time in which Nitrospirota and Acetothermia 1 occur, although they both later disappear.

##### *Intensification*

The beginning of the intensification era is defined by peaks of Acidobacteriota ASVs before they drop to insignificant abundance. The start of this period also has the only occurrences of Acetothermia.1 and Nitrospirota, both of which occur and disappear from the record simultaneously for less than 200 years between 1600-1850 (95% CI: 1530-1870 CE). Within the most recent 200 years of the record, four ASV groups appear for the first time: Acetothermia, Acidobacteriota, MBNT15 and Firmicutes. Of these groups, both Acetothermia, Acidobacteriota and MBNT15 reach abundances of approximately 6% which is the highest any of the groups reach, with Chloroflexi being the only other to reach this abundance at the beginning of the record.

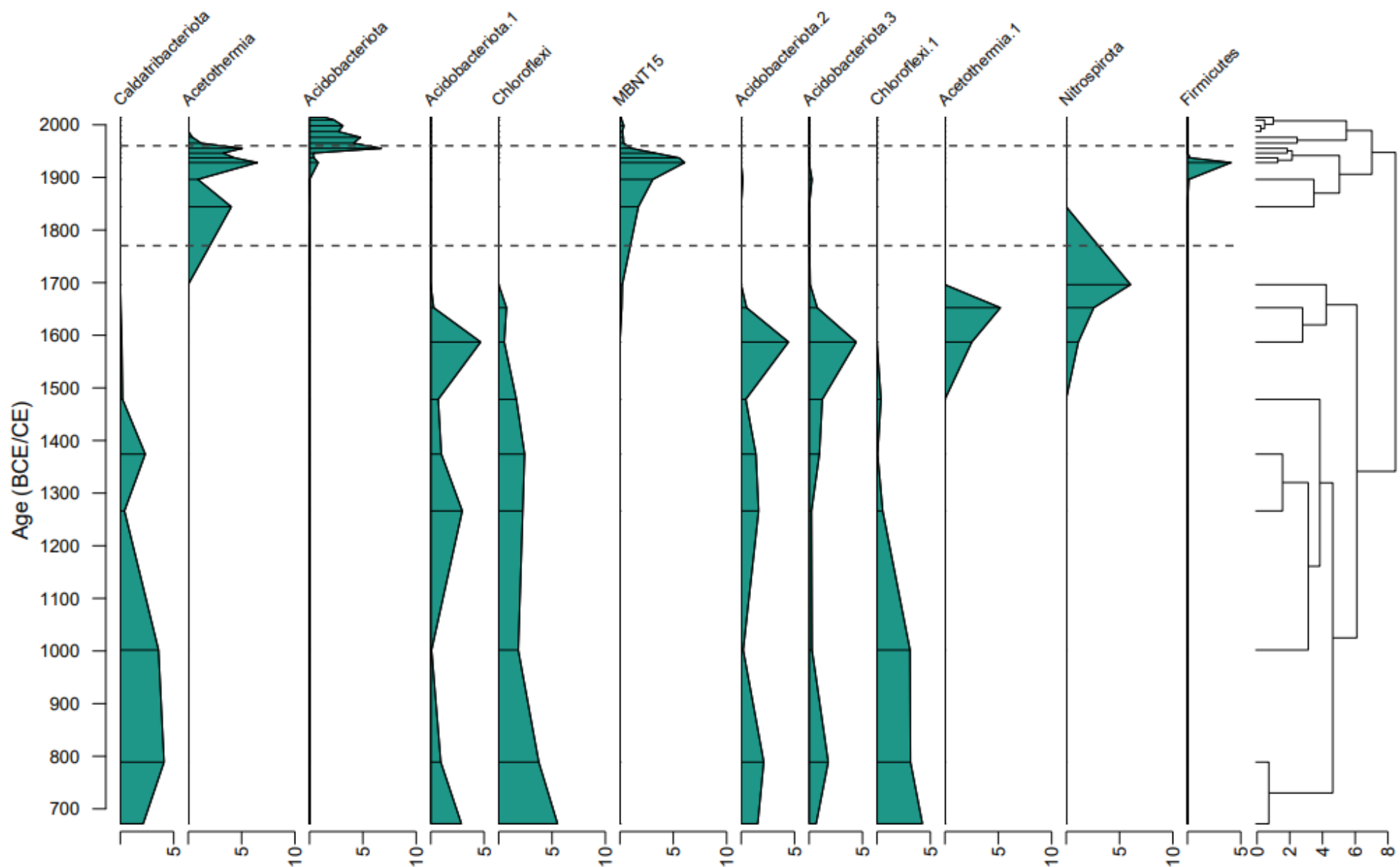


Figure 21.1: The y-axis constrains age, while the x-axis shows the abundance of different bacteria species using the 16S gene against core depth (cm) and age (calendar years before the present). Dotted lines= indicate major changes in the community structure

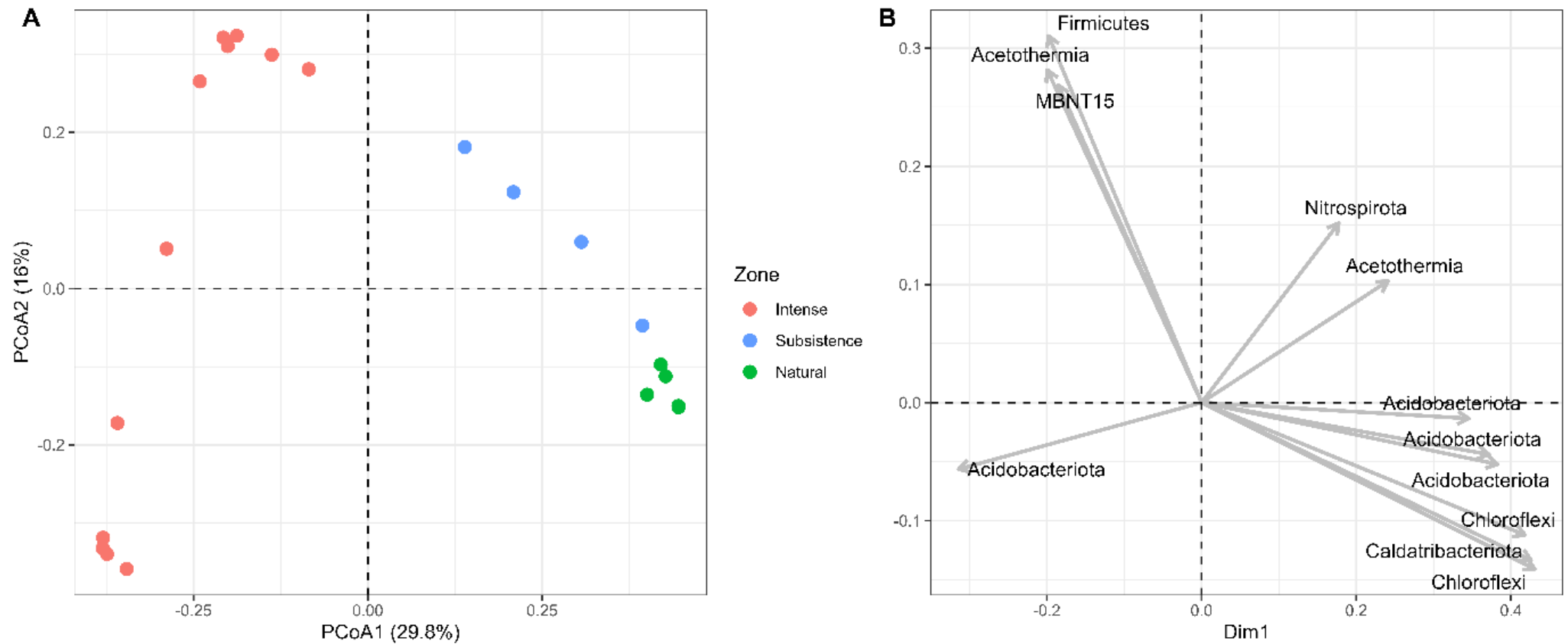


Figure 21.2: Principles coordinate analysis (PCoA) summarizing the variation in the composition of the different bacteria species using the 16S gene community across the three eras of land use in Aotearoa-New Zealand.



