

THE BIO-PHYSICAL AND ECOLOGICAL RESPONSE OF LAKE OKATAINA, BAY OF PLENTY, NEW ZEALAND FOLLOWING THE NATURAL DISTURBANCE OF THE 1886 ERUPTION OF MT TARAWERA

By

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Abstract

The health of New Zealand's lakes is central to the environmental, social and cultural wellbeing of the country and its people. However, less than 5% of New Zealand lakes are monitored, and of those that are, monitoring records are often short in duration and only begin once a lake has already begun to deteriorate. This makes it challenging to determine the natural or undisturbed condition of a lake. Paleolimnological reconstructions from sediment cores have the potential to allow the development of high-resolution time series records that can be used to enhance understanding of how and why lakes and the land around them have changed over many centuries.

While the impacts of press disturbances, such as land-use change, have been well studied using paleolimnological approaches, there are only a few studies on the effects of natural pulse disturbances, such as earthquakes, storms and volcanic eruptions and most have focused on a single proxy or only explored recovery over a short time period. This study uses a paleoecological approach to investigate how geochemical proxies and biological communities of Lake Okataina (Bay of Plenty) responded to a significant natural perturbation – the 1886 Mt Tarawera eruption.

Lake Okataina is a deep (max. 70 m), oligotrophic, crater lake. Unlike most other lakes in this region, its 69.2 km² catchment is largely vegetated by native podocarp forest (approximately 80%). This makes it an ideal location to study the impact and recovery of a lake to a pulse disturbance in the absence of other major land-use effects. A 127-cm sediment core was collected from the lake and was analysed using a multi-proxy approach that incorporated palynology, hyperspectral and ITRAX imaging, DNA bacterial metabarcoding and the morphological analysis of chironomids.

Prior to the eruption, primary productivity was relatively high, geochemical proxies revealed an oxygen-rich environment and the bacterial and chironomid communities were stable and settled. Post-eruption the palynological data illustrated a major decrease in the abundance of species of green algae (*Boytrococcus*) and an increase in the abundance of tree ferns. The ITRAX data highlighted a series of major geochemical fluxes to the system following the eruption, including the addition of new soluble elements such as Ca, K and S as well as increases in elemental ratios such as Fe/Mn and Ti/Mn, suggesting the water column become relatively depleted in oxygen. The hyperspectral data outlined a significant decrease in primary productivity post eruption and the community composition of bacteria also shifted considerably. Chironomid species switched from a *Paucispinigera*-dominated community to a more diverse one, where species of *Chironomus*, a low-oxygen tolerant taxon, also thrived. The state of Lake Okataina following the initial disturbance

appears to be returning to something similar to its pre-eruption state; however, many of the ecological communities (particularly bacteria) remain different.

Collectively these data show that the eruption initiated a major regime shift in the system of Lake Okataina across multiple different trophic levels. Geochemical characteristics within the water column shifted dramatically and indicated an almost instantaneous switch from an oxygen rich, aerobic environment to a more anoxic state. Biological communities also shifted considerably to adapt to the new abiotic conditions they faced. This study highlights how pristine lakes respond to pulse disturbances and how when a system is perturbed, it can trigger a regime shift to a new state. Further research should look to expand the suite of paleoecological evidence (from Lake Okataina) to add additional understanding of the changes identified in this study. Studies on a wider range of lakes in the region would assist in ascertaining if the patterns observed in Lake Okataina also occur in other lakes which experienced varying degrees of impact from the 1886 Mt Tarawera eruption.

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Table of Contents

Contents

Abstract	2
Acknowledgements.....	4
Table of Contents	5
List of Figures.....	8
List of Tables	10
List of Equations	10
<i>Chapter 1: Thesis Introduction</i>	<i>11</i>
1.1 Preface (Over-riding significance of research)	11
1.2 Thesis Overview	13
1.3 Wider Literature Review	15
1.3.1 Paleoecology – the “pros” and “cons”	15
1.3.2 Natural disturbance to lacustrine systems	18
1.3.3 Impacts of volcanism on lake systems	19
1.3.4 Tephra	19
1.3.5 Ecological response	21
1.3.5.1 Bacteria	22
1.3.5.2 Phytoplankton.....	23
1.3.5.3 Chironomids.....	24
1.4 Study Site.....	26
1.5 Research hypotheses and objectives.....	35
<i>Chapter 2: Methods and Methodology.....</i>	<i>36</i>
2.1 Methodology/rationale for reconstruction approach	36
2.1.1 Usefulness of Paleolimnology	36
2.1.2 Drivers of lake ecosystem change.....	36
2.1.3 Measures of lake ecosystem response	38
2.1.3.1 Primary productivity (hyperspectral imaging)	38
2.1.3.2 Environmental DNA (eDNA).....	39
2.1.3.3 Chironomids.....	40
2.1.4 Importance of dating lake sediments and establishing a chronology	41

2.2 Methods	43
2.2.1 Core collection and subsampling	43
2.2.2 Chronology sampling	45
2.2.2.1 ¹⁴ C Sampling	45
2.2.2.2 ²¹⁰ Pb Sampling	46
2.2.3 Palynology	47
2.2.4 ITRAX u-XRF Scanning	48
2.2.5 Hyperspectral Imaging	48
2.2.6 DNA Extractions and Polymerase Chain Reaction Amplification	50
2.2.6.1 DNA Extraction	50
2.2.6.2 Polymerase Chain Reaction (PCR)	50
2.2.6.3 High Throughput Sequencing	51
2.2.6.4 Bioinformatics	51
2.2.7 Morphological Analysis of Chironomids	52
2.2.8 Statistical Analysis	53
2.2.8.1 ITRAX	53
2.2.8.2 Hyperspectral Data	53
2.2.8.3 16S rDNA Bacteria	54
2.2.8.4 Chironomids	55
2.2.9 Sampling Summary	55
 Chapter 3: Results	 57
3.1 Core stratigraphy and correlations	57
3.2 Age Depth Model	60
3.3 Palynology	62
3.4 ITRAX	64
3.5 Hyperspectral Data	68
3.6 16S rDNA Bacteria	69
3.6.1 Univariate/Composition Analysis	69
3.6.2 Beta Diversity Analysis	70
3.6.3 Alpha Diversity Analysis	72
3.6.4 Indicator Species Analysis	74
3.7 Chironomids	77

Chapter 4: Discussion	80
4.1 Prelude.....	80
4.2 Pre-Tephra phase – The “steady-state”	81
4.3 Post-Tephra phase – The “regime shift”	83
4.4 Post 1930 phase – The “new state”	86
4.5 Comparing to previous literature on Lake Okataina.....	89
4.6 Limitations	90
4.6.1 DNA variability and fragility	90
4.6.2 Classic paleo uncertainties.....	90
4.6.3 Greater breadth of system.....	91
4.6.4 Ground truth hyperspectral data with eDNA to show aquatic plant changes/diatoms.....	91
4.6.5 Chronology	92
 Chapter 5: Conclusion	 93
 References	 95
 Appendices	 106

List of Figures

Figure 1: Summary diagram of natural and human induced drivers impacting lakes (Page 15)

Figure 2: Summary diagram highlighting the overlap between the sampling domains of ecology and paleoecology (Page 17)

Figure 3: Study Site map of Lake Okataina and the catchment (Page 26)

Figure 4: Map of the Okataina Volcanic Centre (Page 27)

Figure 5: Map of land-use and vegetation types in the Lake Okataina catchment (Page 28)

Figure 6: Climograph chart highlighting average temperature and precipitation for the Lake Okataina catchment (Page 30)

Figure 7: Average chlorophyll-a concentrations in Lake Okataina (2000 – 2008) (Page 32)

Figure 8: Overview of the Constant Rate of Supply sedimentation model (Page 42)

Figure 9: Summary diagram of the Uwitec gravity corer used in this study (Page 43)

Figure 10: Overview flow-diagram of the methods for the hyperspectral analysis of lake sediments (Page 49)

Figure 11: Summary of the sampling strategy for the different proxies used in this study (Page 56)

Figure 12: Core correlations for Lake Okataina (Page 58)

Figure 13: Polynomial regression curves used in the core correlation process (Page 59)

Figure 14: Age-depth model (Page 61)

Figure 15: Summary pollen diagram depicting species of interest in Lake Okataina (Page 63)

Figure 16: Results of the PCA analysis run on the ITRAX dataset for Lake Okataina (Page 64)

Figure 17: Changes to the geochemical system of Lake Okataina (from the ITRAX data) (Page 65)

Figure 18: Changes to the productivity measures within Lake Okataina (from the ITRAX data) (Page 66)

Figure 19: Changes to water column properties within Lake Okataina (from the ITRAX data) (Page 67)

Figure 20: Boxplot depicting RABD index value differences among the phases (Page 68)

Figure 21: Bar plot of the bacteria community composition in Lake Okataina (Page 70)

Figure 22: Ordination plot depicting the results of a Principal Coordinates Analysis for the 16S bacteria community (Page 71)

Figure 23: Multi-box plot of alpha diversity measures for the 16S bacteria community (Page 73)

Figure 24: Heatmap from the indicator species analysis depicting changes to the Gammaproteobacteria class across the different phases (Page 76)

Figure 25: Stratigraphic plot of relative chironomid abundance (by species) (Page 78)

Figure 26: A PCA plot of the chironomid community in Lake Okataina (coloured by phase) (Page 79)

Figure 27: Regime shift summary figure (Page 80)

Figure 28: Aerial photograph highlight land clearance in the Lake Okataina catchment (Page 87)

Figure 29: Multi proxy summary of ecological change in Lake Okataina (Page 94)

Included in the Appendices:

Figure 30: Full set of ITRAX elements plotted downcore (Page 107)

Figure 31: RABD changes downcore (Page 108)

Figure 32: Full pollen summary for Lake Okataina (Page 109)

Figure 33: Correlation matrix for the ITRAX dataset (Page 111)

List of Tables

Table 1: Outline of contributing researchers and data collaborations for this thesis (Page 14)

Table 2: List of Pb^{210} samples used in the chronological analysis (Page 46)

Table 3: Summary of the indicator species (at Class level) for the different phases in the 16S Bacteria dataset (Page 74)

Table 4: Summary of the indicator species, multipatt analysis run on the Gammaproteobacteria class (Page 75)

Included in the Appendices:

Table 5: Summary of the Pb^{210} results (Page 110)

Table 6: Summary of the radiocarbon results (Page 110)

List of Equations

Equation 1: Constant Rate of Supply calculation (Page 42)

Equation 2: Polynomial equation for LC1U regression (against LC4U) (Page 58)

Equation 2: Polynomial equation for LC2U regression (against LC4U) (Page 58)

Equation 2: Polynomial equation for LC3U regression (against LC4U) (Page 58)

Chapter 1: Thesis Introduction

1.1 Preface (Over-riding significance of research)

In recent decades, New Zealand's freshwater quality has significantly deteriorated. These changes are largely facilitated by anthropogenic impacts such as land-use change and increases in nutrients reaching water bodies. The government has committed to improving water quality in the next five years, with the ambitious target of restoring water quality to a general "healthy" state within a generation (Ministry for Environment, 2020). Determining what a healthy target for water quality actually entails is challenging, as most monitoring records only start after the water quality has already deteriorated. Natural events including storms, earthquakes and volcanic eruptions can also impact water quality. However, there are few, if any, studies which have documented the impact of natural disturbances on freshwater quality in New Zealand.

In New Zealand, scientific knowledge of the bio-physical and ecological response of lake systems to natural and anthropogenic perturbations is limited; there is currently only scientific data available for approximately 5% of lakes greater than 1 ha in size (Ministry for Environment, 2020). Although some of the key drivers of ecosystem health decline are relatively well understood, restoration is complex and requires a deeper understanding of how lakes respond to change. A significant challenge is that, even after release from the key drivers of degradation such as invasive species or increased nutrient inputs, the components of the lake ecosystem that once conferred resilience are unknown, and therefore cannot be restored fully.

In lakes, sediment may provide an accurate and effective record of temporal environmental change. Lake sediments act as natural archives that continuously record environmental history, providing measures of current and historic aquatic communities and water quality (Smol, 1992). Detailed analyses of sediment cores taken from a lake can enable scientists to reconstruct accurate environmental histories. The combined analysis of environmental DNA, terrestrial macrofossil records and u-XRF (ITRAX) and hyperspectral imaging technology provide an unparalleled opportunity to quantify the impact of key drivers of lake ecosystem change. Issues with disentangling long-term pathways of degradation are rarely resolved by conventional short-term monitoring of lake ecosystems, which is where multi-proxy paleoenvironmental reconstructions shine.

Lake Okataina is an oligotrophic lake system, among a cluster of moderate-large sized lakes near Rotorua in the Bay of Plenty region of the North Island, New Zealand. The lake has been subject to a range of natural and anthropogenic, regional and within-lake scale changes and is thus an ideal study site to explore how lakes respond to a variety of disturbances.

This thesis focuses on the impact of a significant natural disturbance; the 1886 eruption of nearby Mt Tarawera. The paleoecological data gathered in this study, will provide insights into how aquatic ecosystems have changed in the lake. This thesis will also explore the impact these natural impacts had in the context of modern anthropogenic disturbances of Lake Okataina's health.

1.2 Thesis Overview

This thesis has been laid out in 5 chapters. Chapter 1 provides an introduction to the topic, including a comprehensive review of the impact of natural disturbances on lake systems, with a particular focus on the effects of volcanic eruptions and tephra. A brief history of Lake Okataina and an overview of the surrounding catchment characteristics are detailed in the study site section. Chapter 2 outlines the rationale for the multi-proxy approach used in this thesis and provides an extensive summary of the specific methods and methodologies used to answer the key research questions and objectives outlined in Chapter 1. Chapter 3 highlights the key results of this research. Chapter 4 uses the results of the research to address the research questions identified in Chapter 1 and discusses these findings in relation to existing literature, whilst also outlining any major limitations. Finally, Chapter 5 summarises this study and provides a series of general conclusions as well as suggesting areas for future work.

Table 1: Outline of data collaborations in this thesis and who completed initial sampling and/or analysis before the results are published in this work

Data type	Primary Investigator	Secondary Investigator
^{210}Pb	Adelaine Moody (Victoria University of Wellington)	Environmental, Science and Research , Christchurch, New Zealand
Radiocarbon	Jenny Dahl (GNS Science)	Stuart Caird (author)
Palynology	Xun Li (GNS Science)	Stuart Caird (author)
ITRAX	Chris Moy (University of Otago)	Andrew Rees (Victoria University of Wellington), Stuart Caird (author)
Hyperspectral Imaging	Claire Shepherd (GNS Science)	Marcus Vandergoes (GNS Science), Stuart Caird (author)
16S Bacteria (eDNA)	Susie Wood and Mailys Piccard (Cawthron Institute)	Stuart Caird (author)
Chironomids	Andrew Rees and Valerie van den Bos (Victoria University of Wellington)	Stuart Caird (author)

1.3 Wider Literature Review

The following section will discuss and outline the relevant literature for this thesis. Starting broad, paleoecology is defined and its significance for this study, identified. Following this, natural disturbances to aquatic systems are discussed, specifically the various impacts of volcanic eruptions on lakes. From here, the implications for aquatic ecosystems are also delineated with a particular focus on environmental indicators that I detail in Chapter 2. A summary of the site description is also included before the research aims are presented.

1.3.1 Paleoecology – the “pros” and “cons”

Paleoecology, formed from paleo – meaning older or ancient, relating to the geological past, and ecology – meaning the study of relations between different organisms and to their surroundings, is an inference driven branch of science, in comparison to the “applied” ecology type of science which draws on experimental and observational style – approaches and data (Dodd and Stanton, 1990). Paleoecologists, on the other hand, seek to reconstruct pre-existing environments from indirect evidence, using a range of indicators of biotic and abiotic change, preserved by natural archives (see Figure 1 below).

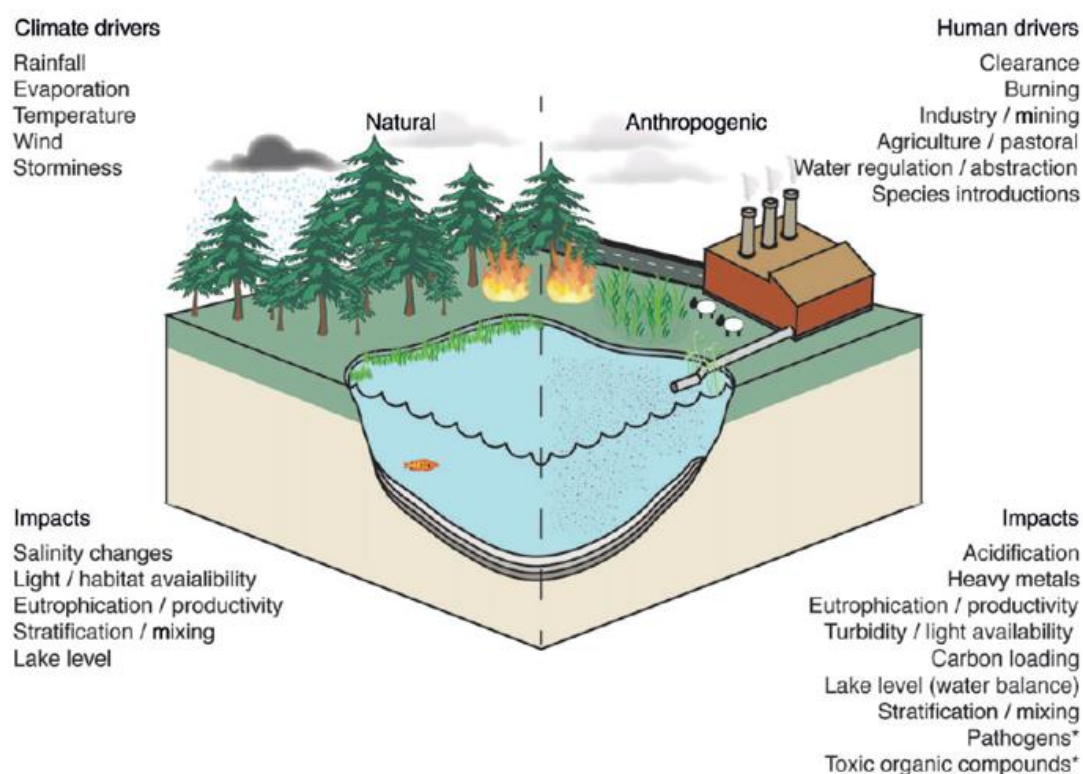


Figure 1: A summary diagram outlining different natural and human induced drivers and the resulting impacts on lake systems. These processes can be unearthed using a paleoecological approach (Mills et al., 2017). Note this figure does not include the impacts of volcanism; these effects will be discussed in-depth throughout this thesis.