#### 4.4 Species Summary

From the summary table (Table 1) where most of the dominant species transitions often either pre- or post-dates the land-use change boundaries, indicating that the ecosystem has a delayed response to the major catchment shifts. The first change of dominant taxa of the pollen taxa, is a direct response to the introduction of human induced land clearance with the Chironomid shift occurring just prior to the pollen change which may indicate the response was due to the fires eliminating the tall forest canopy, more so than *P. esculentum* itself. The eDNA, particularly CO1 and 18S experienced more diversity shifts of the dominant taxa than the other groups which may be signifying more fine scale changes of the lake chemistry throughout the land-use changes.

#### 4.5 Temperature reconstruction models

In general, most chironomid transfer functions for SmT overpredicted temperature on the cooler end of the gradient and underpredicted temperature at the warmer end (Figures 22.1 and 22.2). Based on predicted vs observed SmT and cross-validated model performance (Table 2), the WA-PLS performed the best. Overall, fossil samples were well represented by surface samples, with most samples having a close modern analogue (i.e., less than the 10<sup>th</sup> percentile), good fit to temperature, and few fossil samples with taxa either absent from or poorly modelled by the modern training set (Figure 23).

Table 1: Summary table of the most dominant taxa of each proxy across the different land-use phases.

Age BP	Fossil			EDNA		
		Pollen	Chironomids	CO1	18S	16S
	2000	<i>Pteridium esculentum</i> <i>Pinus</i>	<i>Naonella kimihiia</i> <i>Chironomus</i>	Chlorophyta Tubifex	Labyrinthulaceae Potamogeton	Acidobacteria Aetothermia
	1850					
Pre-human	1250	<i>Fuscospora</i>	<i>Corynocera</i>	Ochrophyta Cardiida	Cryptomycotina Potamogeton	Chloroflexi
500						

Table 2: Table of performance diagnostic of models for temperature reconstruction of subfossil Chironomid (WA-PLS= Weighted averaging partial least squares, PLS= Partial Least Squares regression, WA= Weighted average, MRLC= Maximum likelihood response surfaces, BRT= Boosted regression tree). Model used indicated in bold.

Model		Object					Cross evaluation						
		RMSE	r <sup>2</sup>	Avg.Bias	Max.Bias	Skill	RMSE	r <sup>2</sup>	Avg.Bias	Max.Bias	Skill	delt.RMSE	p
WA-PLS	Comp01	1.432	0.765	-0.085	2.075	76.418	1.55	0.727	-0.145	2.37	72.41	-47.474	0.001
	<b>Comp02</b>	<b>1.172</b>	<b>0.842</b>	<b>-0.014</b>	<b>1.458</b>	<b>84.217</b>	<b>1.357</b>	<b>0.789</b>	<b>-0.065</b>	<b>1.818</b>	<b>78.851</b>	<b>-12.448</b>	<b>0.004</b>
	Comp03	1.049	0.874	-0.009	0.855	87.36	1.318	0.802	-0.042	1.255	80.048	-2.87	0.199
	Comp04	0.996	0.886	-0.015	0.683	88.596	1.36	0.792	-0.071	1.082	78.754	3.192	0.874
	Comp05	0.976	0.891	-0.017	0.658	89.044	1.38	0.787	-0.067	1.022	78.109	1.506	0.794
PLS	Comp01	1.459	0.755	-2.637	2.931	75.55	1.633	0.694	-0.012	3.331	69.357	-44.644	0.001
	<b>Comp02</b>	<b>1.151</b>	<b>0.848</b>	<b>-3.571</b>	<b>1.12</b>	<b>84.773</b>	<b>1.309</b>	<b>0.803</b>	<b>0.005</b>	<b>1.553</b>	<b>80.292</b>	<b>-19.804</b>	<b>0.002</b>
	Comp03	1.091	0.863	-3.553	0.992	86.323	1.261	0.817	0.009	1.44	81.719	-3.687	0.092
	Comp04	1.031	0.878	-3.035	0.696	87.776	1.249	0.821	-0.002	0.925	82.08	-0.993	0.332
	Comp05	0.999	0.885	-2.424	0.676	88.521	1.243	0.823	-0.004	0.905	82.248	-0.469	0.444
WA	WA.inv	1.446	0.777	0.129	3.172	75.964	1.508	0.758	0.065	3.288	73.872	-	-
	WA.cla	1.463	0.758	0.193	2.202	75.422	1.53	0.732	0.11	2.376	73.087	-	-
MRLC	MLRC	1.423	0.816	-0.229	1.671	76.751	1.526	0.775	-0.278	2.669	73.238	-	-
BRT	BRT	-	-	-	-	-	1.436	0.741	-0.026	3.787	-	-	-

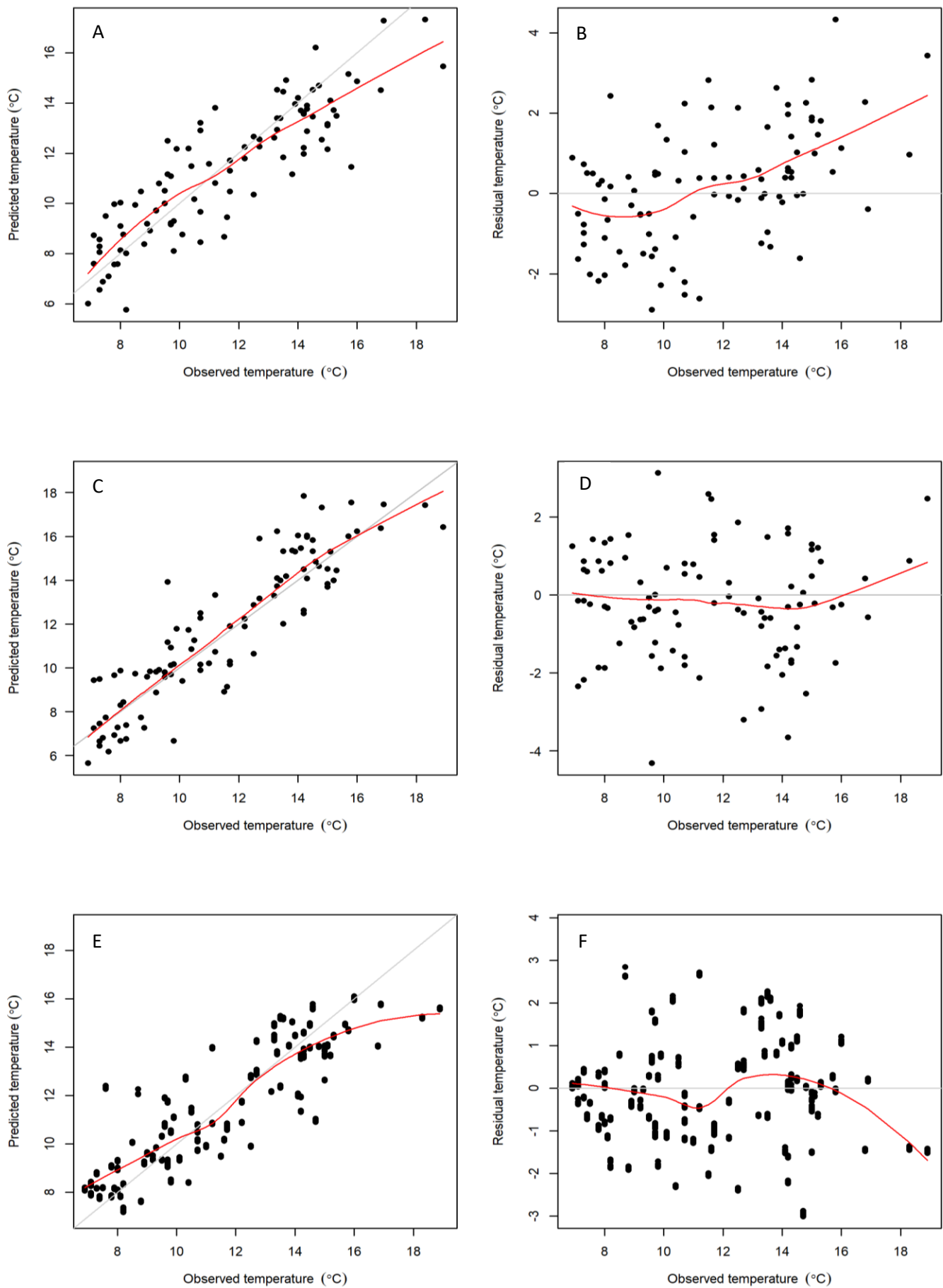


Figure 22.1: Panels A, C, E illustrate the relationship between observed and predicted SmT, while B, D, F depict the residuals of each model. Models include the second component WA-PLS (A, B), second component PLS (C,D), and inverse weighted averaging (E, F).

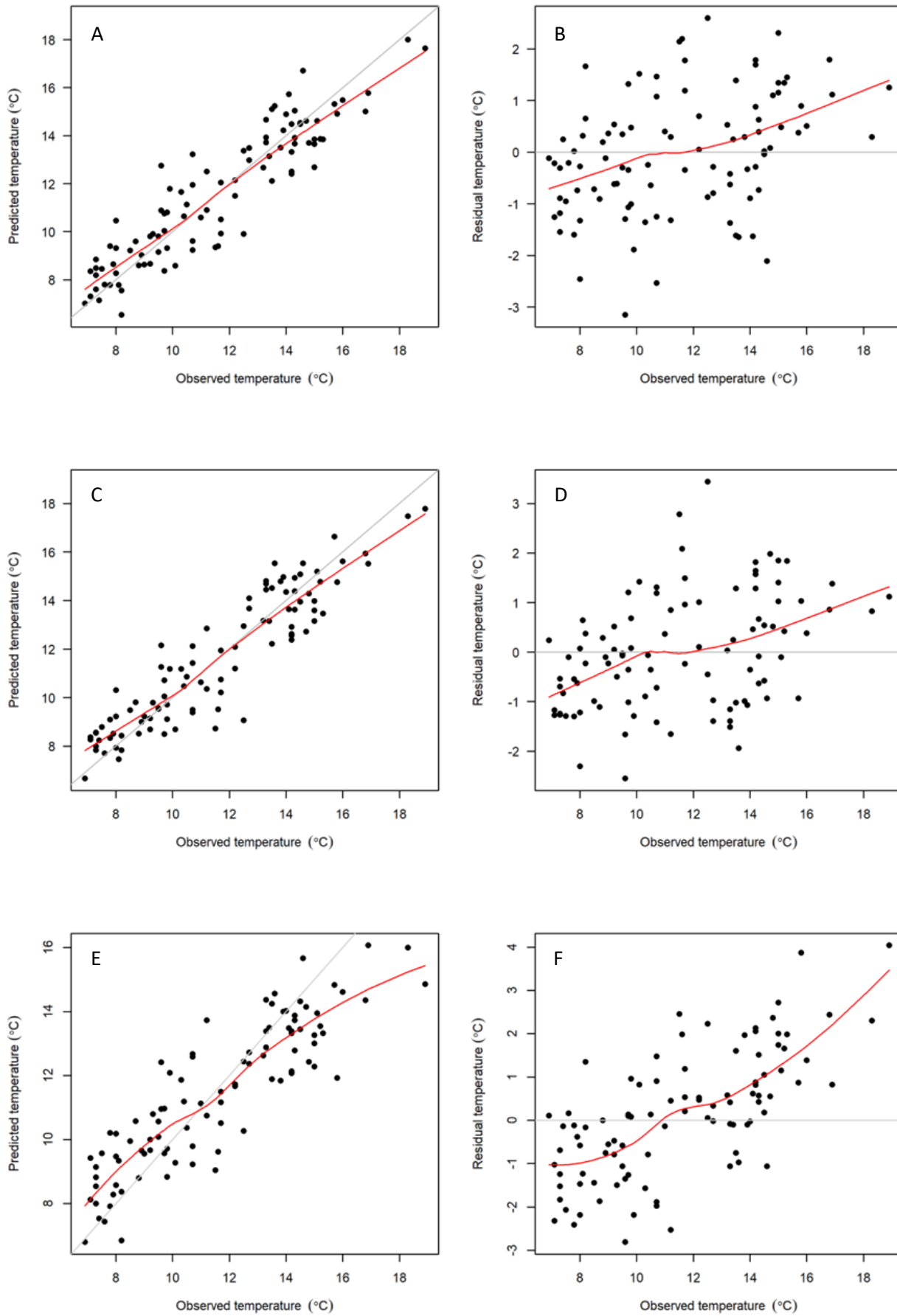


Figure 22.2: Panels A, C, E illustrate the relationship between observed and predicted SmT, while B, D, F depict the residuals of each model. Models include the second component classic weighted averaging (A, B), Maximum likelihood response surfaces (MRLC) (C,D), and Boosted regression tree (BRT) (E,F).

The amount of dissimilarity between the fossil sample and modern analogue remains with a “close” fit throughout the record (Figure 23). Goodness of fit of fossil samples to the modern analogue remains with “good”. Fit as all chi-squared distance remains below both the 2<sup>nd</sup> and 5<sup>th</sup> percentiles. From the outcomes of the model testing, WA-PLS and PLS are the appropriate models for temperature reconstruction diagnostics.