Natural archives in this setting, constitute a depositional environment where the accumulation of material is chronological (Meyers and Ishiwatari, 1993; Smol, 1992), whereas indicators or proxies of environmental change entail phenomena that can be either quantitatively or qualitatively linked to an environmental gradient of interest (Dixit et al., 1992). This approach is complementary to applied ecology and environmental science, among other disciplines because paleoecology supplements understanding of environmental change. Paleoecological approaches help to provide context for modern day observations (such as CO₂ levels in the atmosphere) and work to extend instrumental records (such temperature records before historical records began), (Smol, 1992). Paleoecology can also be used to analyse the stability or resilience of ecosystems and understand restorative ecology pathways (Schoonmaker and Foster, 1991) as well as assess the relevant impacts from human induced changes and natural variability.

Ecological approaches rely on hard and concrete evidence: data that is generated for a specific purpose that directly informs a research question or particular theory. Whilst important and informative for modern day scientific research, ecological approaches cannot provide information on paleoenvironments. Paleoecology makes use of a host of different environmental proxies. These proxies provide insights into the environmental conditions that once existed in a given system but they do not always tell the full story. Conversely then, paleoecology can be viewed as a form of community ecology, stretched backward through time, offering unique and powerful insights into past patterns, processes and changes to different phenomena (Schoonmaker and Foster, 1991). However, the paleoecological signal is often smeared by taphonomic and post-depositional processes. In short, both “neo” and “paleo” approaches have their merits and shortcomings, but when used in conjunction, the disciplines can be complementary. Especially for lake systems, finding a balance between the different approaches (as shown below in Figure 2) can be key for long-term insight into system behaviours.

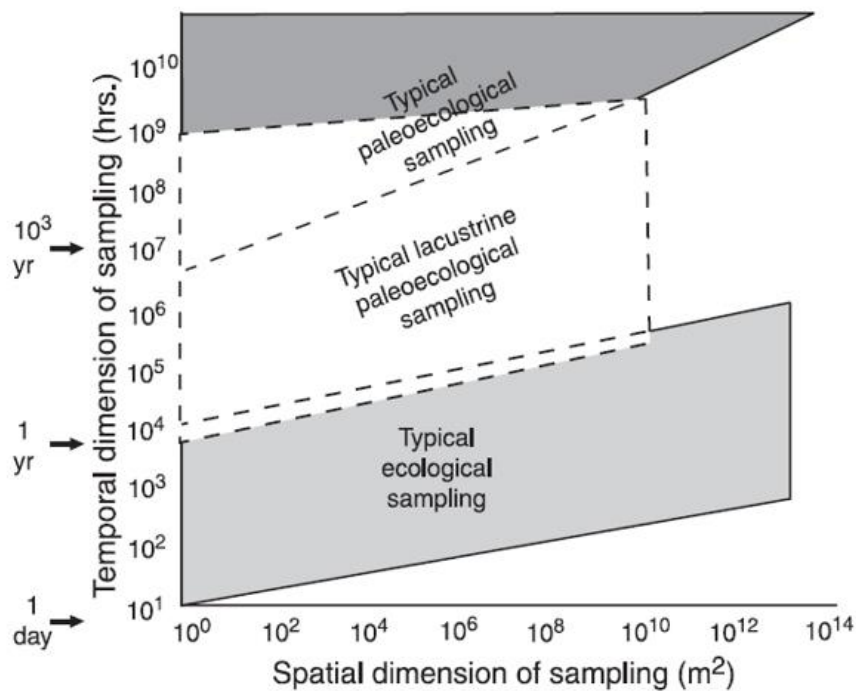


Figure 2: Sampling domains for ecology and paleoecology, demonstrating the overlap specifically between paleolimnology (paleoecology focused on lake systems) and ecology (Schoonmaker and Foster, 1991).

The paleo-based approach to ecology is very valuable but caution is required when applying the resulting data and making specific inferences about a given paleoenvironment. The field is complex and multi-dimensional, underpinned by key assumptions that must be acknowledged. When analysing the paleoenvironment of a lake for instance, caution must be exercised when assigning importance or significance of inputs into the system and ascribing relationships between cause and effect.

Whilst specific fluxes of nutrients, for instance, could be attributed to a change in the ecological community structure whereby a new organism is introduced or removed, they could also be explained by a range of different external inputs from the catchment such as climate, land-use changes and hydrological processes (Cohen, 2003). Thus, it is often hard to precisely discern exactly what environmental driver is responsible for the features observed in the data.

To increase the reliability and validity of inferences based on paleoecological data, multi-proxy datasets are often used. This allows the environmental scientist to compare, contrast and holistically interpret and analyse any patterns, trends or noteworthy features that are present. This limits the likelihood of misguided conclusions and the misinterpretation of biological changes to systems. This type of multi-proxy approach is key to disentangling a range of natural and anthropogenic disturbances to lacustrine systems.

1.3.2 Natural disturbance to lacustrine systems

Natural variability is largely a product of disturbance in combination with hydrology and climate. Together these factors shape and structure lake ecosystems across space and time (Sousa, 2001; White, 1979). Disturbances that cause variability in lacustrine environments, alter species composition and diversity, however, the impacts of these variations are strongly reliant on the scale of disturbance. The true effects of any natural perturbation depend on (1); the specific characteristics of the disturbance, and (2); the underlying stability or resilience of the system (Folke et al., 2004; Scheffer et al., 2012).

Lake systems are often impacted by a range of stochastic natural disruptions such as severe floods, landslides, earthquakes or volcanic eruptions. These pulse-events occur suddenly and potentially with intense force and can cause significant changes to existing aquatic communities (Smol, 1992). These disruptions manifest in a variety of different forms, ranging from minor abiotic changes to the environment such as increased or reduced sedimentation rates or fluxes (Howarth et al., 2012; Hsu et al., 2004; Rea and Ruff, 1996), through to entire biological regime shifts (Folke et al., 2004; Randsalu-Wendrup et al., 2016; Van Nes and Scheffer, 2007).

1.3.3 Impacts of volcanism on lake systems

Volcanic eruptions are one of the key natural, stochastic events that have the potential to perturb lacustrine systems and communities in New Zealand. Eruptive products such as tephra, interact with environments to induce a range of physical, chemical and biological changes (Massaferro et al., 2018). Eruptions of different magnitudes and strengths can trigger a cascade of different environmental responses that directly alter the catchment characteristics of a lake (Lucht et al., 2002). The consequences for affected lake systems and associated communities may have either an immediate impact, or smaller initial changes but far-reaching implications.

These longer-term impacts often traverse multiple trophic levels and encompass a range of bio-physical relationships (Ayriss and Delmelle, 2012; Massaferro et al., 2018; Wolinski et al., 2013). This difference can be viewed in the terms of direct “pulse” effects and longer-term, more indirect “press” effects. Both of these types of stresses can impact water quality and their biological limnetic communities (Anderson, 2014).

1.3.4 Tephra

Tephra is one of the most widespread and common materials deposited following volcanic eruptions. Classified as any material of a pyroclastic nature ejected during an eruption, tephra forms in one of three ways: (1) as a product of the rupture of gas bubbles within brittle rocks (Busby and Bassett, 2007), (2) through the shear forces involved in accelerating magma (Zimanowski et al., 2003), and (3), as a by-product of the interaction of magma and water or ice (Morrissey, 2000). The physio-chemical properties of tephra particles (density, mineralogy, chemical composition and size) largely dictate the range of interactions the material has with the system it encounters (Telford et al., 2004). The environmental effects of tephra deposition on aquatic ecosystems are often problematic to quantify and link to other bio-physical system changes (Telford et al., 2004).

Tephra deposits can initiate significant changes in lakes and their respective catchments and the resulting effects can be both physical, chemical and biological. Several studies have identified and isolated a detrimental effect of tephra deposition on lake systems, following volcanic eruptions (Collier, 2002; Fazlullin et al., 2000; Kurenkov, 1966). However, these studies only encompass a short duration, limiting our understanding of the longer-term effects on aquatic communities. Important interactions for lake systems include residence time (of the tephra in the water column) and

chemical reactions where the tephra meets the water body of the lake (Ayris and Delmelle, 2012). Volcanic events effect nearby lake systems primarily through two distinct pathways; directly via aerial deposition on the lake surface, resulting in limnological changes and, indirectly, via catchment-scale changes as a result of the eruption (Ayris and Delmelle, 2012; Dale et al., 2005; Massaferrero et al., 2018; Telford et al., 2004).

Tephra deposition in lakes commonly triggers a response in the Si/P ratios in the water column (dependent on the elemental composition of the tephra). Si and P budgets and cycling control rates of algal growth, limit volumes of phytoplankton biomass and help to define the trophic level status of lakes (Stauffer, 1986). Changes in the Si/P budget can be further influenced by leaching and run-off from soils within the catchment that have also been exposed to tephra (Ayris and Delmelle, 2012; Lotter et al., 1995; Massaferrero et al., 2018). This flux in the amount of bio-available Si and P, can alter the nutrient load present in the system. This in turn can initiate a multi-trophic level response, manifesting itself initially in rates of primary productivity, which in turn has flow on effects for a range of aquatic plants and organisms (Telford et al., 2004; Wolinski et al., 2013). This type of response fits well with the theory that eruptive events (and resulting products such as tephra and ashfall), have a fertilising effect on lake ecosystems, prompting substantial increases in planktonic biomass volumes (Hamme et al., 2010; Lin et al., 2011).

Tephra deposited in lakes also impacts the distribution and scattering of light throughout the water column. Upon deposition, suspended tephra particles increase turbidity, by increasing the volume of total suspended solids (TSS), (Ayris and Delmelle, 2012). An increase in turbidity and TSS, reduces the capacity of light to penetrate through the water column. Some living organisms in aquatic systems require access to light to carry out photosynthesis (Ayris and Delmelle, 2012; Modenutti et al., 2013; Telford et al., 2004). Much of the existing research, focusing on the impact of volcanic events on lake systems, overlooks the importance of light intensity and availability, particular in direct comparison to nutrient budgets (Karlsson et al., 2009). In some instances, particularly in shallow, well-mixed lake systems, stained by dissolved organic matter (DOM) the amount (and natural colour) of DOM actively reduces overall light intensity throughout the lake. Williamson and Rose (2010), suggest that DOM acts as the “ozone layer of the underwater world”. Contrastingly, in deeper, clearer and more oligotrophic systems, like Lake Okataina, light intensity appears to be a much more critical factor in shaping rates of low-level biomass productivity, namely plankton (Modenutti et al., 2013).

Deposition of tephra on lake floor sediments also can trigger the creation of an impermeable benthic barrier, impeding nutrient exchanges across the dynamic sediment-water interface (SWI); (Barker et al., 2000; Telford et al., 2004). This inhibits the degree of benthic P recycling that occurs in the system by preventing the resuspension of sediment via bioturbation, as well as providing a physical barrier to the diffusion of P (this is dependent on the thickness of the tephra). This process directly influences rates of growth in macro-phytic plants, diatoms and other benthic sediment dwelling organisms (Dale et al., 2005; Einarsson et al., 1993).

1.3.5 Ecological response

As outlined above, the deposition of tephra has a multitude of implications for the physical properties of lakes. Similarly, the limnetic ecological communities in affected lake systems also experience changes in response to perturbations initiated by the deposition of tephra. Abrupt changes to geochemical properties and abiotic conditions in the water column, are believed to drive a series of shifts in aquatic community structures.

Previous paleoecological work has analysed ecosystem disturbance, and dynamics of system resilience and rates of response; however, much of the work centred on aquatic systems, has only focused on short-term ecological scales (Folke et al., 2004; Massaferro et al., 2018; Telford et al., 2004). Studies have examined the impacts of volcanic events on systems, highlighting the range of limnological property changes (such as turbidity, pH, nutrient concentrations and light intensity) and how these directly translate into reduced or increased availability of food to biota in the system (Barker et al., 2000; Okorafor, 2011). The following reviews key indicators that are used in environmental reconstructions and that are relevant to this study, and reviews any published work related to responses to volcanic eruptions.

1.3.5.1 Bacteria

Similar to phytoplankton, bacterial communities make up a key component of lower trophic levels in aquatic systems. Bacteria are highly stenotopic and extremely sensitive to environmental changes in the lake systems. Understanding of bacterial community composition and response to stochastic events, specifically volcanic eruptions, is limited (Modenutti et al., 2016). Very little is known about how these communities respond to mass changes and shifts in the limnological properties of the systems they occupy. Of the research that exists, studies hypothesise that both nutrient and organic carbon availability play a leading control on rates of bacterial production and growth (Sterner et al., 1997). Both of these factors are directly affected by the deposition of tephra and volcanic eruptions. P increases with more ash input, and the nutrient balance increases. Light availability then decreases, triggering a flux in organic carbon (Chrzanowski and Kyle, 1996). Bacterial communities in lake systems are also shown to reflect the volume of primary productivity. This relationship is relatively intuitive as both bacterial and phytoplankton communities seem to exhibit similar responses to abiotic changes in their environments (Lipson et al., 1999).

A study conducted in 2016, isolated and examined the response of bacterial communities to the impacts of volcanism (Modenutti et al., 2016). The research revolved around an experiment, whereby pumice and ash particles (common post volcanic event features) were added to water samples from two contrasting lake systems. Samples from both lakes displayed distinct, bacterial community assemblage changes in response to the “volcanic” conditions (that were artificially created). A non-metric dimensional scaling (NMDS) analysis, clearly identified differences between samples, which clustered based on pre-and post-addition of the ash and pumice. Notable community shifts were observed for genera such as *Proteobacteria* and *Bacteroidetes*. The authors posited that fluxes in the availability of light and nutrients could be driving these changes. They further suggested that bacteria are reliant on the dissolved organic matter pool in freshwater ecosystems and that phosphorus (a key nutrient impacted by tephra deposition), is important for regulating rates of organic consumption by aquatic bacteria (Modenutti et al., 2016).

1.3.5.2 Phytoplankton

Phytoplankton communities are primary producers and act as the base of most lake food-web systems; they provide key nutritional and biological bases for zooplankton, invertebrates and fish, among others (Emmanuel and Onyema, 2007). Phytoplankton exist as the pioneers of an aquatic ecosystem and as such, the productivity (and health) of such a system is directly linked to the density of phytoplankton present (Narasimha and Benarjee, 2013).

Phytoplanktonic communities are susceptible to the impacts of volcanic disturbance. The availability of light, a property that is directly influenced by the deposition of tephra, is a vital factor for growth of phytoplankton (Ayrís and Delmelle, 2012). The presence and settling of tephra in the water column of a lake reduces light intensity and availability, limiting rates of photosynthesis – the key life process for growth among phytoplankton (Eilers and Peeters, 1988). Previous studies also posit that tephra can act as a direct source of nutrients for phytoplankton (Eicher Jr and Rounsefell, 1957; Kurenkov, 1966). Independent paleolimnological studies in Iceland (Einarsson et al., 1993), Mexico (Telford et al., 2004) and Chile (Modenutti et al., 2013), all noted marked increases in chlorophyll-derived pigments in sediments following the deposition of eruptive products. In these studies, the chlorophyll pigments were used as a proxy for phytoplanktonic biomass.

Across a set of North Andean Patagonian lakes, there were a series of fluctuations in derived chlorophyll-a values following volcanic eruptions. These fluctuations occurred without noticeable shifts in the balance of P (and other nutrients) in the system, indicating that other mechanisms may have been driving these changes. Modenutti et al. (2013), postulate that reduced chlorophyll-a levels reflect lower light intensities at depths throughout the water column. This suggestion is supported by the results of a multi-regression analysis that identified light intensity as the environmental variable that is primarily associated with variation in chlorophyll-a (Modenutti et al., 2013).

1.3.5.3 Chironomids

Studies focusing on community changes following natural disturbance are predominantly centred on climate driven forcing. There is however, some knowledge on the response of chironomid communities to volcanic disturbance (Araneda et al., 2007; Massaferrero et al., 2005; Massaferrero and Corley, 1998). Chironomids are insects with aquatic larvae, which are a cornerstone of many aquatic food webs (Armitage et al., 2012). There are mixed conclusions with regard to the behaviour of chironomids in affected lake systems which is largely due to differences in the catchment properties, as well as the severity of the limnological changes, triggered by the disturbance (Araneda et al., 2007; Massaferrero et al., 2018).

In a recent study from Patagonia, two geographically and limnologically similar lake communities (Lakes Verde and Tonck) were assessed, following volcanic disturbances (with the most recent eruption occurring in 1960). Chironomidae community responses were different among the lakes. A Principal Components Analysis (PCA) and resulting ordination bi-plot, suggested that samples from Lake Tonck appeared to form two distinct clusters of pre tephra and post tephra samples (Massaferrero et al., 2018).

Contrastingly, samples from Lake Verde showed no discernible clustering (between pre tephra and post tephra samples). Given the proximity of the two lakes to one another, and the similarity in the observed impacts of the 1960 tephra deposition on both sites, there is an inference that Lake Verde has a higher degree of ecological resilience to disturbance than Lake Tonck. Upon assessing the physical characteristics of the two systems in the study, key differences soon became apparent. Lake Verde has extensive, closed-canopy forests in its catchment and widespread macrophytic plant growth within the lake, whereas the catchment of Lake Tonck is largely cleared of tall trees and has a limited abundance of macrophytes. The sheltering mechanism offered by vegetation cover and aquatic plant growth, protects or lessens the impacts of tephra on the lake system (and minimised the impacts of the in-wash period following the eruption). This process appears to exert a leading control on chironomid community resilience and recovery across these two, otherwise similar, lake systems (Massaferrero et al., 2018; Randsalu-Wendrup et al., 2016; Telford et al., 2004).