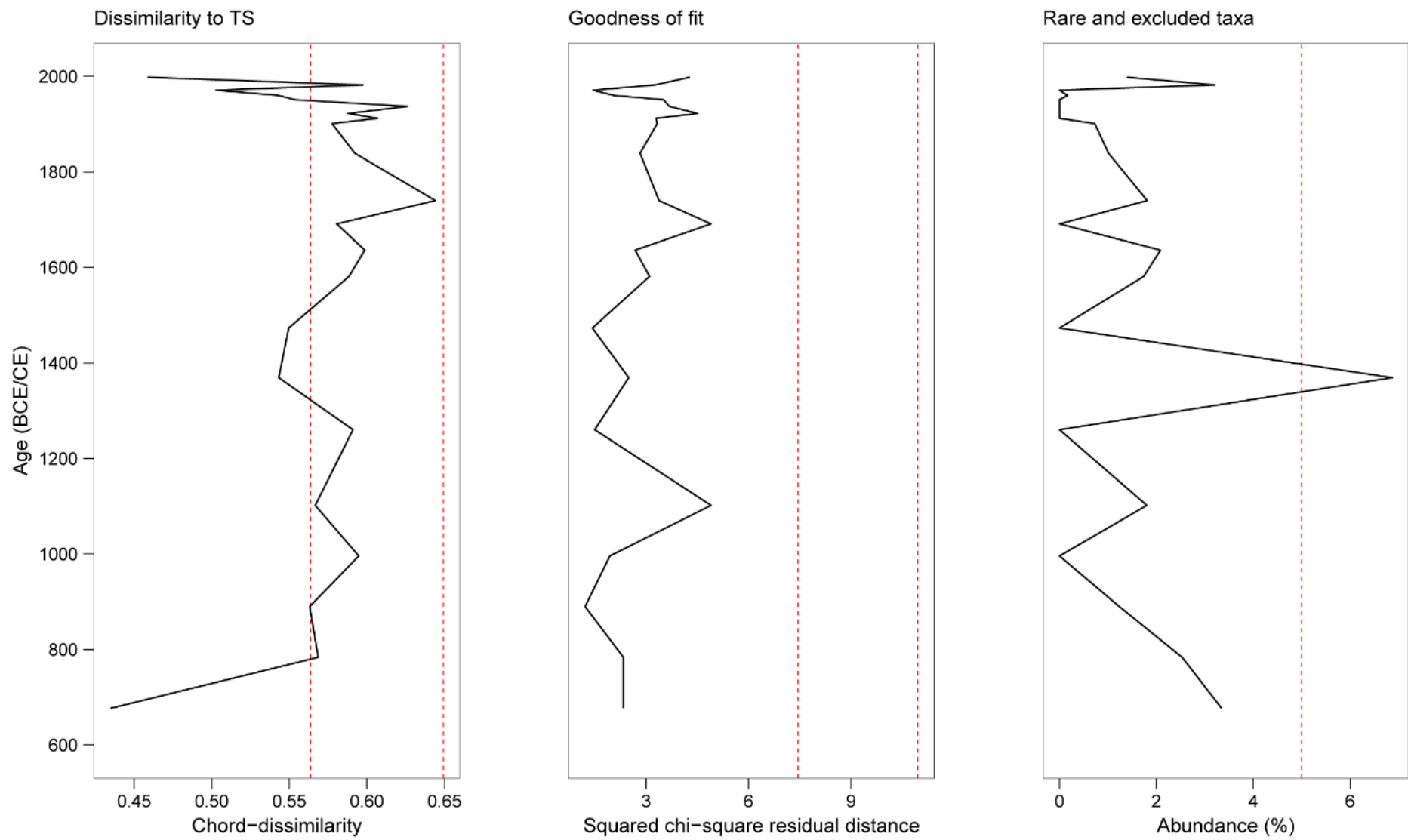


Figure 23: Chosen temperature reconstruction diagnostic model (WA-PLS) appropriateness testing. Red dotted lines= model fitness.

The rate of change throughout the entire timeline has a continual upwards trend (Figure 24). However, this rate of change flattens and remains steady throughout the subsistence farming era before increasing again as practices on the catchment are intensified. As the phase transitions into intensification, the rate of change has its sharpest increase, which continues throughout the period. This sharp incline occurs simultaneously as the first diversity shift of CO1 and 16S.

Estimated summer temperatures, throughout the prior to the humans, continually increase, reaching a peak temperature of approximately 15°C around the onset of the 16<sup>th</sup> century, where subsistence farming practices have been occurring for approximately 150 years. This temperature peak aligns with the second major divert shift of Chironomids and the first shift of 18S. From this high, temperatures have been continually declining until 2000 where average summer temperatures are approximately 14°C.

Aside from three large troughs at approximately 1000, 1090 and 1250 CE chlorophyll *a* remains relatively steady throughout the pre-human era before a drop which occurs around 1250 CE (95% CI: 1200-1300 CE), right on the onset of subsistence farming. This decline continues throughout this time period, reaching its lowest point during the 19<sup>th</sup> century after when values sharply incline as agricultural practices are intensified. This low point coincides with the first CONISS cluster delimiter of both CO1 and 16S.



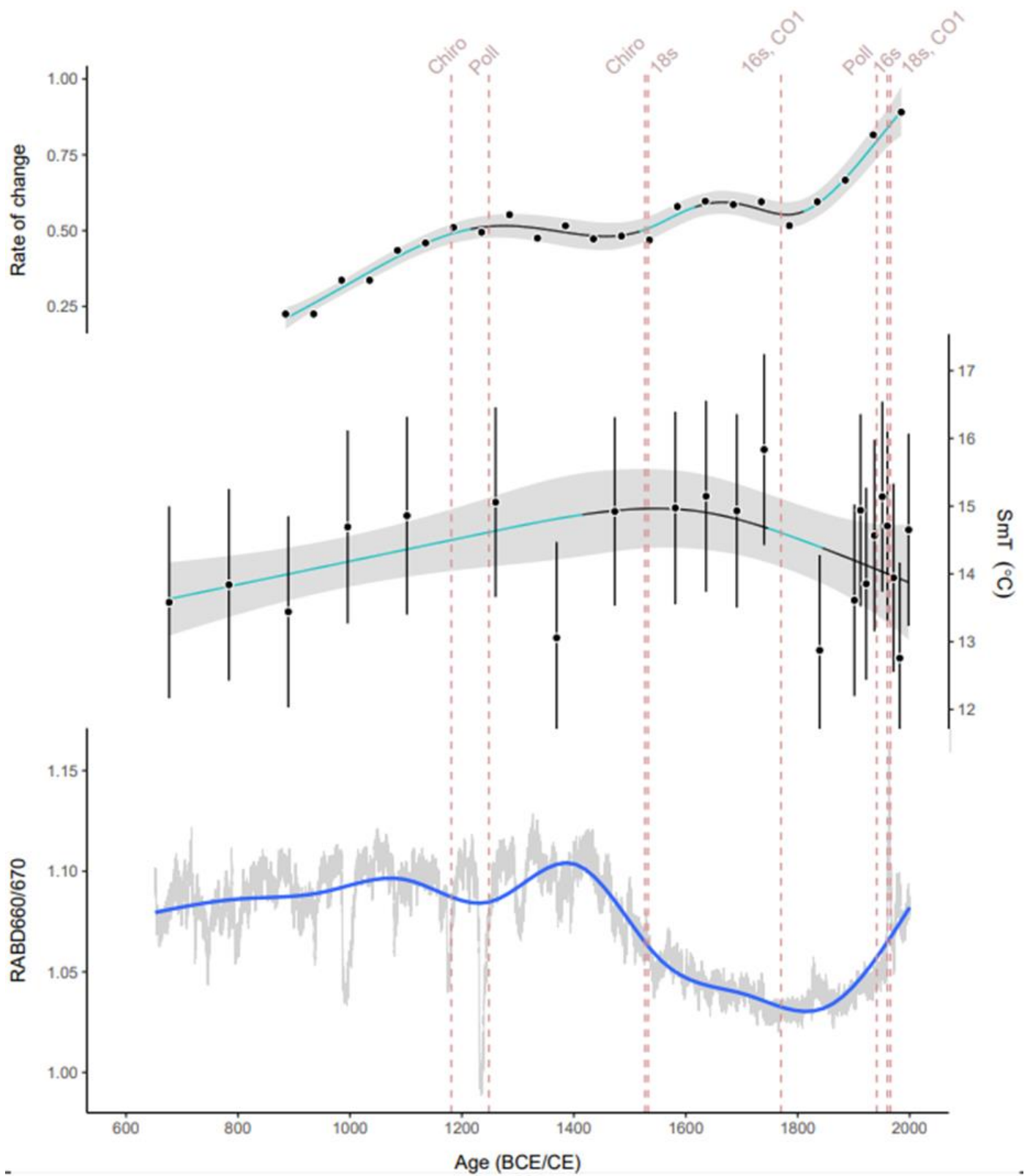


Figure 24: Summary plot. Top graph= Rate of change analysis; middle graph= mean summer temperature reconstruction; bottom graph= hyperspectral graph of RABD 660/670 (Chlorophyll a). Dotted lines= based on CONISS (constrained cluster analysis) of all proxy assemblages.

## Chapter 5: Discussion

Chapter 5 aims to reconstruct environmental changes surrounding Lake Kaweka, to examine the impacts of the sudden environmental shifts which are associated with anthropogenic climate change and changing land use and how the ecosystem shifts in response. The two aims are tried, 1) Whether there is evidence of anthropogenic climate change in a lake of good ecological condition in Aotearoa-New Zealand; 2) How does ecosystem diversity change in response to climate and catchment pressures? In order to achieve these aims, a chronology of the different land use regimes within the Lake Kaweka catchment is generated over the last 1,000 years, encapsulating pre-human settlement, through the introduction of early settlers' subsistence farming and the later intensification of agriculture.

### 5.1 Key Species Distribution

#### 5.1.1 Ecology of the most abundant chironomid taxa

Knowledge of the ecology and distribution of the chironomid fauna of Aotearoa-New Zealand is poor due to incomplete taxonomic knowledge and insufficient ecological data (Boothroyd, 2012). This is especially true for the subfamily Orthoclaadiinae, from which two of the most abundant taxa were identified, *N. kimihia* and *Corynocera*. *N. kimihia* is known to occur in the shallow, littoral zones of both deep and shallow lakes with records across both the North and South Islands in lowland and upland lakes. *N. kimihia* lives epiphytically on stems and leaves of submerged aquatic vegetation with no preference between native or introduced species (Boothroyd, 2012). *Corynocera* thrives in ecosystems with heavy algae growths, often due to excessive nutrient enrichment, as they are known to feed on a range of streambed algae and organic detritus.

The other three most abundant taxa belong to the subfamily Chironominae. *Corynocera* is also a species which thrives in ecosystems with heavy algae growths, often due to excessive nutrient enrichment, as they are known to feed on a range of streambed algae and organic detritus. *Chironomus* is a generalist species found in a variety of environmental conditions including oxygen-depleted, nutrient-rich ecosystems, thriving in sewage ponds and profundal zones where oxygen availability is low, and the temperature fluctuates dramatically. *Chironomus* species are typically found in the soft sediment of slow-flowing streams, ponds, or

lakes, feeding on a wide fine organic matter that settles in pool habitats. *Tanytarsus funebris* is a species belonging to the tribe Tanytarsini which tends to be the dominant taxa in small lakes at high altitudes in the North Island, suggesting they prefer cooler, open waters as well as harsh environments typical of developing lakes, favouring low conductivity (Dieffenbacher-Krall et al., 2007). *T. funebris* occurs frequently in middle-range temperatures (Dieffenbacher-Krall et al., 2007), although they have been observed in temperatures reaching above 25°C in geothermal regions of Taupō. The separation of different *T. funebris* is based on antennae pedestal height to mentum height, with the types with long antennae tending to cluster and occur more frequently in warmer lakes with higher chlorophyll- $\alpha$  content (Dieffenbacher-Krall et al., 2007).

#### 5.1.2 Environmental tolerances

An ecological optimum is a combination of a variety of environmental variables which is optimal for the existence, growth, development, and reproduction of a species where the environmental tolerances are the range in which the species needs to survive (Figure 25). Species can occur outside these temperature ranges by living in microhabitats near banks where water temperature may be different from that recorded from the main water column (Duggan et al., 2007).

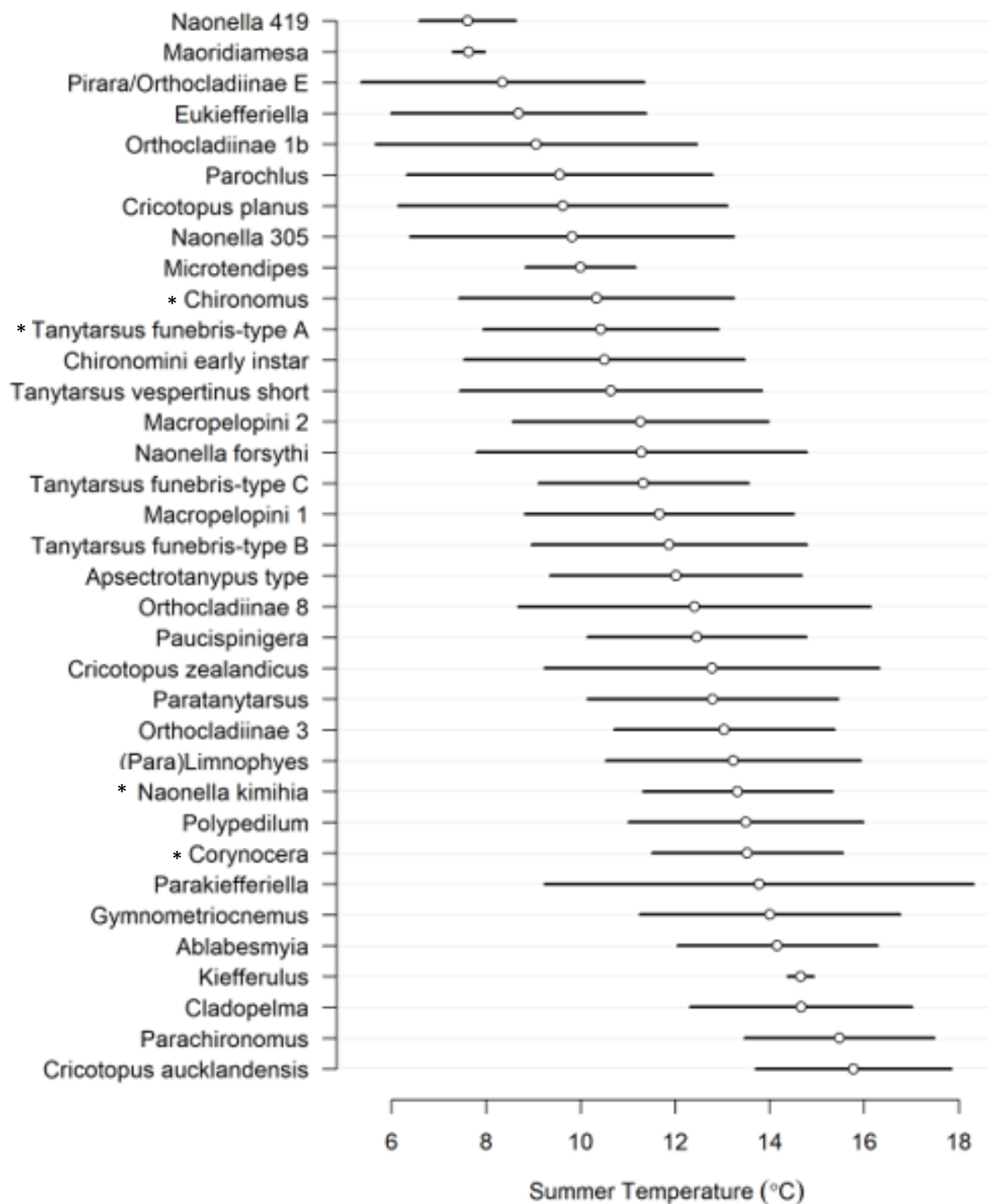


Figure 26: The most abundant chironomid species from Kaweka Lake environmental optima with tolerance range in °C. Derived from information collected from Dieffenbacher-Krall et al., 2007. \*= indicated most abundant species of the entire record.