A study focused on Lake Kilpoola, in British Columbia, showed a clear community shift following tephra deposition (Heinrichs et al., 1999). The authors suggest that the deposition of a grey-silty layer intermixed with tephra particles, increased erosion in the lake basin and the surrounding catchment. They also posited (supported by geochemical data) that this deposition of tephra led to an instantaneous increase in salinity in the aquatic system, driving the response in chironomid communities. A paleoecological study on a New Zealand lake system – Lake Maratoto, south of Hamilton, found little in terms of impacts on chironomids as a result of tephra deposition (Boubee, 1983). Despite containing a number of tephra layers, chironomid communities showed no noticeable response, although the sampling interval used in the study (5cm – ca. 500 year based on sedimentation rates) was potentially too coarse to detect any signals in the composition of chironomid communities present (Araneda et al., 2007; Matthews-Bird et al., 2017; Telford et al., 2004).

1.4 Study Site

Lake Okataina ($38^{\circ} 07''$ S; $176^{\circ} 25''$ E) is a deep, oligotrophic, crater lake in the Okataina Volcanic Centre (OVC), located in the Bay of Plenty region, in the North Island of New Zealand (see the darker shaded lake in the centre of Figure 3 below). The name Okataina means the lake of laughter, an abbreviated form of the original name Te Moana-i-Kataina-a-Te Rangitakaroro which translates to “The Ocean Where Te Rangitakaroro Laughed”. The mana whenua of the lake are Ngāti Tarāwhai and they recognise Lake Okataina as a significant natural taonga that once played an important role as a primary transport route (via waka), pre-European settlement (Smith, 2009).

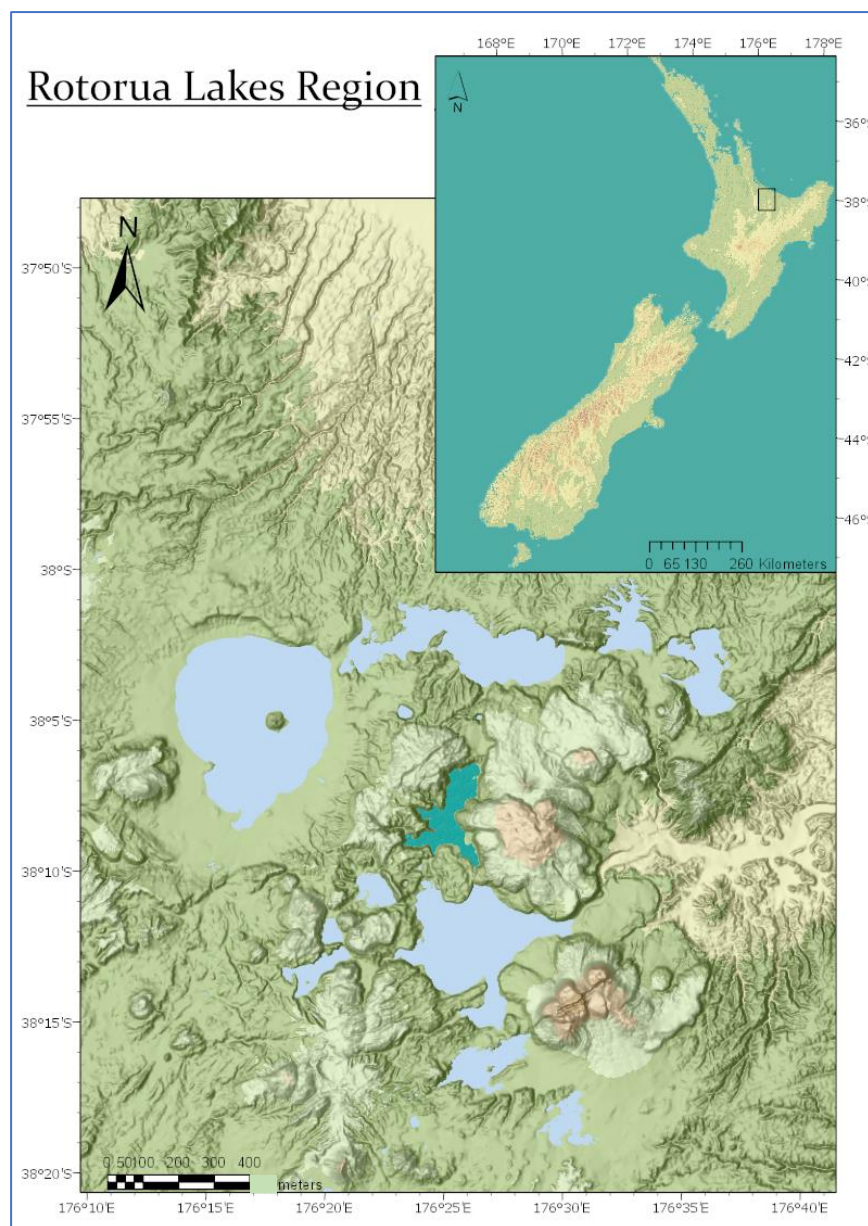


Figure 3: Map of the Rotorua Lakes region (centred on Lake Okataina in the green shade). Inset map highlighting the location of Lake Okataina relative to New Zealand.

Situated at an altitude of 311 m above mean sea level (msl). Okataina's 62.9 km² catchment is largely vegetated by native bush (80%) and there is also no surface inlet or outlet. These features starkly contrast most other lakes in the region, which have high inputs from agriculture and other intensive land-uses. The lake has a high-water quality (with a 2.5 TLI index value representing an oligotrophic level). The following section outlines the specific physical characteristics of the limnetic system, giving an overview of Lake Okataina's ontogeny, catchment soils and vegetation, climate and anthropogenic impacts.

The OVC is a geologically rich section of the larger Taupo Volcanic Zone (TVZ), home to many of New Zealand's most severe and violent volcanic eruptions in the last 20,000 years, such as the 1310 CE and 1886 eruptions of Mt Tarawera and the Taupo (Hatepe) eruption of 180 CE (Wilson et al., 2009). The plateau upon which the OVC sits has abundant dormant and extinct volcanic cones and a raft of volcanically formed, crater lakes (see Figure 4 below), similar in geomorphic nature to Okataina (Cole et al., 2010). Lake Okataina was formed during an eruptive event in the OVC, approximately 7000 years ago. The lake originally existed as an arm of Lake Tarawera; however, a rhyolitic lava flow deposit formed a land bridge (noted in Figure 4), (Kpodonu et al., 2016).

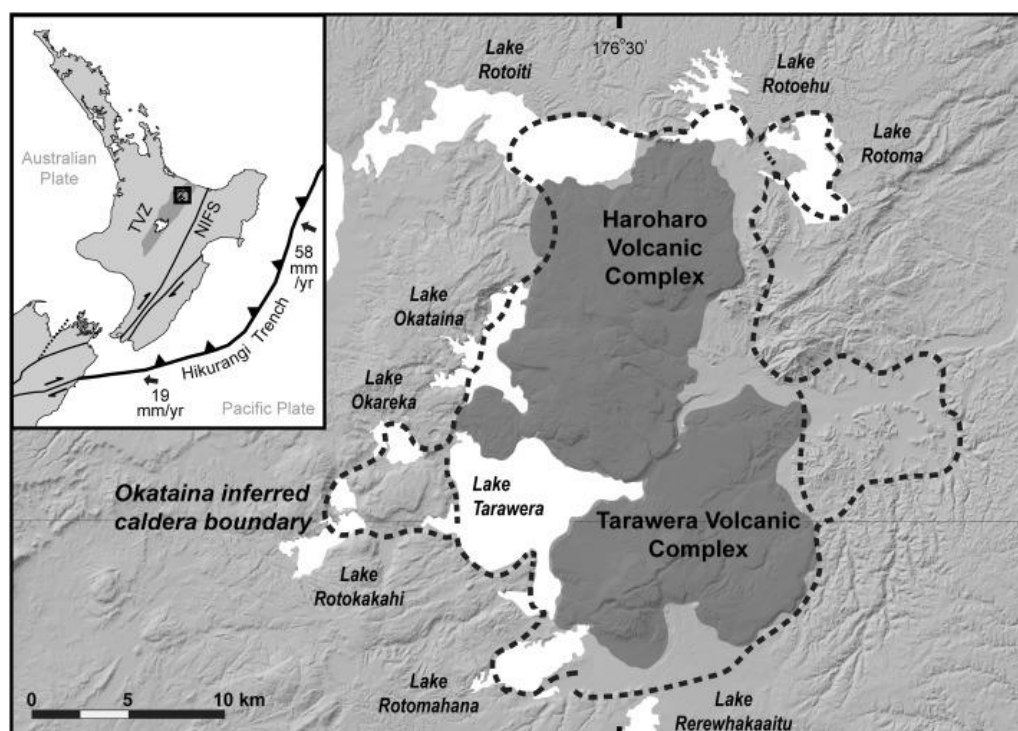


Figure 4: The Okataina Volcanic Centre (OVC; inset showing location relative to New Zealand), highlighting the boundary of the dominant Okataina caldera (shown by the dotted line) and the lakes that it encompasses. Note the small land bridge between Lake's Tarawera and Okataina (modified from (Sas et al., 2019).

Soils:

The soils comprising Lake Okataina's catchment are characteristic of previous volcanic events. They are well-drained, highly permeable recent pumice soils, rich in allophanic material dominated by aluminium and silica (Parfitt, 1990). These types of soils are prone to erosion when they become saturated; vegetative cover provides limits on these erosional processes in the Okataina catchment (Rijkse and Guinto, 2010). Due to their volcanic origin, the catchment soils are also high in phosphorus and other nutrients. These nutrients, derived from the underlying layers of pumice and bedrock, in turn promote high growth rates of plant matter on top of the soils, further reducing the likelihood of erosion by increasing the availability of root structures (Harnilton, 2005).

Vegetation:

Lake Okataina has one of the more unique catchments in the Rotorua Lakes region, largely due to the types of vegetation present (see Figure 5 below).

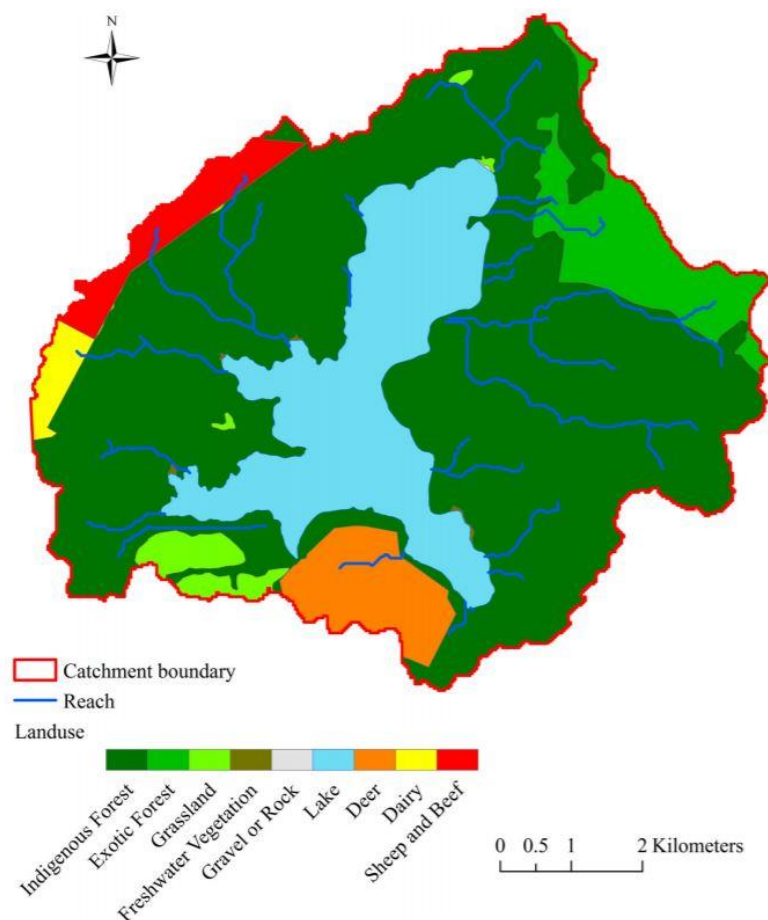


Figure 5: Land-use and vegetation types present in the Lake Okataina catchment (Kpodonu, 2019)

Okataina's modern catchment predominantly is covered by native forest (totalling approximately 80%), with dry-stock agriculture making up 10%, exotic forests between 5-8% (mainly plantations of pine) and roading and infrastructure 1-2% (Kpodonu et al., 2019; Scholes and Bloxham, 2007). The native vegetation is dominated by podocarps such as rimu (*Dacrydium cupressinum*), totara (*Podocarpus totara*), northern rata (*Metrosideros robusta*) and kahikatea (*Dacrycarpus dacrydioides*).

Since the mid 1970's, these proportions of land use have remained relatively constant, and this, coupled with minimal inputs from agriculture and pastureland, render Lake Okataina as close to a natural-reference state as possible in the Rotorua lakes region.

However, this stability has not always been the case. Being in a volcanically active zone, the vegetation in the catchment has experienced significant disruption since the lake formed 7000 years ago. Eruptions have a range of immediate and longer reaching biophysical impacts on vegetative systems (Ayriss and Delmelle, 2012). Ferns are well known for their resilience to fire and disturbance among other common plant types and this proves to be the case again here. *Pteridium esculentum* appears to be particularly abundant after eruptive events such as the 1886 eruption of Mt Tarawera, as well as other tree ferns *Cyathea dealbata* and *Cyathea smithii* (Clarkson, 1990). Since European arrival following this eruption, the abundance of grass species has grown along with forests of *Pinus radiata*, whilst species of indigenous tall trees (namely *Dacrydium cupressinum*) have declined (Clarkson, 1990; Kpodonu et al., 2019).

Climate:

Lake Okataina experiences a warm and temperate climate, similar to most of New Zealand. The region has a Koppen-Geiger climate classification of Cfb (labelled as a “temperate ocean climate”). Lake Okataina has an average annual air temperature of 12.3°C and has a mean annual rainfall of 1600-2200mm (Figure 6). This range is similar to other lakes in the region (e.g., Lake Tarawera has a mean annual rainfall of 1500 - 2000 mm and Lake Tikitapu receives between 1400 - 1600 mm annually).

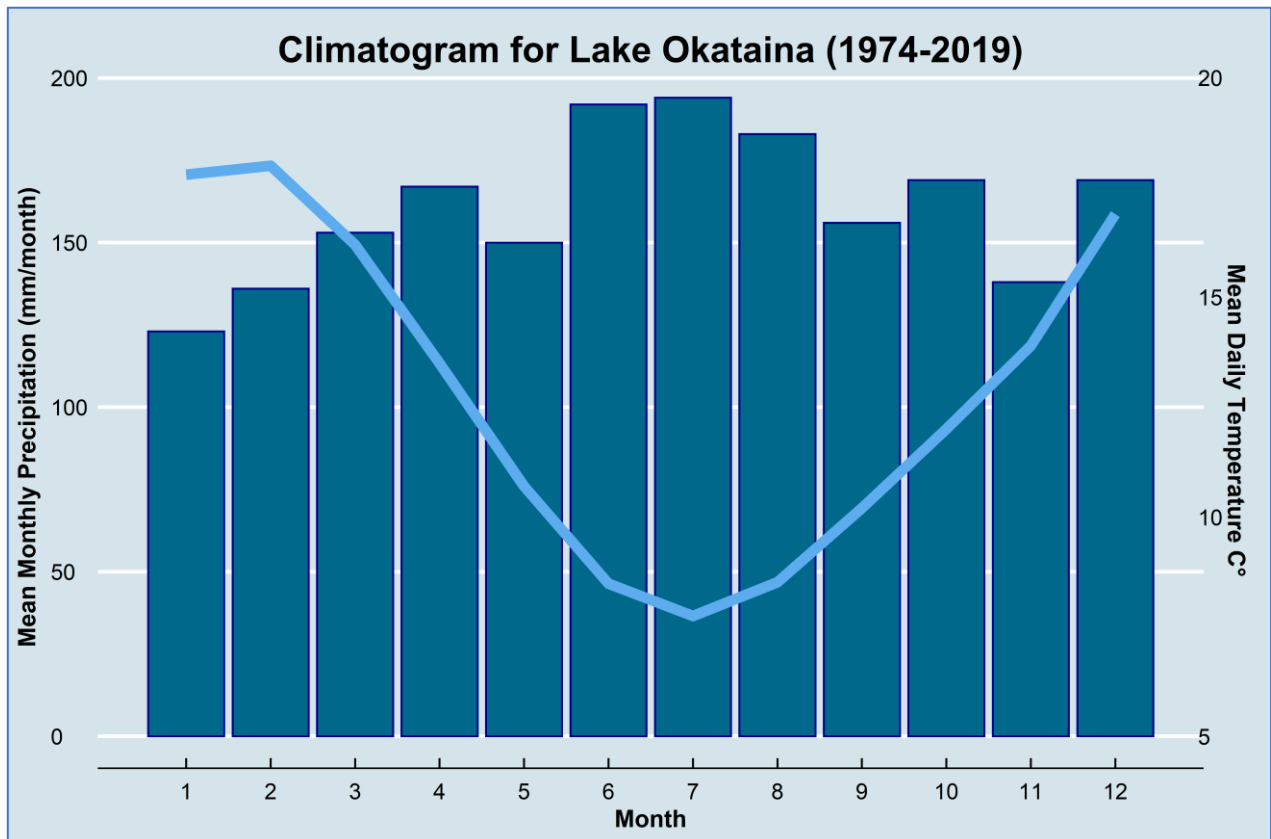


Figure 6: Climograph depicting mean average daily temperature (°C) as a blue line and mean monthly precipitation (mm/month) as bars. Data was collected between 1974 and 2019 at a climate station 5.9km from Lake Okataina. Sourced from NIWA’s CliFlo National Climate Database.

Limnology:

Okataina has a surface area of 10.8km², and a maximum depth of 72 m, with an average depth of 39 m, approximately 60% (665 ha) of the lake is deeper than 40 m (Kpodonu et al., 2016).

Lake Okataina has no true surface water outlet. Instead, drainage occurs primarily through southward flowing seepage towards Lake Tarawera. This results in dramatic water level fluctuations, dependent on rainfall in the catchment. The lake level has risen and fallen by as much as 10 m in the last 100 years alone (Kpodonu et al., 2016). There are only two permanent streams feeding into Lake Okataina, however, these streams have substantially low base flow rates, far below what would be anticipated, given the catchments rainfall volumes. Thus, storm-flow and sub-surface springs are assumed to provide the major sources of water entering the basin (McColl, 1972).