## 5.2 Pre-human landscape

Consistent with findings by Wilmshurst *et al.*, (1997), the pollen record prior to human settlement within the catchment largely consisted of a continuous cover of beech-broadleaf-podocarp forest. The forest was primarily composed of *Fuscospora* spp (beech), *Prumnopitys taxifolia* (matai), and *Dacrydium cupressinum* (Rimu), indicating that a majority of the catchment was forested with these species forming a tall overstory. *Fuscospora* is typically a light-demanding tree found in lowland and montane forests with a preference for well-draining, fertile soil. However, while these preferences remain true for red beech, mountain beech (which is also included within *Fuscospora*, and both are currently found within Kaweka Lake's catchment) grows to form forest tree lines, growing at higher elevations. Due to Kaweka Lake mid-altitude location with surrounding alpine peaks, the predominant beech within *Fuscospora* spp. pollen is therefore likely to be mountain beech (Māori name: Tawhai rauriki) although it is important to note that beech pollen is able to be wind-dispersed and thus is relatively mobile. *D. cupressinum* is a type of podocarp which is typically an emergent, forming pure stands which can exclude *Fuscospora*, commonly found from lowland into montane forests in well-drained, fertile soils with rainfall in exceedance of 1,000 mm/yr and mean annual temperatures >11°C (Lorrey & Bostock, 2017). Therefore, the catchment during this period was likely highly vegetated, with *Fuscospora* dominating the higher altitudes in the surrounding catchment while *D. cupressinum* occupied the lower altitudes around the edge of the lake.

## 5.3 Ecosystem and catchment responses

### 5.3.1 Chironomids

The Chironomid fossil record prior to human settlement had the lowest abundance and lowest diversity, mainly consisting of the warm tolerant genera *Corynocera* (Subfamily: Chironominae) (Figure 17.1). *Corynocera* is a shallow, littoral-type species which can tolerate acidic conditions (Nazarova *et al.*, 2017). They are a common species often found in productive lakes and, typical of its subfamily, has a strong significant relationship with chlorophyll- $\alpha$  (Dieffenbacher-Krall *et al.*, 2007). These traits all indicate that Kaweka Lake was likely eutrophic, and vulnerable to algae blooms due to the high levels of natural erosion

in the area which increases nutrients in the system and potentially warm summers reconstructed from the chironomid assemblages. A relatively more eutrophic state is supported by the elevated values of chlorophyll- $\alpha$  inferred from the hyperspectral measurements. The high abundances of *Corynocera* and *Chironomus* particularly indicate high levels of total phosphorus (TP) (Zang, et al., 2011). TP is an essential element in freshwater systems and occurs naturally in rocks and minerals. The weathering of the rocks and minerals allows TP to bind itself to the sediment where it can enter waterways through erosion, encouraging algal blooms (LAWA, 2023). *Chironomus*, although a cool-type genus, also thrives in highly productive, low-oxygenated lakes (Zang, et al., 2011) supporting the pre-human state of Kaweka Lake being eutrophic and prone to algal blooms. The presence of *Macropelopini* within the lake sediments, throughout the entire record, also correlates with high erosion levels, or flood events, as this taxon is more often associated with stream habitats (Siri & Donato, 2015) so has likely been washed into Kaweka Lake from the surrounding streams of the catchment.

#### 5.3.2 eDNA

The CO1 gene sequence is a component of the mitochondria, an organelle found within the cells of most eukaryotic organisms, with 18S sequences more targeted at fungi, and 16S primarily used for bacterial detection. Prior to the arrival of humans, the most abundant ASVs from the CO1 and 18S records were Ochrophyta 1, which belongs within the division of red algae (Rhodophyta)(Figure: 18.1), and *Potamogeton* (Figure: 19.1). Red algae are not likely to produce nuisance growth, choking the environment, often found in shadier habitats or deeper in the water column and are unlikely to produce toxins (MWLR, 2023) with Ochrophyta being a saline-tolerant taxa (Astorg et al., 2022). It is likely the species of *Potamogeton* is *P. suboblongus*, as it is the only native species which can occur at montane altitudes, which thrives in high nutrient environments but lower temperatures. After a sharp incline, the species has a dramatic decline where it flattens out, before beginning to increase again just prior to human arrival. Throughout this time Dinophyceae cycles through periods of high and low abundance. Dinophyceae is the most abundant group of Dinoflagellate, which has the ability to produce a dinotoxin which can be highly toxic with the capability of poisoning wildlife if concentrations are high.

The most abundant bacteria are two different Chlorofelxi (Figure 20.1) which play an important role in ecosystems by providing a scaffold for flocs, creating an ample primary food source (Speir et al., 2015). Chlorofelxi is a filamentous bacterium which is being used globally in sludge wastewater treatment as an effective way to remove nitrogen and phosphorus in anaerobic conditions (Speir et al., 2015). When in a natural setting, this may maintain high nutrient levels within Kaweka Lake, levels where ecosystems still function, by controlling algal blooms and reducing the risk of suffocating or poisoning the environment

#### 5.4 Subsistence farming land use

Following the arrival of the Māori and the introduction of subsistence agriculture land use, Kaweka Lake's pollen record was characterised by the sudden increase in charcoal (50-100 µm), as well as a decline in tall trees, which is contemporaneous with an increase of grasses and shrubs, particularly *P. esculentum* (Wilson, 2005). Similar rapid transitions from a tall, closed-canopy forest type to early successive type species such as *P. esculentum*, followed by the appearance of other fast colonising species like *Coriaria* and *Leptospermum* are well documented within Aotearoa-New Zealand palynological records, interpreted to be a result of early Māori land clearance (Cook et al., 2002; McGlone et al., 2005; McWethy et al., 2014; Newnham et al., 2013; Perry et al., 2014; Wilson, 2005; Woodward & Shulmeister, 2005). The increase of these species may also be the result of intentional planting from local iwi to support the growing population later in this time period. The need for these species would have increased as both were highly cultivated for medical properties which they provide resulting in these species being highly valued by Māori. The increase and continually high abundance of *P. esculentum* alongside the other culturally significant species, as well as the influx of charcoal found within Kaweka Lake, indicate local land clearances likely for agricultural purposes to support growing populations in the area. Increased planting in the lake catchment limits both the sediment and nutrient inputs, in turn, reducing lake productivity, restricting the growth of algae and consequently the productivity of benthic organisms (Wilby et al., 2010).

*Fuscospora* experiences the most drastic decline of the entire pollen record, dropping by approximately half.

This rapid decline may have been due to the species preferring the drier ridges making them more

susceptible to fire. *Fuscospora* is, however, the only tall tree species during this time period to also increase in abundance near the end of the phase, indicating a potential recovery. This increase could be attributed to the now open canopy, which permits more light to penetrate into the system, allowing for greater reproductive success rates.

For Aotearoa-New Zealand, charcoal is the primary evidence of fire (McWethy et al., 2014). Charcoal particles in lake sediments which are greater than 125  $\mu\text{m}$  are likely derived from distances of no more than 1-2 km away and are the minimum size fraction for evidence of local fires, as it is difficult for larger particles to travel great distances. Smaller particles (less than 100  $\mu\text{m}$ ) can however travel much farther distances with dust-sized charcoal able to disperse thousands of kilometres from its original source (McWethy et al., 2014). After a fire, charcoal is able to remain in the environment on charred wood and on the ground in soil layers for many years and any disturbance in the catchment, such as heavy rain, can lead to abrupt spikes within the sediment. The most abundant size fraction of charcoal in Kaweka Lake sediments are intermediate (50-100  $\mu\text{m}$ ) which implies that a majority of fires occurred in the surrounding catchment, not directly around the lake. This charcoal reaches its peak just at the end of this period but could possibly be a delayed signal from an influx of charcoal entering the system from a sudden disturbance, such as a flood.