Trophic Level Index (TLI) values are calculated and assigned to lakes throughout New Zealand based on measurements of four water quality variables: total (available) nitrogen, total (available) phosphorus, water clarity and chlorophyll-a (Burns and Schallenberg, 1998; Ministry for Environment, 2020); the lower the value, the healthier the lake. Lake Okataina currently has a TLI value of 2.5, indicative of oligotrophic status. Lake Okataina's phosphorus concentrations are relatively low – contrary to other lakes in the region, however, during the past 15 years, concentrations of phosphorus have slightly trended upwards, while the total nitrogen concentration has decreased (Scholes and Bloxham, 2007).

The depth of Lake Okataina exerts a higher-order control on natural processes that define many of its limnological features (Sigee, 2005). The lake experiences continuous thermal stratification for approximately 9 months of the hydrological year and undergoes vertical mixing between June and August (Jolly, 1968). The thermo-stratification occurs approximately in October when the terrestrial temperature begins to warm, separating distinct layers of water (warmer closest to the surface and coldest near the lake floor); (Dake and Harleman, 1969). The mean depth of the thermocline is estimated to be 22.7 m below the lake surface (McColl, 1972). The lake water remains stratified until approximately June, when there is significant mixing of surface and bottom water layers, largely driven by wind action, associated with winter atmospheric circulation. Concentrations of chlorophyll-a (measured in the top 17 m of the water column) vary throughout the year, with the highest levels coinciding with the mixing period in winter (Figure 7).

Although early records indicated that the hypolimnion of Lake Okataina (the lower layer of water in a stratified lake) remained oxygenated throughout stratification (Fish, 1970; Jolly, 1968; McColl,

1972), more recent data has highlighted that anoxia occurs throughout a large proportion of the hypolimnion volume (Pearson et al., 2010).

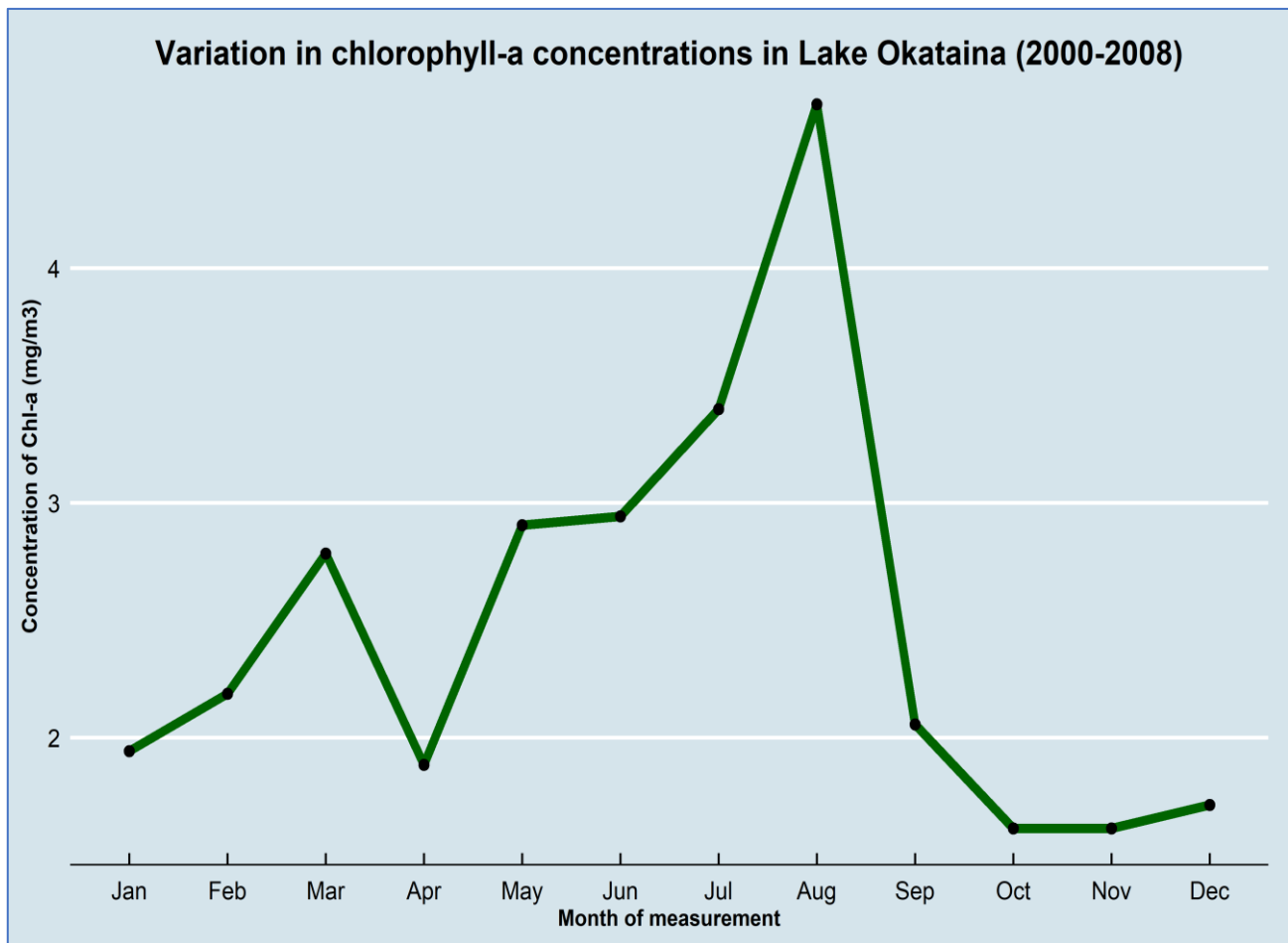


Figure 7: Chlorophyll-a concentrations, averaged across 8 years of data collected by the Bay of Plenty Regional Council. Data sourced from LERNZ database.

External disturbances to Lake Okataina:

The catchment of Lake Okataina has undergone significant natural and anthropogenic disturbance over the last millennium. Early Polynesian settlers are believed to have arrived in the Bay of Plenty region (and the wider Okataina catchment) between the late 13th and early 14th century, immediately prior to the destructive Kaharoa eruption (estimated 1314 +/- 12 AD); (Hogg et al., 2002). Polynesian settlers used large-scale fires to clear sections of forest and to enable small-scale logging operations to take place in the mid-late 19th century, primarily for the production of Māori canoes and infrastructure (Stafford, 1967).

On the 10th June, 1886, a violent basaltic, plinian eruption of nearby Mt Tarawera - caused a severe natural disturbance to the area surrounding Lake Okataina (Walker et al., 1984). This event remains New Zealand's largest and most destructive eruption since historical records began. The event resulted in the formation of a 17km long rift from Mt Tarawera, through another nearby lake (Rotomahana) and into a nearby valley. Large volumes of scoria (produced from exploded basaltic magma) and finer ash and tephra blanketed surrounding areas. It's estimated that 2 km³ of tephra was erupted and the resulting deposits extended as far away as Gisbourne, approximately 150 km south-east of Mt Tarawera (Walker et al., 1984).

The tephra covered and damaged vegetation throughout the catchment and instigated a major ecological response. The lake system was also affected by the deposition of tephra, fine ash particles and pyroclastic mud. Widescale geochemical changes to the system initiated a range of limnological property shifts, both in the immediate and long term. Tephra percolated through the water column and would have altered characteristics such as availability of light and nutrients, silica and phosphorus budgets and turbidity. The tephra settled on the lake floor, influencing benthic ecological processes. The history and scientific understanding behind these types of responses will be further explored in this thesis and in the context of the wider literature.

Following the 1886 eruption, Europeans began to settle in the area in the early stages of the 20th century and introduced a series of mammals into the surrounding forest such as the dama wallaby (*Macropus eugenii*), feral pigs (*Sus scrofa domesticus*), red deer (*Cervus elaphus*) and the Australian brushtail possum (*Trichosurus vulpecula*) as well as a population of Rainbow trout (*Oncorhynchus mykiss*) to the lake for recreational purposes (Kpodonu et al., 2016). The introduction of these land-dwelling species has opened up the forest canopy, exposing soils to higher amounts of

run-off and increasing rates of erosion on susceptible hillslopes in the catchment (Kpodonu et al., 2019).

Little is currently known about the impacts of the introduction of the predatory Rainbow trout on the Lake Okataina system. Rainbow trout were introduced into Lake Okataina in the early 1930's (initially volumes of approximately 200,000 individual fry) and populations have blossomed ever since (Eastern Fish and Game, 2020).

The modern-day catchment is dominated by native forests and whilst logging operations have increased, the lake is largely exempt from extensive runoff and intensive forms of land-use such as pasture and dairy farming. Lake Okataina is used for a range of recreational water activities such as boating, kayaking and trout fishing and there is a small (largely seasonal) community on its shores.

1.5 Research hypotheses and objectives

This thesis aims to reconstruct environmental change at Lake Okataina over the past approximately 300 years using a suite of paleolimnological methods. A specific focus is placed on the response of the lake to the 1886 eruption of Mt Tarawera and the resulting impact that this event had on the wider lake ecosystem. To achieve this aim, sediment cores from Lake Okataina were studied to address the following primary research hypothesis:

- The instantaneous deposition of tephra following the eruption of Mt Tarawera resulted in both a widespread and permanent ecosystem change within Lake Okataina, that transcended multiple trophic levels and initiated a regime shift in the system towards a more nutrient-rich state

Testing this hypothesis requires the following objectives to be achieved:

- 1) Use of paleoenvironmental data and radiometric dating approaches to establish a chronology and record of system change in Lake Okataina and the surrounding catchment to delineate historical phases
- 2) Develop a paleo reconstruction of ecosystem response and change across the phases identified above
- 3) Assess the differences between ecological communities before and after the eruption

Chapter 2: Methods and Methodology

The following sections outline the specific methods used in this thesis. The rationale and methodology behind the reconstruction approach is first supported and then the key processes and analyses used in the study are summarised.

2.1 Methodology/rationale for reconstruction approach

2.1.1 Usefulness of Paleolimnology

Paleolimnological and paleoenvironmental reconstructions are important and well-recognised tools that provide insight into both historical and current lake ecosystem health. Sediments, that are constantly deposited over time, create a natural archive of lake health, catchment conditions, changes in land-use and impacts from natural events, such as volcanic eruptions (Rawlence et al., 2014; Smol, 1992). Thorough examination of these sediments can provide deeper understanding of a lake's history and evolution, whilst simultaneously offering insight into the inter-relationships between key drivers of change and wider system response. This degree of archival knowledge is not attainable with current-day monitoring approaches, which in general have only been implemented over the last few years (Meyers and Ishiwatari, 1993; Randsalu-Wendrup et al., 2016; Schoonmaker and Foster, 1991).

2.1.2 Drivers of lake ecosystem change

Lake systems are prone to both naturally and anthropogenically induced changes. Natural cycles in regional and local climate, hydrological events within the catchment, vegetation fires, earthquakes, landslides and volcanic eruptions are common phenomena that can drive significant shifts in aquatic ecosystems and communities (Scheffer et al., 2012; Schoonmaker and Foster, 1991; Smol, 1992). Stochastic events such as earthquakes, landslides and volcanic eruptions can instantaneously alter the limnetic properties of a system; this can have immediate implications for the response in the

ecological communities that reside in the lake. These sudden events can also trigger longer term responses that may take months or even years to manifest before their effect on the ecosystem is truly realised (Randsalu-Wendrup et al., 2016; Telford et al., 2004).

Increasingly, anthropogenic activities and forcing's have initiated a series of changes within aquatic systems. Intensified types of land-use such as heavy pastoral farming, industrial and infrastructural work and increased urbanisation, continue to place pressures and create new environmental stressors for aquatic systems globally and in New Zealand (Ministry for Environment, 2020). Many of these drivers are “slow burners” in that they take a while to effect a system, Once impacted, lake systems are very hard to reverse and restoring the system to its previous state, can be a generational problem to solve (Bennion et al., 2011; Folke et al., 2004).

In this study, the wider catchment of Lake Okataina plays host to a number of key natural drivers that initiate changes within the lake system, most notably the eruption of Mt Tarawera (the key foci of this thesis). ITRAX u-XRF scanning technology is used in this thesis to document the geochemical changes initiated by this eruption.

The following sub-sections describe indicators of environmental change (which will be deployed in this thesis), archived in Lake Okataina's sedimentary record and how these indicators link to natural and anthropogenic forcing mechanisms such as the 1886 eruption of Mt Tarawera.

2.1.3 Measures of lake ecosystem response

2.1.3.1 Primary productivity (hyperspectral imaging)

Phytoplanktonic communities act as the foundation of aquatic productivity in a lakes as they provide a series of environmental services through mechanisms such as carbon and nitrogen fixation and oxygen production (Rabalais, 2002). Consequently, understanding of their health and abundance downcore, is vital for an effective and comprehensive paleolimnological reconstruction. Chlorophyll-a exists in almost all organisms that carry out photosynthesis; chlorophyll-a is the primary pigment that absorbs light in the blue, red and violet wavelengths of the photoelectric spectrum (Butz et al., 2015; Wolfe et al., 2006). In-situ imaging spectroscopy of lake sediment cores allows for the high-resolution analysis of sediment composition, throughout a core section, highlighting changes in different pigments. In contrast to other scanning methods such as ITRAX- μ XRF (micro x – ray fluorescence), spectrometric methods detect changes in the electromagnetic spectrum and process this information to help identify the presence of materials such as pigments like chlorophyll-a.

The visual to near-infrared range (VNIR) imaging spectrometer, used in this study, measured the spectral reflectance downcore and derived spectral indices that were then used to estimate relative concentrations of chlorophyll-a in the sediment core. Provided that chlorophyll-a can be attributed to the presence of algae and other macrophytes in an aquatic system, then the hyperspectral scanning technology provides a high resolution proxy for autogenic productivity for a given lake (Butz et al., 2015). Algae species and concentrations can shift abruptly to disturbances in aquatic systems and thus can provide useful insights into how lakes respond to natural or anthropogenic disturbance. Studies from the existing literature suggest that the reflectance trough at 660-670 nm, aligns with chlorophyll-a and its diagenetic products (Butz et al., 2017; Grosjean et al., 2014). Thus, in this study, this spectral index is used as the main estimate and reference for primary productivity and phytoplankton biomass.

2.1.3.2 Environmental DNA (eDNA)

Recent developments and technological advancements in molecular biology, permit scientists to detect the presence of many organisms in sediment cores. Whilst still in its infancy as a technique, particularly in comparison to more traditional paleo methods such as the study of diatoms or the morphological analysis of chironomids, the use of environmental DNA (eDNA) in paleoecology, is increasing, alongside its apparent scope and scientific significance (Domaizon et al., 2017).

Traditional methods are highly labour intensive and often require time consuming and highly skilled microscopic work to create accurate paleo-reconstructions from core samples. eDNA methods eliminate many of these issues and the widely available taxonomic reference databases for selected organisms, allow for a relatively time and labour-efficient process for assessing ancient taxa.

Where eDNA proves invaluable to the paleoecologist, is in its ability to document and track changes in taxa that do not leave diagnostic morphological features in the sediment. This technique instead relies on the premise that organisms leave behind traces of their DNA signatures in paleo environments, such as on the bed of a lake system. Following careful laboratory and biostatistical analysis, these DNA signatures can then be retrospectively matched to different taxa that can help to provide insight into complex community assemblages and how these shift through time (Capo et al., 2017; Domaizon et al., 2017; Ficetola et al., 2018).

eDNA has been used in paleolimnology to quantify and trace the historical abundance of bacterial communities, species of aquatic macrophytes and invertebrates to name a few specific organisms. In this study, bacterial communities were assessed using 16S rDNA gene metabarcoding.

2.1.3.3 Chironomids

Larvae of the Chironomidae (Insecta: Diptera) are among the most ubiquitous, abundant and diverse components of the macrozoobenthos of lakes (the invertebrate community that resides on or in the sediment, and is retained on a 1mm² sieve); (Massaferro and Brooks, 2002). Chironomids are a family of true flies, or non-biting midges: holometabolic insects that undergo complete metamorphosis. During their life cycle, worm-like larvae hatch from an egg and begin larval growth. They generally moult four times, then pupate before emerging as a fully winged adult. The head capsule of the larva is highly resistant and remains preserved in the sediments after moulting; the soft-bodied larvae does not (Walker, 1987).

Chironomidae exhibit a range of characteristics that make them well suited to being useful environmental indicators. They have relatively short generation times (from larva through to adult), ranging from a week to multiple months, depending on the species and time of year (e.g. one or two generations per year can emerge in temperate climates such as New Zealand). This, coupled with the rapid dispersal by winged adults, means that chironomids can quickly respond to environmental changes such as climate or the deposition of tephra (Massaferro and Brooks, 2002). Many taxa are also highly stenotopic, having narrow ecological optima for a range of environmental parameters, furthering their value as a paleoecological indicator (Massaferro et al., 2018). Chironomids have been used as an effective indicator for freshwater since 1922 (Thienemann, 1922).

The morphological analysis of chironomids is used, in this study, to explore how the composition may have changed as result of a volcanic eruption and the resulting natural fluxes in the system.

2.1.4 Importance of dating lake sediments and establishing a chronology

The quality of a paleoenvironmental reconstruction is heavily dependent and reliant on the accuracy of the chronology, namely the independent timing of events (Gamrod, 2009; McGeehin et al., 2001). Several methods can be used to help establish a time scale for a lake system: the most common of which includes the radioactive decay of lead (^{210}Pb with a half-life of 22.3 yr.), (Appleby and Oldfield, 1978; Von Gunten and Moser, 1993) and the conventional radioactive decay of Carbon (^{14}C with a half-life of 5730 yr.), (Björck and Wohlfarth, 2002). Different sediment records can thus be correlated by establishing independent age-depth relationships for each record (from the methods above), or by matching dated environmental events, such as the first detection of a dated introduced species or the presence of distinct natural markers such as tephra deposits from known volcanic events.

^{210}Pb has been widely used to provide chronology across the last century, most commonly by the Constant Rate of Supply (CRS) model, as this method meets the required modelling assumptions across the greatest variety of depositional settings (Appleby and Oldfield, 1978; Oldfield and Appleby, 1984). The CRS model assumes a constant (unsupported) ^{210}Pb flux to the sediment, but permits the sediment supply (e.g. sedimentation rate) to vary, compared to other dating models where both ^{210}Pb flux and sediment supply are assumed to remain constant throughout the sediment profile (Appleby and Oldfield, 1978; Ravichandran et al., 1995; Silva et al., 2009). The CRS model equation is given below (and is illustrated in Figure 8):

Equation 1: Constant Rate of Supply calculation

$$t = \lambda^{-1} \times \ln(A_{\infty}/A_x)$$

where λ is the ^{210}Pb decay constant ($0.031/\text{year}^{-1}$),

A_{∞} is the integrated activity from the surface to A_0 (and A_0 is the ^{210}Pb excess activity in the top layer of the sediment core in Bq/kg

A_x is the integrated activity from x to A_0 ,

and (t) is the sedimentation rate ($\text{cm}/\text{year}^{-1}$)

Note: Specific ages are calculated by dividing core depth by sedimentation rate.

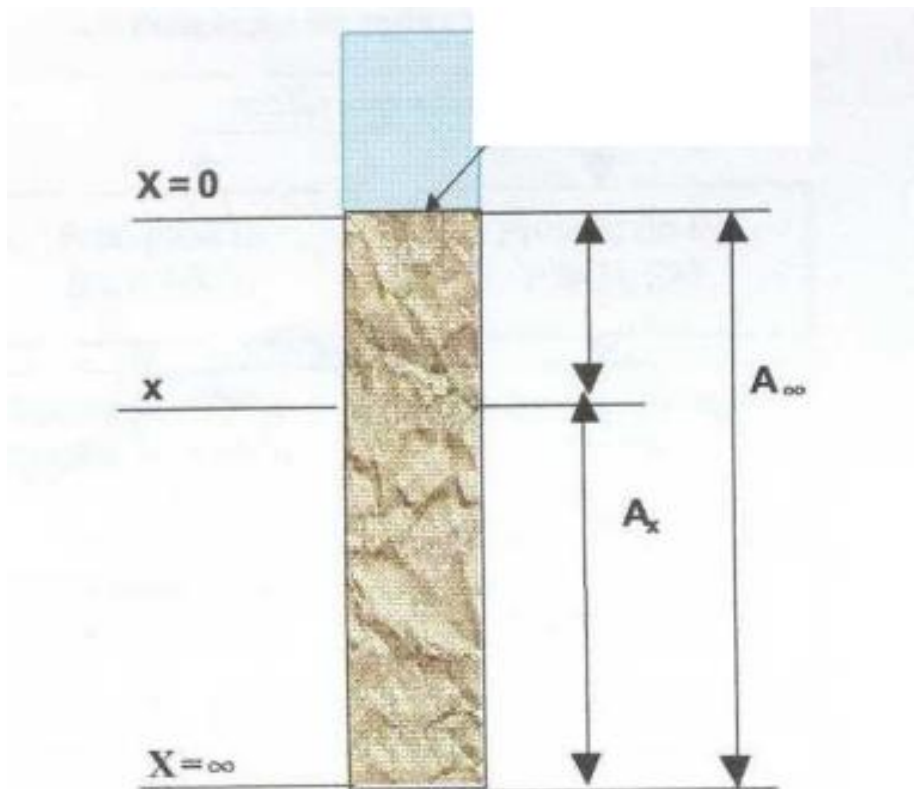


Figure 8: Schematic depicting the CRS constant supply model (Silva et al., 2009)

2.2 Methods

2.2.1 Core collection and subsampling

Four sediment cores were retrieved from Lake Okataina using a Uwitec gravity corer, with a 2-m long, 90 mm diameter polyvinyl chloride barrel (see Figure 9 below). The Uwitec corer was selected because it is operated by hand, is easily transportable and allows for relatively quick and effective capture of the upper 2 m of sediment covering a lake-bed. Individual cores were then cut to <1 m sections for later sub-sampling and analysis.

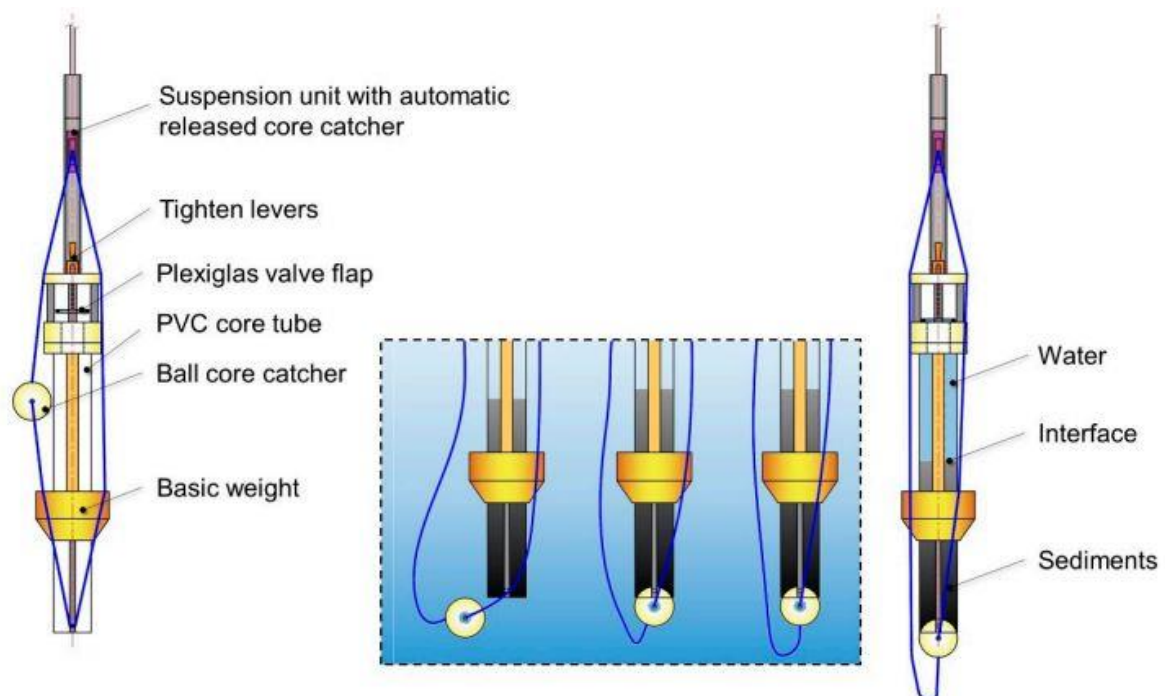


Figure 9: Sketch outlining the components of a conventional Uwitec gravity corer, similar to the one used to collect core samples from Lake Okataina in this study (Gong et al., 2019).

The cores were retrieved from a location, close to the depocenter of the lake's main basin towards the north-eastern end (38° 6'45.43"S, 176°25'8.63"E). Taking a core from the depocenter of a lake is widely accepted as best practice because this environment usually archives the highest-resolvable record and is distal from confounding factors that obscure environmental reconstructions like slumping (Lu et al., 2014; Smol, 1992).

The cores were collected on 3 April 2019 and transported back to the GNS Science, National Isotope Centre in Lower Hutt, Wellington, where they were chilled at 4°C and kept in complete darkness until subsampling.

The four core measured:

- LC1U: 78cm
- LC2U: 94 cm
- LC3U: 119 cm
- LC4U: 125 cm

All four cores were sliced along the longitudinal plane with a specialist core splitting machine and were then separated into two halves using a guillotine. The top 2-3 millimetres of each half were then scraped back and removed using a sterile spatula. In order to reduce the effects of oxidation on the cores, one half was prepared for later hyperspectral and ITRAX u-XRF imaging and then wrapped and stored, while the other was immediately visually logged (noting colour, texture, structure, core deformation and abundance of organic material).

LC4U was selected as the “master core” as it was the longest and had little evidence of deformation during the coring process. The primary core, LC4U was sub-sampled at 1cm for the analysis of chironomids, pollen and eDNA. Some material from this core was also used for radiocarbon dating.

Cores LC2U and LC3U were predominantly used to help establish a chronological record for Lake Okataina (refer to section 3.1 for core correlations). LC2U was selected as the primary core for radiocarbon sampling and LC3U was selected for Pb²¹⁰ sampling. LC1U was maintained as an archive.

2.2.2 Chronology sampling

2.2.2.1 ^{14}C Sampling

Two core sections were sieved (LC3U and LC2U) for possible ^{14}C targets. A sterilised metal strip was placed in the middle of the core to prevent contamination before sub-sampling. Sediment was washed through a 1-mm sieve with deionised water and organic material of interest was picked out using sterile forceps. Two samples were collected and were deemed to have enough mass to begin the ^{14}C treatment process.

Isolated terrestrial macrofossils were prepared for ^{14}C dating by mechanically cleaning the sample followed by the standard Rafter Radiocarbon Lab protocol for acid-alkali-acid (A-A-A) treatment. This treatment removed calcium carbonate, humic and other mobile carbon contaminants from the macrofossil. The last acid step broke any bonds the sample had created with atmospheric CO_2 during the alkali step. Chemical treatment was individualised for each sample based on fragility and sample mass by adjusting the molarity, temperature or length of treatment to avoid sample mass loss.

Samples prepared for ^{14}C measurement were loaded into quartz tubes and carbon dioxide was generated by sealed tube combustion and converted to graphite by reduction with hydrogen over an iron catalyst (Turnbull et al., 2015). $\delta^{13}\text{C}$ was measured offline on samples with sufficient mass using a continuous flow isotope-ratio mass spectrometer (EA-IRMS) in the Stable Isotope laboratory at GNS Science. Radiocarbon dating was performed at Rafter Radiocarbon Laboratory, GNS Science on the 0.5 MV XCAMS AMS. Results were produced using the measurement of all three carbon isotopes provided by XCAMS which corrects for any mass-dependent fractionation that may have occurred before or during measurement (Turnbull et al., 2014). Results were normalized against the NIST standard Oxalic Acid I. Blank correction was applied to the results using a process blank target of matching mass which was included in measurement with the experimental samples and normalised to $\delta^{13}\text{C}$ of -25‰ (Donahue et al., 1990). Radiocarbon results are reported as ^{14}C ages (yr BP) with a 1-sigma error. Samples were calibrated using Winstcal calibration program with the SHCal20 calibration curve (Hogg et al., 2020).

2.2.2.2 ²¹⁰Pb Sampling

One core section (LC3U) was sampled for ²¹⁰Pb by Adelaine Moody (Victoria University of Wellington). N = 15 samples were taken from the core and weighed (see Table 1 below). These samples were frozen and then freeze dried before being sent to the Institute of Environmental Science and Research (ESR) laboratory in Christchurch, New Zealand, where 0.3g of each sample was analysed using alpha spectrometry.

Table 2: List of ²¹⁰Pb samples used in the analysis

Sample Depth (cm)	Wet Weight (g)	Dry Weight (g)
1-2	12.44	2.51
3-4	13.09	2.85
5-6	12.48	4.01
7-8	10.35	2.25
9-10	9.45	2.04
11-12	13.2	2.94
14-15	13.36	2.92
17-18	12.63	3.17
19-20	12.57	2.37
26-27	14.84	5.94
31-32	12.67	6.71
35-36	15.89	7.76
74-75	9.44	2.28
79-80	9.78	2.25
83-84	11.65	2.66

An age depth-model was developed from the 25 ^{210}Pb and 2 ^{14}C dates, along with the calendar age of the Mt. Tarawera eruption and a uniform prior for first appearance of pine that ranges from 1870 to 1920 CE. The age-depth model was created in OxCal v4.4.4 (Ramsey, 2001) using the P Sequence function (Ramsey, 2008).

2.2.3 Palynology

The pollen stratigraphy was used to identify changes to regional and local vegetation in the wider catchment of Lake Okataina. This helped to place significant events in the lake's history such as the 1886 eruption of the adjacent Mt Tarawera. Palynology sampling was conducted prior to the beginning of this study by Xun Li (GNS Science), who followed an adapted preparation method outlined in Faegri et al. (1989).

This involved a series of processing steps:

- an acid wash (to remove calcium from the samples)
- acetolysis (effectively simultaneous acetylation and hydrolysis)
- heavy liquid floatation (to remove the mineral fraction)
- filtering (through 6 μm nylon cloth mesh)
- and finally, slide mounting

A relative pollen diagram was established by normalising taxa counts across the dryland pollen (this was defined as the sum of the pollen grains from tall trees, small trees and shrubs and herbs). Fern spores and other types of wetland taxa were not included; however, the percentage of fern spores and wetland taxa were calculated against the total dryland pollen sum.

Charcoal analysis was enumerated alongside the palynology sampling. Charcoal counts were converted to concentrations (charcoal particles per cm^3) by dividing counts of charcoal fragments by the total volume of sediment sieved per sample (Perry et al., 2012). Charcoal counts on pollen slides were used to assess fire history, with the microscopic fragments being $<100 \mu\text{m}$ and macroscopic referring to fragments $>100 \mu\text{m}$.

2.2.4 ITRAX u-XRF Scanning

Another type of non-destructive scanning was carried out on the LC4U core section. The ITRAX scanning instrument recorded optical, radiographic and elemental variations at high resolution (1000 microns). An intense micro-X-ray beam was used to irradiate the core to enable x-radiography and x-ray fluorescence analysis. Two different tubes were used in the analysis: a Cr tube for all elements lighter in mass than and including Fe and a Mo tube for all elements heavier than Fe, except for Zr, which was measured with the Zr tube. The XRF voltage and current were 30kV and 55 mA respectively and the exposure time was 10 s.

2.2.5 Hyperspectral Imaging

Hyperspectral imaging was used to derive the relative absorption band depth (RABD) at 660-670 nm as a direct proxy for volumes of chlorophyll-a and as an indirect proxy for within-lake productivity. All cores were prepared for scanning by scraping the surface sediment using a sterilised tool, to ensure a smooth and flat surface, free of pockets or deviations that can create false readings within the hyperspectral data.

Hyperspectral imaging scans were then collected for each sub-section of the LC4U core using a Specim SISU single core scanner, equipped with a sCMOS-50-V10E spectral camera. The spatial resolution of the scanner was set to 1mm/pixel at a spectral resolution of 660-670 nm. Image pre-processing and normalisation procedures followed standard methods (Butz et al., 2015). The four-step method mirrored the workflow outlined in Figure 10 below (Butz et al., 2015). The spectral indices were calculated using R version 4.0.3, applying the RABD ratio R_{660}/R_{670} to provide a simple estimate of primary productivity changes downcore.

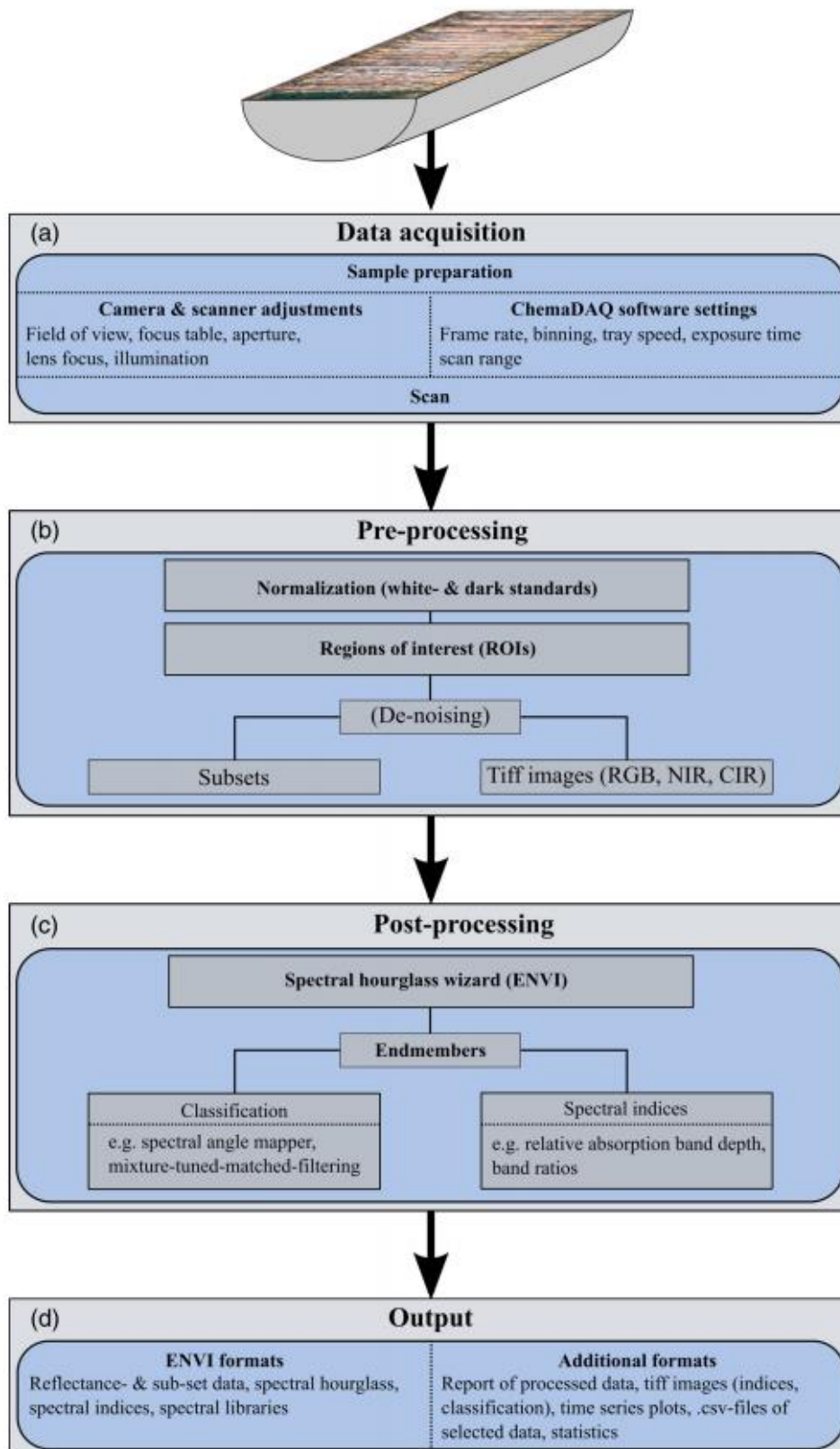


Figure 10: The general workflow-methodology for the hyperspectral analysis of lake sediments (Butz et al., 2015)

2.2.6 DNA Extractions and Polymerase Chain Reaction Amplification

The environmental DNA process from DNA extraction (post sample collection) to bioinformatic analysis, is described in the following sections (for a simpler overview of the entire DNA process, refer to Figure 34 in the Appendix). The 16S ribosomal DNA (16S rDNA) bacteria gene was analysed, using material sampled from the LC4U master core. The dataset contained n = 61 samples from throughout the entire core section.