## 5.5 Ecosystem and catchment responses

### 5.5.1 Chironomids

Following the arrival of humans and the beginnings of subsistence agriculture, there is a sudden decline of *Corynocera*, a species which disappears from the record by the end of this era, aside from a small occurrence in the 20<sup>th</sup> century. The drastic decline of *Corynocera* left an open niche for two other species to exploit: *Naonella* and *Chironomus*. This could suggest a change in the primary production within the lake, namely a transition from a majority algae-dominated environment to macrophyte-dominant, which is also supported by the hyperspectral scanning (figure 19). An environment which has a higher composition of macrophytes promote greater *Naonella* abundance, particularly *N. kimihia*, as this species lives in this ecosystem type. This transition may also indicate a change in the geomorphology of the lakebed; elevated influx of eroded



materials may support expansion of macrophyte communities, which typically require sandy sediments to grow; many macroalgal species require solid substrates (Peters & Lodge, 2009). The decline of tall trees in the catchment to allow for subsistence agriculture on the landscape likely increased surface and wind erosion. The increase of *Chironomus* also supports this change, as they are typically found in soft sediments, feeding on fine organic material settled on the lake bottom (Larocque et al., 2006). The increase in the number of other Orthoclaadiinae species (*Cricotopus*, *Eukiefferiella* and *Limnophytes*) also suggests greater erosion, as this subfamily is more likely to be found within stream environments, suggesting these genera were probably washed into the lake system due to erosion from the reduction of soil stability by the removal of tall trees.

While the chironomid-inferred summer temperatures peak during the subsistence agriculture phase, it is important to note peak temperatures coincide with a potential rearrangement of the ecosystem from algae- to macrophyte-dominance. This rearrangement could confound estimated temperatures. The reconstruction diagnostics suggest the majority of the record is comprised of well-modelled taxa that are sensitive to summer temperature (Table: 1). The resultant estimated temperature from the sample is conspicuously cold. Despite the strong diagnostics, however, drivers of chironomid community composition other than temperature cannot be ruled out.

#### 5.5.2 ASVs

Subsequent to the introduction of subsistence agriculture to the landscape, Kaweka Lake's ecosystem and water quality are characterised by a general decline at the beginning of the phase in bacterial taxonomic composition and algal productivity. Both Chloroflexi and Acidobacteria are capable of chlorophyll-based phototrophy (Jagannathan, & Golbeck, 2009), and the general decline of these groups may be a result of less light entering the system, a common symptom of increased sediment in the environment. However, different groups of Acidobacteria have other modes of gaining nutrients through consuming atmospheric H<sub>2</sub> and being a slow-acting decomposers of plant, insect and fungi-derived polymers (Dedysh & Sinninghe

Damsté, 2019). These different modes of gaining nutrients are likely the cause of the three different groups within the record, and the different environmental responses of each.

A recently discovered fungus or fungal-like eukaryote known as Crytomycota is believed to have a vast amount of unstudied diversity and is present in both terrestrial and aquatic ecosystems, indicating that it likely plays an important ecological role, though the specifics of that role are yet unknown (Lazarus & James, 2015; Rojas-Jimenez et al., 2017). The sudden appearance and disappearance of this class was likely due to a novel environmental factor of this era, but that factor is unknown due to a lack of information on the taxon's environmental tolerances.

Ascomycetes is a common fungus which can be divided into two broad categories based on how they gain their nutrition: either parasitising or endophytic on aquatic macrophytes and algae or the more common method, saprophytic on dead plant material (Shearer, 1993). Some of the Ascomycete's occurrences may have been due to allochthonous input from increased erosion, especially as they are commonly found on a variety of *Fuscospora* species (Shearer, 1993). This is likely the cause as Ascomycetes appears suddenly in high abundance and then rapid decline to zero, paralleling the abundance of *Fuscospora* in the pollen record. There are several aquatic Ascomycetes, species that require water to disperse, but these would theoretically be more constant throughout the record.

It is likely the occurrences of both Nitrospirota and Acetothemia, which only occur in this era, are indicative of the environment going through a period of greater salinity, as both species are halophilic (Daims, & Wagner, 2018; Baricz et al., 2021). The traditional subsistence agricultural techniques of Māori used ash as a fertiliser (MWLC, 2023), a product which contains reasonably high levels of sodium, which may have leached into Kaweka Lake from the catchment. The increase in sodium may have been the influential factor of this era which allowed the growth of Crymycota.

Finally, bivalves (Unclassified Cardiida) have a global distribution and perform important roles in the functioning of freshwater ecosystems with dispersal often relying on the movement within the stream

network (Kappes & Haase, 2012). The introduction and rapid dispersal of Mollusca within Kaweka Lake may have been aided by the movements of humans across the landscape, as they are typically slow dispersers in freshwater ecosystems.

## 5.6 Intensification land use

Most indigenous fauna experiences a decline during the intensification phase of agriculture, a trend which is observed globally (Cairns, 2015; Contreras-Hermosilla, 2000; McGlone, 2009; McWethy et al., 2010; Suarez & Sajise, 2010) and is also observed in the catchment of Lake Kaweka. The intensification period within Kaweka Lake is characterised by the introduction of exotic pollen types, specifically *Pinus*, and an increase in Poaceae. These increases are preceded by a small spike in charcoal (50-100  $\mu\text{m}$ ), before dropping post-1950 CE, suggesting much of the land within Kaweka Lake's catchment had already been cleared for agricultural purposes. The spike in charcoal occurs simultaneously with a drop in *P. esculentum*, indicating the area this species once occupied was replaced with Poaceae to support growing sheep and cattle numbers.

The first introduction of *Pinus* into the catchment slightly predates historical records of the intentional planting of *P. contorta* by approximately 50 years, which could be a result of wind dispersal from a nearby source or uncertainty of the age-depth model. Even with the modern controls of *P. contorta*, *Pinus* pollen continues to rise, likely due to the introduction and continual rise in forestry agriculture in the country, 90% of which is *P. radiata* (MPI, 2022)

## 5.7 Ecosystem and catchment changes

### 5.7.1 Chironomids

The intensification of agriculture on the landscape had strong effects on the chironomid community, with species becoming unstable with a transition to more environmentally tolerant species. This is a trend which is witnessed globally when different land use practices, including agriculture and forestry, are intensified (Cairns, 2015; Contreras-Hermosilla, 2000; McGlone, 2009; McWethy et al., 2010; Suarez & Sajise, 2010). The most dominant species of this era is *N. Kimihia*, which reaches peak abundance at the end of the record

of approximately 50% of individuals identified. *N. Kimihia*, being an epiphytic species living on submerged aquatic vegetation, implies that Kaweka Lake remains a lake dominated by macrophyte flora more so than algae. *Macropelopini* and *Chironomus* and early Chironomini instars are species which thrive in a high TP environment, with both types reaching peaks at the beginning of this era. This may result from the introduction of artificial fertiliser to replenish soil nutrients to support the introduction of the pine industry in the catchment (Zavišić et al., 2018). The many fluctuations of *Macropelopini* may also be related to the increase in high-intensity precipitation events in the area (MfE, 2020, NIWA, 2020).

There does not appear to be a clear trend of global warming within the topmost chironomid samples. Interestingly, the phase post 1950 CE has the most rapid rate of change for the entire record, with four of the five proxy records possessing CONISS cluster delimiters; the Chironomidae are notably absent from this list. Summer temperatures of the last century are highly variable, ranging between about 13.5 and 15°C, which is likely a function of the increased sampling resolution.

#### 5.7.2 ASVs

The intensification phase of land use contains the greatest diversity of CO1 ASVs and is characterised by the introduction of Annelida and the reintroduction of Ochrophyte. The most common type of Annelid from the record is *Tubifex* spp., colloquially known as a “sludge worm”, which occurs in a variety of freshwater habitats but is most prominent in fine, inorganic substrates. *Tubifex* spp. has been known to withstand adverse environmental conditions, becoming renowned for its ability to thrive in deoxygenated and highly polluted environments, including sewage discharge. Within these environments, *Tubifex* spp. are often associated with the littoral zone but can be found in great numbers within periphyton or algal mats. When Annelida is first recorded, it coincides with the increase of *Potamogeton*, with both groups declining at similar rates. This could indicate the annelid was reliant on *Potamogeton* as a food source. *Tubifex* spp, however, is somewhat sensitive to heavy metals in the environment, especially when temperatures reach 15°C, which may result in a future decline of the group when the pine forestry is felled as these practices increase heavy metals in the environment (Rathore & Khangarot 2002).