2.2.6.1 DNA Extraction

Sub-samples (~0,25 g) of sediment from each depth were weighed in the first tube provided in the DNeasy PowerSoil™ DNA Isolation Kit (QIAGEN, Germany). DNA was extracted following the manufacturer's protocol, with DNA eluted in 100 µL of buffer. Extraction of DNA was performed in batches of eight to ten samples including a negative control every two batches. This contained all the reagents but no sediment. DNA concentrations and quality were measured using a spectrophotometer (Eppendorf AG, Hamburg, Germany).

2.2.6.2 Polymerase Chain Reaction (PCR)

The V3-V4 regions of the bacterial 16S rDNA gene, were amplified by Polymerase Chain Reaction (PCR), using the bacterial-specific primers 341F: 5'-CCT ACG GGN GGC WGC AG-3' and 805R: 5'-GAC TAC HVG GGT ATC TAA TCC-3 (Herlemann et al., 2007; Klindworth et al., 2013). The primers were modified to include Illumina™ overhang adaptors following the dual-indexing method described in Kozich et al. (2013).

PCR reactions were performed in 20 µL volumes in triplicate for each sample. The reaction mixture contained 10 µL of MiFi 2 × PCR mastermix, 2 µM of each primer (final conc.) and 2 µL of template DNA. The reaction mixture was then held at 94°C for 1 min followed by 30 cycles of 95°C for 15 s, 52°C for 15 s, 72°C for 15 s, with a final extension step at 72°C for 7 min. Negative PCR and negative extraction controls were included.

2.2.6.3 High Throughput Sequencing

The triplicate PCR products and negative controls were pooled and 20 μL of the pooled PCR products were cleaned and normalized using SequalPrep Normalization plates (ThermoFisher Scientific, USA), resulting in a concentration of $\sim 1 \text{ ng } \mu\text{L}^{-1}$. Water blanks were also included as sequencing blank controls

The samples were sent to the Auckland Genomics Facility for sequencing on an Illumina MiseqTM platform. The samples were prepared for sequencing following the Illumina 16S metagenomics library prep manual with the exception that after the indexing PCR, 5 μL of each sample (including water samples acting as sequencing blank) was pooled and a single clean-up was undertaken on the pool instead of samples being individually cleaned.

The library pool quality control was undertaken on a bioanalyzer before the library was diluted to 4 nM, denatured and diluted to a final loading concentration of 7 μM with a 15% PhiX spike. Raw sequence reads were deposited in the NCBI short read archive under the accession number: PRJNA606991.

2.2.6.4 Bioinformatics

Bioinformatics were carried out by John Pearman and Mailys Piccard of the Cawthron Institute.

Primers were removed from the raw reads using cutadapt with 1 mismatch allowed (Martin, 2011) and were then subsequently processed within R (R Team, 2014), using the DADA2 package (Callahan et al., 2016). Reads were truncated (230 and 228 bp for both forward and reverse reads respectively) and were then filtered with a maximum number of “expected errors” (maxEE) threshold of two (forward reads) and four (reverse reads). Those reads not matching this specific criterion were discarded from further analysis. A parametric error matrix was built, based on the first 10^8 bp of the sequences. Following sequence dereplication, sequence variants for both the forward and reverse reads were inferred based on this error matrix.

Singletons were discarded and remaining paired-end reads were merged with a maximum mismatch of 1 bp and a required minimum overlap of 10 bp. Within the DADA2 package, the script *removeBimeraDenovo* was used to remove chimeric sequences. The resulting chimera checked, Amplicon Sequence Variants (ASVs), were taxonomically classified using the SILVA 132 database for 16S (Pruesse et al., 2007).

The sequences were then classified based on the rdp classifier (Wang et al., 2007), with a bootstrap of 50 to allow for classifications to occur at higher taxonomic levels. The results were combined into a *phyloseq* object (McMurdie and Holmes 2013). Sequences assigned as microeukaryotes, chloroplasts and mitochondria were removed. Negative controls were assessed and read numbers for ASVs found in the negative blanks were removed via subtraction.

Samples were rarefied at 8962 reads. Four samples in the dataset (14-15cm = 5470 reads, 21-22cm = 4418 reads, 41-42cm = 2960 reads and 96-97cm = 888 reads) were removed, as the number of reads was below the rarefaction threshold.

2.2.7 Morphological Analysis of Chironomids

For the morphological analysis of chironomids 2 – 6 cc. of sediment was extracted per sample from the LC4U core. 35 samples were prepared according to standard procedures (Walker et al., 1991). Samples were mixed and deflocculated in hot 10% KOH solution under a fume hood for 15 min. and were then sieved over a 90 - μ m nylon mesh. The exact volume of sediment retrieved was determined by the density of head capsules per sample. Where possible sediment was extracted and sieved to retrieve at least 50 whole head capsules per sample (Heiri and Lotter, 2001), though only a maximum of 6 cc of. sediment was available. Studies suggest between 40 and 50 head capsules are sufficient for use in inference models, where diversity is relatively low (Quinlan and Smol, 2001; Rees et al., 2008). After sieving, aliquots of the residue were poured into a Bogorov counting tray and examined under a dissection microscope at 50x magnification. Individual head capsules were hand-picked using forceps until the entire sample residue was processed. Head capsules were then positioned ventral-side up on a coverslip and mounted with Entellan®. Identification was undertaken by Valerie van den Bos and Andrew Rees (Victoria University), using a compound, light microscope at 400x magnification, following standard reference manuals (Oliver and Roussel, 1983; Wiederholm, 1983) and a region specific, detailed identification guide (Dieffenbacher-Krall et al., 2008).

2.2.8 Statistical Analysis

Datasets for the different proxies were subject to a range of different non-parametric statistical analyses conducted in R (R Team, 2016).

2.2.8.1 ITRAX

Downcore stratigraphic line plots were constructed to highlight changes to individual elements and elemental ratios in the geochemical system of Lake Okataina. A PCA analysis was also run on this dataset to distinguish between Pre-Tephra, Tephra, Post-Tephra and Post 1930 phases. Note the Tephra phase was only included as there were sufficient geochemical data points for this phase unlike with the other proxies. This analysis was carried out in R using the *vegan* package (Oksanen, 2011).

2.2.8.2 Hyperspectral Data

A box-plot was constructed to compare the RABD averages between the three phases visually using the *ggplot* package in R (Wickham, 2017). A Kruskal Wallis and Nemenyi-Kruskal pairwise, post hoc test were also run in R to assess the statistical significance of the differences between the time phases using the *PMCMR* package (Pohlert, 2014). The hyperspectral data were linearly interpolated to the same resolution as the ITRAX data above and included in that PCA.

Hyperspectral imaging was also used to correlate LC1U, LC2U and LC3U back to the master core of LC4U. Tie points were visually identified using the RABD660/670 profiles of all cores, and then the former three were individually regressed against LC4U to develop equations for cross correlations.

2.2.8.3 16S rDNA Bacteria

To visualise the composition of the 16S rDNA gene data, a composition bar plot was created by merging all samples from the dataset together. Amplicon Sequence Variants (ASV's) were agglomerated at the taxonomic level of class and the number of reads and relative proportion of reads were calculated using the *phyloseq* package in R (McMurdie and Holmes, 2013).

To analyse alpha diversity within the bacterial community, a series of box-plots were constructed, based on Shannon and Simpson index values for each samples, as well as observed (actual richness) values for comparison. Kruskal Wallis tests were run in R, on all three measures separately, to determine if there were significant differences between the three-time phases. Post-hoc Nemenyi-Kruskal tests were also run on the three measures of alpha diversity to isolate the specific differences between the time phases using the *PMCMR* package in R (Pohlert, 2014)

To assess whether there were differences in the community structures between different time phases (Pre-Tephra, Post-Tephra and Post 1930), a permutational ANOVA (PERMANOVA) was run, based on a Bray-Curtis dissimilarity matrix. To ascertain which groups differed from one another specifically, a pairwise PERMANOVA was also undertaken. Both tests were run in the R package *vegan* (Oksanen et al., 2013). A Principal Coordinates Analysis (PCoA) plot was then constructed in *ggplot2* (Wickham, 2017) with points coloured based on time phase.

A multipatt, indicator species analysis was also run on this dataset to identify any significant taxa (at Class level) that appeared as indicators of different phases. This test was also run on just the class of *Gammaproteobacteria* across the different phases to isolate indicator species (at Genus level) within this group. This was carried out using the *indicspecies* package in R (Cáceres and Legendre, 2009).

2.2.8.4 Chironomids

A downcore stratigraphic plot was constructed at species level to highlight community changes across the different phases. A Principal Components Analysis was run on this dataset and points were coloured by time phase. These analysis were completed using the *vegan* and *ggplot* packages in R (González and Déjean, 2012; Wickham, 2017).

2.2.9 Sampling Summary

All proxies and analyses, were correlated back to the master depth of the LC4U core using tie points from the hyperspectral imaging. LC4U, in turn, was sub-divided into three different phases. Pre-Tephra (76 – 127 cm), the Post-Tephra (17-61 cm) and the Post 1930 (0-16 cm). These phases were defined by the physical characteristics of LC4U in combination with the palynology record and geochemical and hyperspectral datasets. Figure 11 below highlights the sampling intervals for the key proxies included in this thesis.

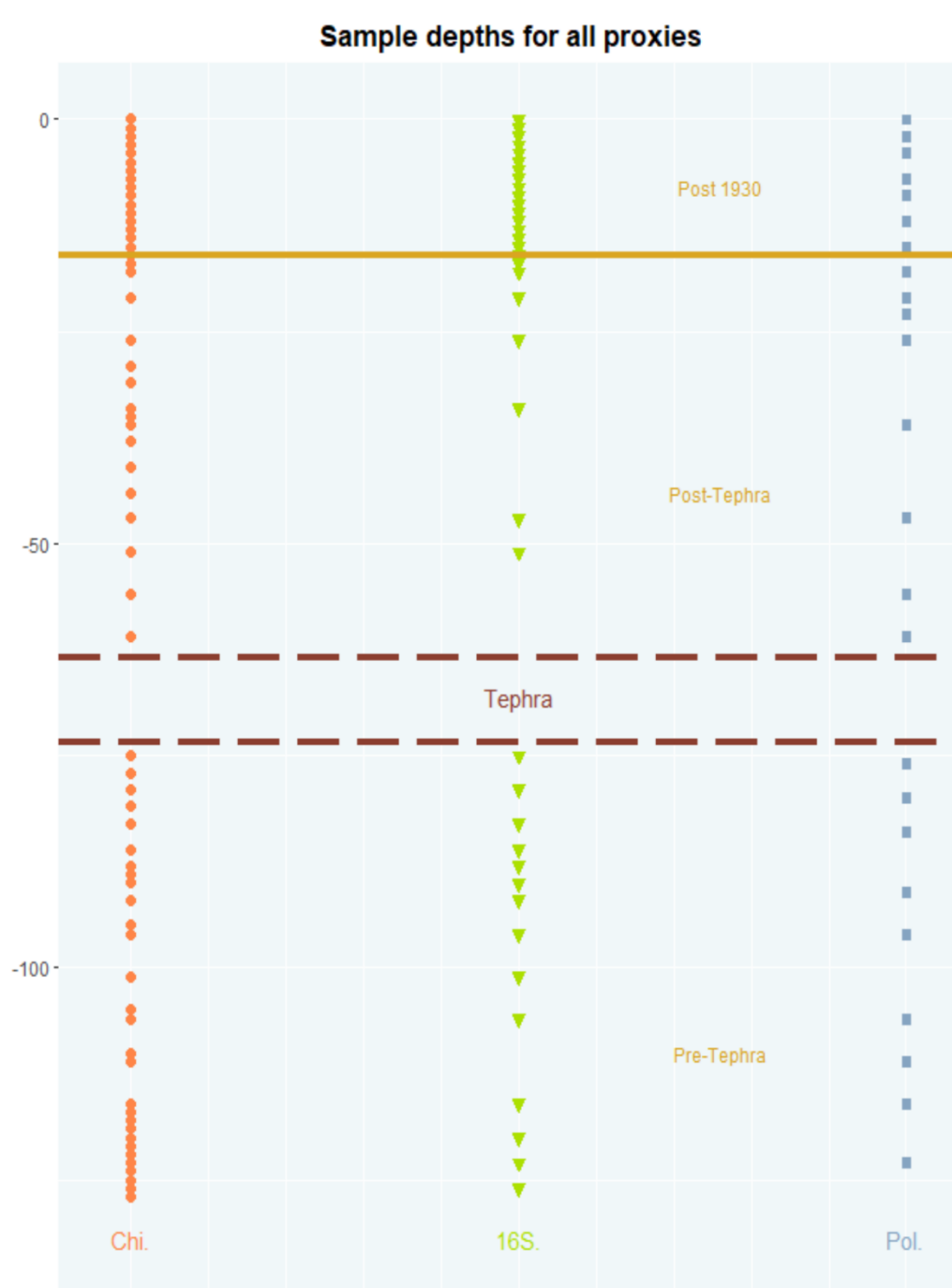


Figure 11: Sampling depths (cm) for chironomids (orange), 16S bacteria (green) and pollen (blue). Note the annotations denoting the different time phases (Pre-Tephra, Post-Tephra and Post 1930).

Chapter 3: Results

Chapter 3 presents the results of the multi-proxy analyses and focuses on the differences between the Pre-Tephra, Post-Tephra and Post 1930 phases in the study. This section begins by detailing the chronology of Lake Okataina. Following this, the results of the ITRAX data and the palynology are detailed. In the next section the results from the ecological proxies (hyperspectral scanning, bacterial metabarcoding and the morphological analysis of chironomids) are also presented.

3.1 Core stratigraphy and correlations

The stratigraphy of Lake Okataina was varied with the most prominent layer deriving from the 1886 Mt Tarawera eruption and the resulting tephra deposition. The following description is taken from the master core (LC4U), which is best exemplified in Figure 12.

The Pre-Tephra environment is characterised by a series of laminated bands ranging from lighter orange, to light orange-dark green and black. The laminations appear to give way to a single unit at approximately 110cm that appears largely brown, with darker mottling throughout. There is a sharp contact between this unit and the tephra (at 74-75cm). The tephra particles appear coarse in size for 1-2cm before then begin to fine right down to silty-sand at the top of the tephra deposit. Another light grey silty unit follows on top of the tephra layer from approximately 63 – 50cm. Following this a series of laminated bands appear, ranging in colour from dark and light grey to dark and light brown, through to approximately 37cm. From here more laminated bands follow, however, there are now very pale, yellow-white layers interspersed between some of the brown layers (described above). At 19-24cm there is a significant continuous yellow-white layer. Following this, there appears to be one main, light and dark orange, silty-mud unit till the top of the core.

Nine (LC1U), twelve (LC2U) and fourteen (LC3U and LC4U) tie points were identified for each respective core from the hyperspectral imaging (RABD 660-670 nm) in order to create a master stratigraphy (Figure 12).

The master stratigraphy was created by individually regressing LC1U, LC2U and LC3U against LC4U using the points identified in Figure 12. These were used to create a series of polynomial regression curves (Figure 13) and equations (2-4). All regressions had strong positive relationships ($R^2 = 0.98$ to 0.99).

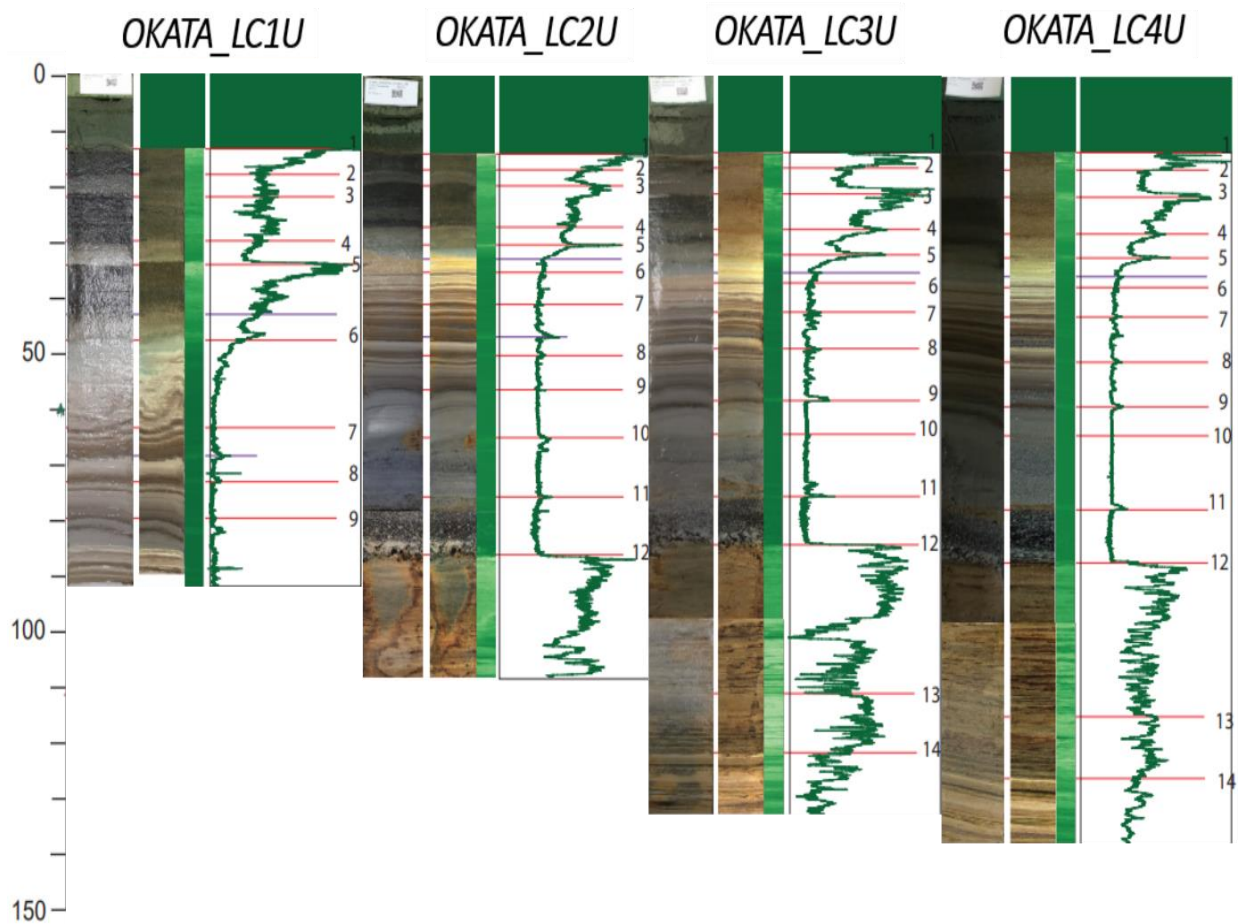


Figure 12: Correlations of cores LC1U (left), LC2U (middle left), LC3U (middle right) and LC4U (right). Correlated points are shown in red and the chlorophyll-a abundance (RABD 660-670 nm) is plotted in green. Points are defined by significant changes in chlorophyll-a throughout the cores. Purple lines indicate significant “tie points” used for the correlation calculations. Note the green blocks at the top of the core represent flora foam (used to plug the

Equation 2: Polynomial equation for LC1U depth (against LC4U depth)

$$LC4U = (-0.0017 \times LC1U^2) + (0.7794 \times LC1U) + 4.5725$$

Equation 3: Polynomial equation for LC2U depth (against LC4U depth)

$$LC4U = (-0.001 \times LC2U^2) + (1.1085 \times LC2U) - 1.0017$$

Equation 4: Polynomial equation for LC3U depth (against LC4U depth)

$$LC4U = (-0.0002 \times LC3U^2) + (1.0152 \times LC3U) - 0.482$$

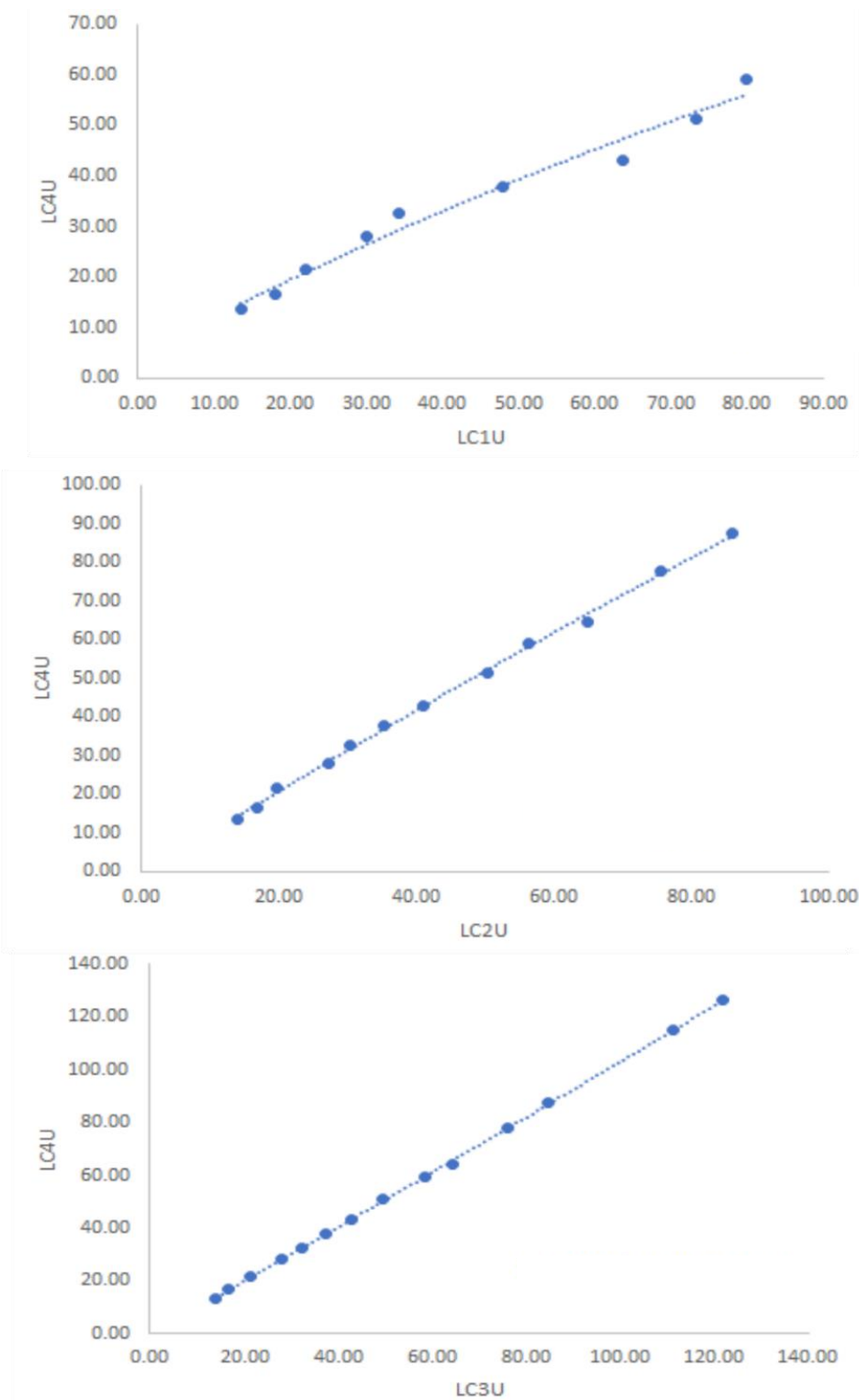


Figure 13: Polynomial regression plots of cores LC1U (top), LC2U (middle) and LC3U (bottom). The correlation curves (blue line) are calculated by regressing depths (blue dots) on one core against the master core (LC4U).

3.2 Age Depth Model

Sediment within Lake Okataina was dated using ^{210}Pb , biostratigraphy (pollen and tephra) and conventional ^{14}C techniques. 25 ^{210}Pb samples were collected from the LC3U core and the CRS model returned a total of 25 dates ranging from AD 2018 (+/- 0.1 AD) to AD 1877 (+/- 5.0 AD). Biostratigraphic ages were based on known events and introductions of taxa to the catchment. The introduction of pine was dated between AD 1869 (earliest maximum) and AD 1895 (latest minimum). The eruption of Mt Tarawera and the resulting tephra deposit was dated to AD 1886. The radiocarbon samples from 30-31 cm and 39-40 cm provided calendar ages (once calibrated) of AD 1890 (95% CI AD 1875 – 1905) and AD 1895 (95% CI AD 1880 – 1910). These different constraints were combined to create the age-depth model (Figure 14). The ages for the older parts of the core were calculated using linear extrapolation because there was no datable material recovered from these older periods.

The age-depth model revealed 20 cm immediately above the tephra to be instantaneously deposited in-wash. As the objective of this thesis is to assess ecosystem response to natural disturbance and not characterise volcanic deposits, the in-wash and tephra were removed from the composite depth stratigraphy. The sedimentation rate also varied markedly. In the top 10 cm, ~40 years are covered (0.25 cm yr^{-1}), ~60 years are covered in between depths 10-20 cm (0.17 cm yr^{-1}) and then ~50 years between 20 -45 cm (0.52 cm yr^{-1}).

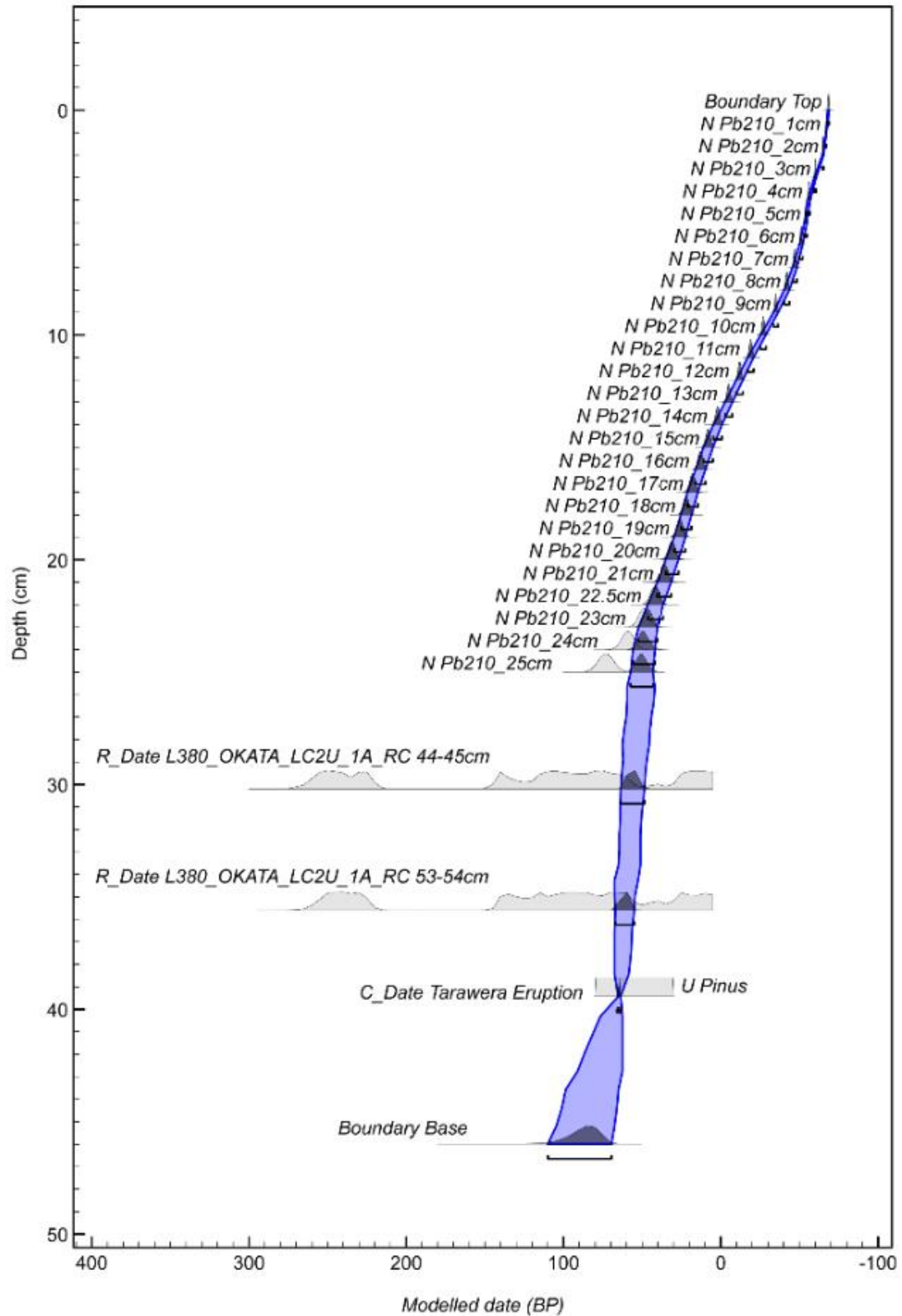


Figure 14: Oxcal age model of Lake Okataina sediment down core using depths to a master core (LC4U). Note, the tephra and subsequent in-wash have been removed from the depth scale.

3.3 Palynology

Dacrydium cupressinum and *Prumnopitys taxifolia* (tall trees) and *Botryococcus* (algae) were generally in higher abundance before 1886 and the eruption of Mt Tarawera (Figure 15). *Pteridium esculentum*, *Cyperaceae* and both micro and macro charcoal also appeared relatively abundant during this time (AD 1700 – 1886). Following the eruption, *Cyathea smithii* and *Cyathea dealbata* increase markedly in abundance until AD 1920 when they decrease again. *Pteridium esculentum* and *Dicksonia squarrosa* increase sharply and remain relatively high during this time until approximately AD 1940. The abundance of *Pinus* begins to increase from approximately AD 1920 and remains high to present day. Species of grasses also increase and remain high in abundance during this time. The abundance of *Botryococcus* decreases noticeably from AD 1886.

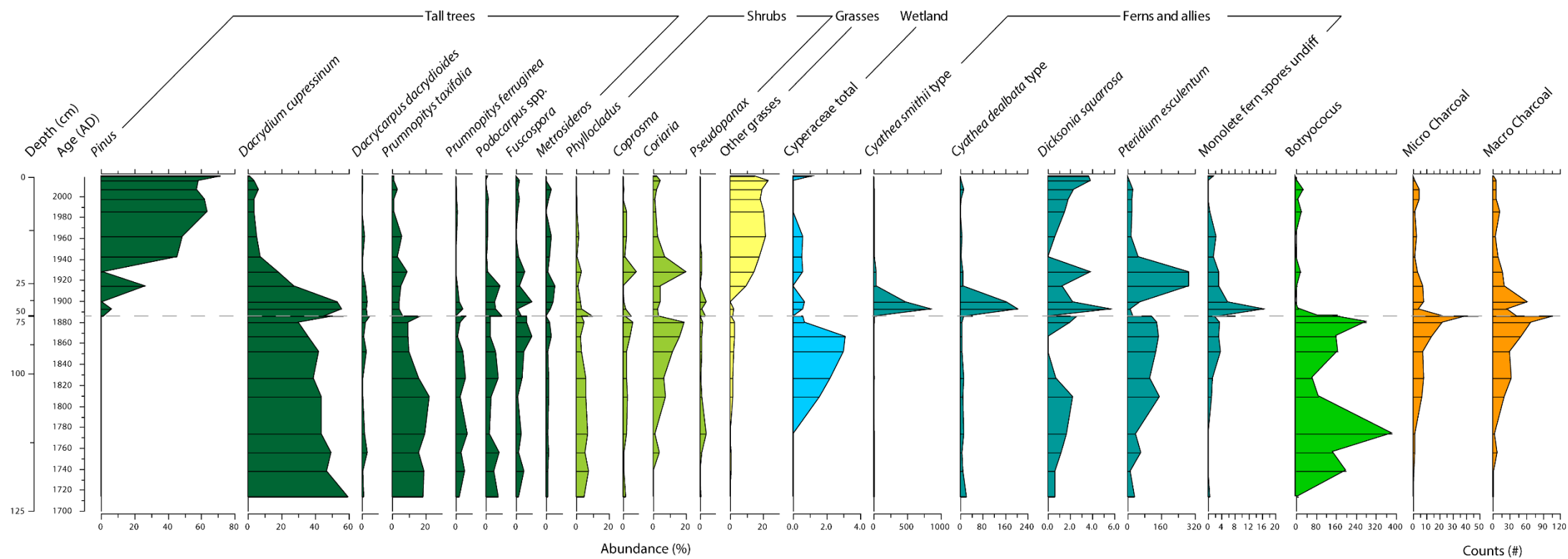


Figure 15: Summary pollen diagram depicting species of interest in Lake Okataina. The 1886 eruption is superimposed in the grey dotted line.

3.4 ITRAX

Based on the PCA, tephra samples possess unique geochemistry with elevated abundances of Fe, Zn, Ca, and, Si. Post-Tephra samples possess these elements as well, with greater contributions from Zr, Rb, and S. Meanwhile, Pre-Tephra and the youngest samples are distinct with elevated P and hyperspectral-inferred chl a. The youngest samples are distinguished by above average As.

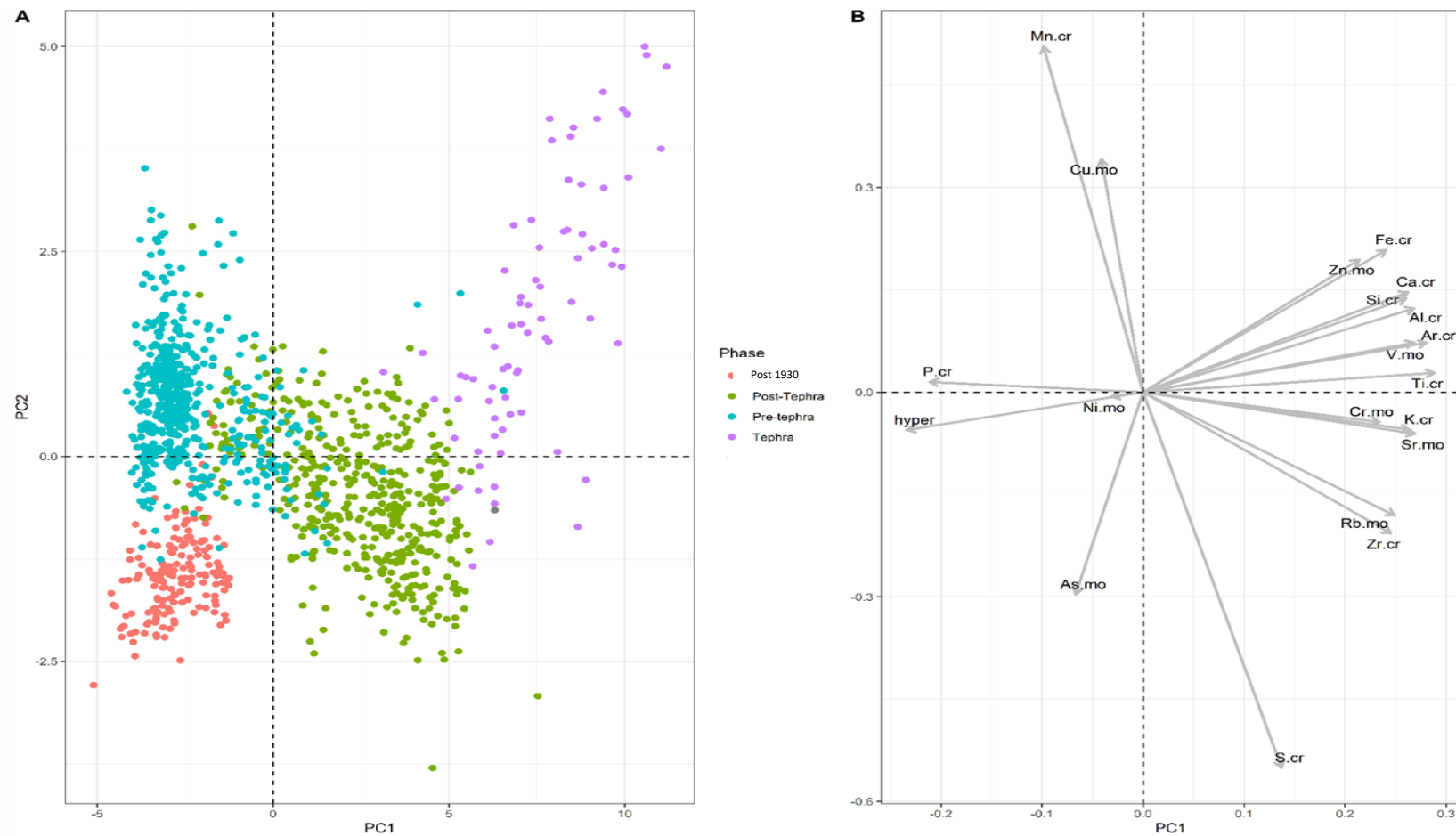


Figure 16: A PCA site scores (A) and species scores (B) for the ITRAX dataset. The points (in A) are coloured by phase (Post 1930 = Red, Post-Tephra = Green, Tephra = Purple, Pre-Tephra = Blue). Plot B has defining elements, superimposed as vectors (arrows). The letters represent elements and the tubes (either chromium or molybdenum) that the analyses were conducted in e.g. P.cr = phosphorus analysed in a chromium tube)

The ITRAX data highlights marked shifts in the geochemical properties of Lake Okataina before and after the eruption of Mt Tarawera and the resulting deposition of the tephra (Figure 17). The abundance of elements such as K, Ti, Ca and Sr increased dramatically following the eruption event (shown where all the elements peak together). The values for all four elements shown remained relatively high for 20-30 years (1886 – 1920 AD) following the tephra. Post ~1950 AD the values return to the levels measured before the eruption.