As an aside, the 18S record of *Potamogeton* seems to completely contrast the appearance of the taxon in the pollen record. *Potamogeton* is rare in the pollen record, with only a few spores counted in the top few layers of sediment. This could reflect the macrophyte's distance from the coring location throughout most of the record, highlighting eDNA's potential to identify broader trends within the lake.

The intensification phase is defined by a complete change in the bacterium community with all species which previously dominated the record (Chloroflexi, Cladribacteriota and Acidobacteria 1,2 and 3) disappearing. Just prior to this phase, Acidobacteria 1, 2 and 3 experience near-simultaneous peaks before vanishing. The more modern bacterium community is comprised of Acetothermia, Acidobacteria and MBNT15, all of which thrive in high-nutrient environments (Begmatov et al., 2022).

## Chapter 6: Conclusion

With the increasing pressure to improve freshwater ecosystems across Aotearoa-New Zealand, it is vital to have an understanding of a lake's history, the effects from previous climate events, environmental degradation and how the ecosystem has changed under these pressures. Paleolimnological is a tool for evaluating historical catchment land use, and how land use has impacted aquatic ecosystems, providing a greater understanding of the environment than is possible through traditional monitoring techniques. To investigate how lake ecosystems of Aotearoa-New Zealand may respond to changes in land use and anthropogenic climate change, this study aimed to reconstruct the past environment of Kaweka Lake from a pre-human reference state, to a warm analogue of the past (MCA), culminating in current intensification.

Evidence of anthropogenic climate change in a lake of good ecological condition in Aotearoa-New Zealand.

To reconstruct the past climate of Kaweka Lake, a summer temperature model was developed from a modern training set and applied to a subfossil chironomid record. The age-depth model indicates the last 1,250 years were captured by the reconstruction, placing the bottom of the core at ~750 CE (95% CI: CE 550-950).

Temperature reconstruction shows that Hawke's Bay was in a state of continual warming, reaching a maximum of 15°C, which is approximately 1°C warmer than current temperatures, around 1550 CE (Figure: 24). This result aligns with current research involving climate patterns around Aotearoa-New Zealand at the time (Cook et al., 2002; Burrows & Greenland, 1979; Lorrey & Bostock, 2017; Lüning et al., 2019; NIWA, 2020; van den Bos et al 2018). The MWA may be the reason *Potamogeton suboblongus*, a the species prefers cooler temperatures, drastically declines simultaneous with peak temperatures. After the maximum, temperature falls to its current annual average of 14°C. This fall in temperature corresponds to an increase in *P. suboblongus*. Estimates of future temperatures around Hawke's Bay shows increases over the upcoming 70 years of 0.5-1.5°C (Cook et al., 2002; Burrows & Greenland, 1979; Lorrey & Bostock, 2017; Lüning et al., 2019; NIWA, 2020; van den Bos et al 2018), meaning ecosystem structures during the MCA are an appropriate analogue for Kaweka Lake's immediate future. Knowledge gained of the different species present and

abundances throughout this time are important for the management of Kaweka Lake, potentially enhancing the resilience of the ecosystem in times of warming.

The temperature reconstruction does not show a distinct warming trend associated with anthropogenic climate change. Despite this, the ecosystem demonstrates community changes that fit within the time frame of global warming. This includes chironomid abundances becoming unstable, with species diversity dropping and shifting to more tolerant species like *Chironomus* and early *Chironomini* instars and *Tanytarsus*, as well as the appearance of more tolerant groups like the Annelida. The bacterial community also experiences a great drop in diversity, with the only types remaining prior to 1950, Acidobacteriota and Acetothermia, becoming unstable. The increase of lotic *Orthocladinae* species, especially in the last 100 years, suggests an increase of erosion, which may indicate an increase of storminess or the introduction of pine forestry; these stressors have notable effects on soil stability. Kaweka Lake appears to have always been a nutrient-rich environment as indicated by the abundance of nutrient tolerant species throughout the record; the hyperspectral data suggests algal levels are increasing in the modern error, which might indicate more nutrients in the environment as well as warmer temperatures.

How did the ecosystem diversity change in response to climate and catchment pressures? Human impacts on the catchment were detected using pollen and charcoal, with ecosystem impacts being observed from environmental DNA and subfossil chironomids. Based on these proxies, three different phases of land use were identified within Kaweka Lake's catchment, these being a pre-human era before ~1250 CE, subsistence agricultural practice from 1250-1850 CE, and agricultural intensification from 1850 CE to present.

Prior to human settlement, the catchment of Kaweka Lake was one dominated by tall trees, particularly beech, matai, and rimu, creating a tall overstory in a completely forested catchment with only a small occurrence of charcoal being recorded. Throughout the record, Kaweka Lake has remained an environment with high nutrient levels, with the chironomid community characterised by nutrient-tolerant, warm-adapted species like *Corynocera*. The high abundance of *Corynocera*, as well as the results of the hyperspectral

scanning, suggests that, prior to human arrival, Kaweka Lake was dominated by algae. Hawke's Bay is a region which experiences a large amount of natural erosion, which may be the explanation for the high nutrient levels in the lake. Another likely cause for the high algae production may also be high bird numbers, which would have been living throughout the forested catchment, providing an alternative allochthonous nutrient input. Along with being a naturally nutrient-rich environment Kaweka Lake was also likely anoxic, which is indicated by both the high algae production as well as the great abundance of Chloroflexi throughout this time period.

The change of phases is characterised by a sharp increase of charcoal, coinciding with the decline of tall trees. This also occurs simultaneously with the introduction of *P. esculentum* into the record. These catchment changes occurred across the country when subsistence agricultural practices involving burning were used to support growing human populations. The transition from a forested catchment to one dominated by *P. esculentum* led to greater erosion into the lake, as a result of weakening soil stability from the removal of large trees and their root systems. Greater erosion throughout the subsistence agriculture phase also would have affected the geomorphology of Kaweka Lake by increasing soft sediments. This is illustrated by the transition in primary production from algae- to macrophyte-dominated, as macrophytes typically grow in soft substrate. A change of the substrate also explains the spike of *Chironomus*.

The period of agricultural intensification in Aotearoa-New Zealand began with the arrival of Europeans in 1850 and was characterised by the introduction of exotic species into the record. For Kaweka Lake, the main exotic species was *Pinus*. There was also a large decline in *P. esculentum*, which opens space for exotic *Poaceae* species that serve as pasture plants for the growing sheep industry of the region. These changes in catchment have drastic community responses. *Corynocera*, previously the most abundant species throughout the core, almost disappears entirely from the record, being replaced by a community currently dominated by *Naonella* species, particularly *N. kimihia*. This large community shift is also observed in the bacterial communities, with the previously dominant taxa entirely vanishing from the record, being replaced with a variety of Acidobacteria. These large community transitions may be explained by the introduction of



artificial fertilisers into the environment, rapidly increasing nutrient levels with chemicals which may not have been previously present.

The information collected through the paleolimnological analysis of Kaweka Lake's sediment record has provided greater understanding of the lake's previous states and how communities adapt to environmental pressures.

The information provided by this thesis will enable greater understanding of how global climate events, such as the MCA, impact the Southern Hemisphere generally and Aotearoa-New Zealand specifically. It provides greater information on previous lake ecosystems and how these respond to major external pressures, which allows for more informed decisions on lake management and how to create a resilient ecosystem that might better cope with anthropogenic climate change.

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