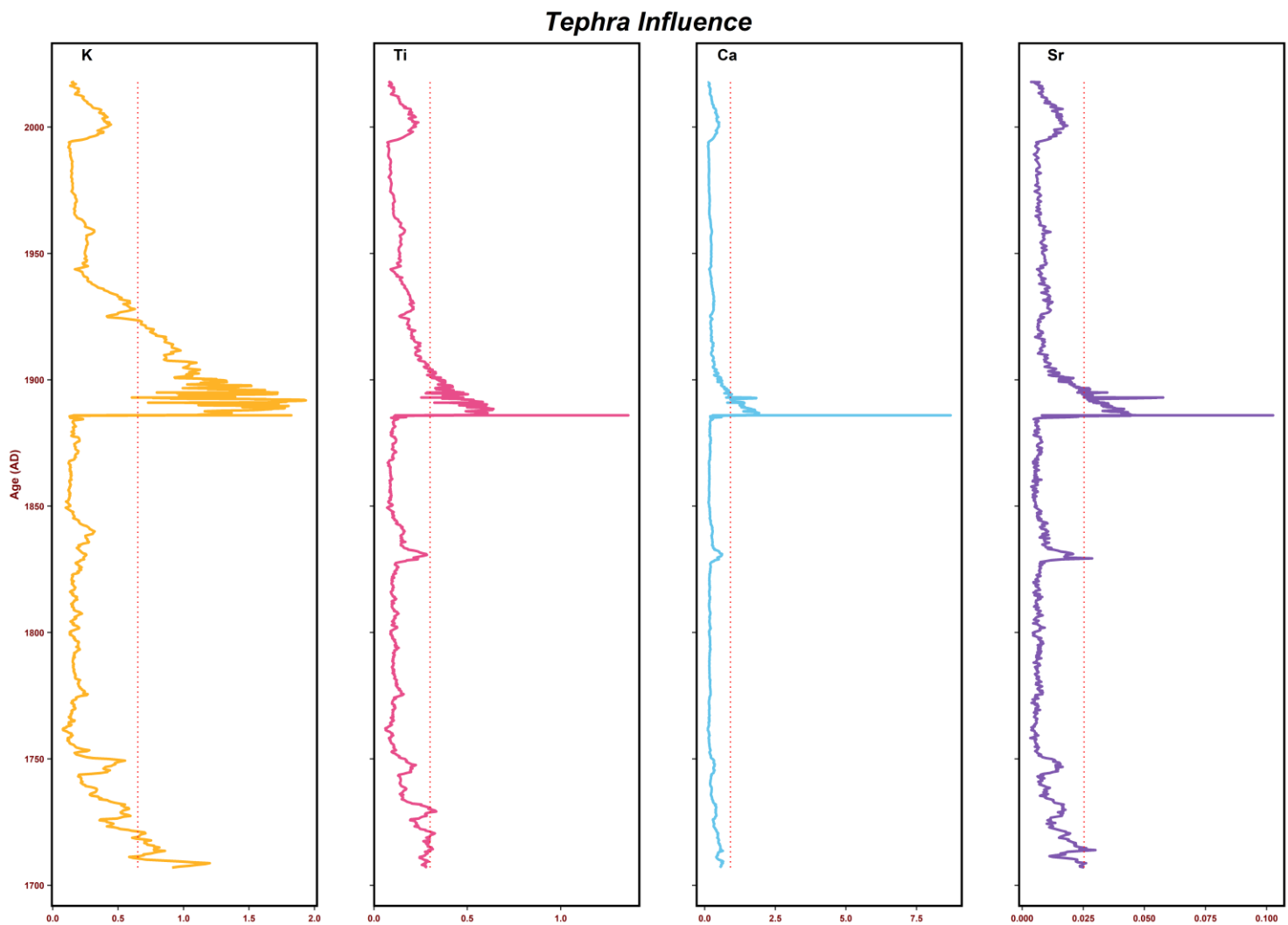


Figure 17: Results from the ITRAX analysis depicting changes in concentration downcore (from left to right) of potassium, titanium, calcium and strontium. The tephra layer from the Tarawera eruption is clearly highlighted by the associated spikes and the dotted vertical lines (red) show the mean value for the element

The ITRAX data indicate that different measures of aquatic productivity shifted considerably following the eruption (Figure 18). The RABD index (from the hyperspectral imaging data) is shown alongside here for reference. Concentrations of P in Lake Okataina fell markedly post eruption and remained low before they increased again from approximately 1970 AD till present. The concentration of Si/Ti (which can be an indicator of biogenic silica (diatoms) or primary productivity in an aquatic system) fell sharply following the eruption and has fluctuated but remained relatively low since the eruption (Croudace et al., 2006; C. Moy, personal communication, April 15, 2021). In contrast to the other three indicators highlighted in the plot, concentrations of S increased following the eruption and largely remained higher than the Pre-Tephra levels. The concentrations appear to decrease for a time between approximately 1890 and 1920 AD before they increase again from approximately 1930 AD till present.

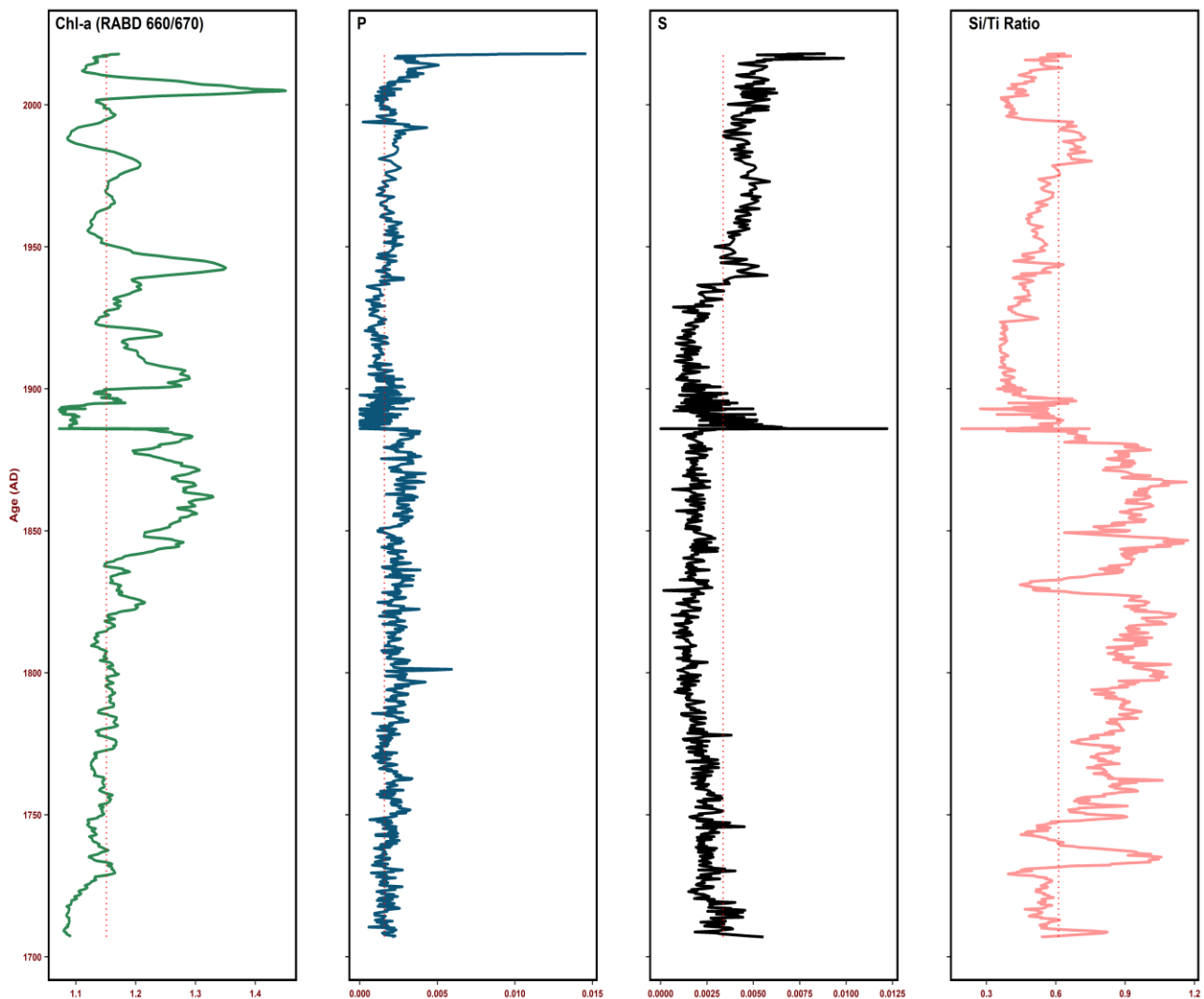


Figure 18: Results from the ITRAX analysis depicting changes in concentration downcore (from left to right) of phosphorus, sulphur and silica/titanium (with the RABD index included as a reference)

The ratios of Fe/Mn and Ti/Mn are very similar and both their concentrations appear to increase significantly following the eruption and remain higher than their pre-existing levels after this event (Figure 19).

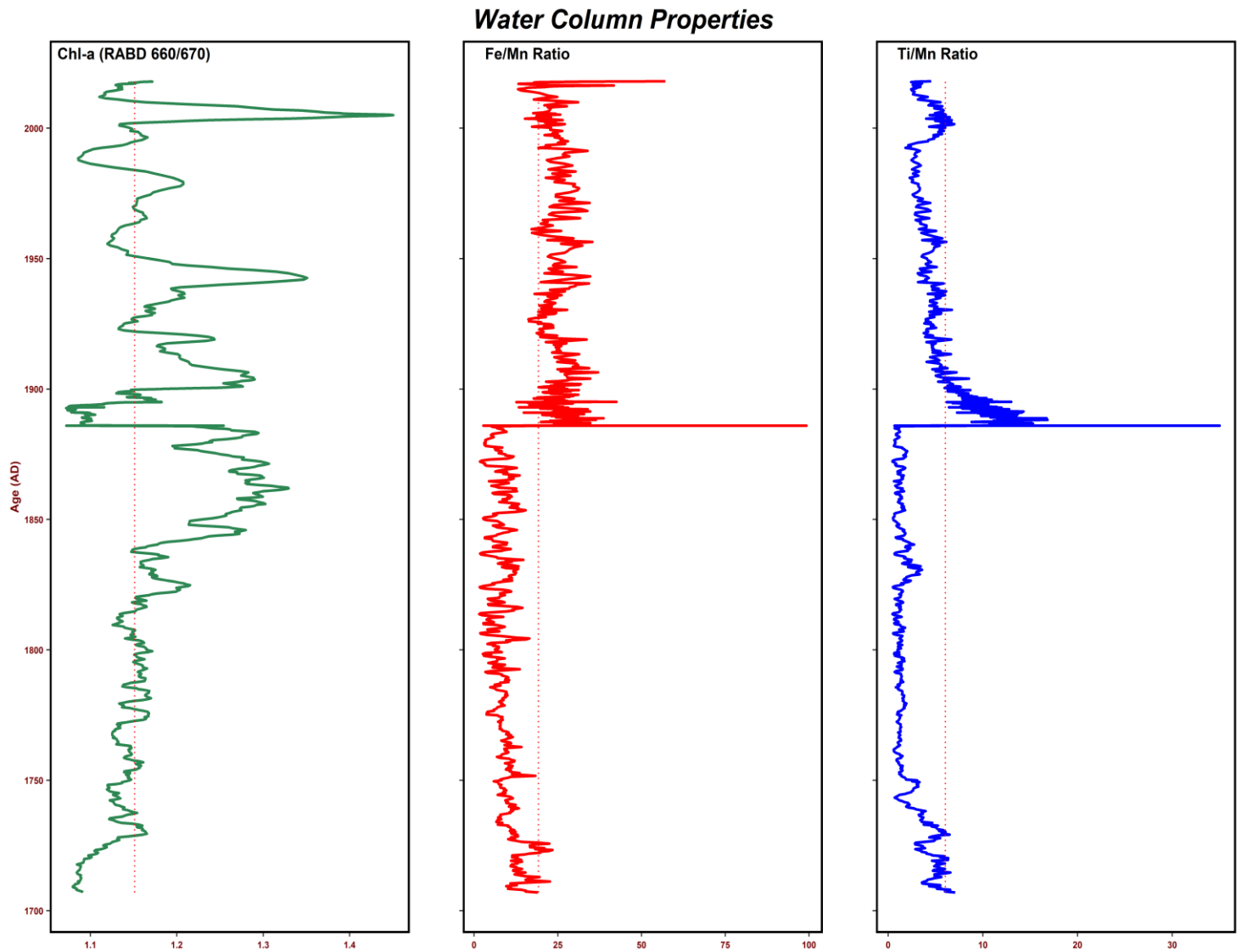


Figure 19: Results from the ITRAX analysis depicting changes in concentration downcore of iron/manganese, titanium/manganese ratios (with the RABD index included as a reference)

3.5 Hyperspectral Data

The Pre-Tephra and Post 1930 phases had mean values of 1.09 and 1.12 respectively, whereas the Post-Tephra phase had a lower mean value of 1.00. The box-plot illustrates clear differences between the average RABD values between the pre-defined phases, most notably, the disparity between the Post-Tephra phase and the Pre-Tephra and Post 1930 phases (Figure 20). The Pre-Tephra and Post 1930 phases have slightly higher RABD averages than the Post-Tephra phase and both these phases also appear to have a greater spread of data.

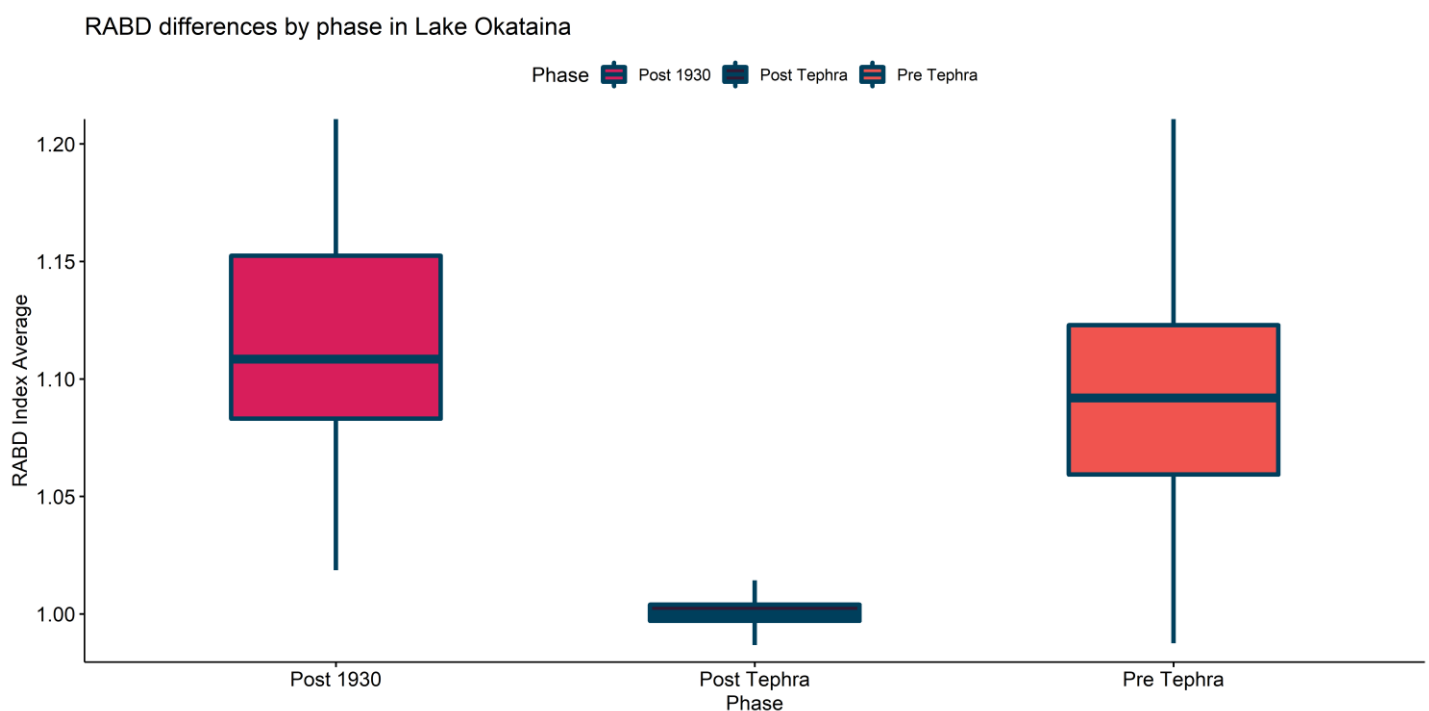


Figure 20: Boxplot depicting differences among phases in the RABD averages from the hyperspectral imaging results (Post 1930 = Pink, Post-Tephra = Black, Pre-Tephra = Orange)

A Kruskal Wallis test was undertaken and found a chi-square test statistic of 21743, with a highly significant p-value of <0.001 . A pairwise, post-hoc Nemenyi-Kruskal test was also run on this dataset and p-values for comparisons between all the different groups were highly significant (<0.001).

3.6 16S rDNA Bacteria

3.6.1 Univariate/Composition Analysis

The Pre-Tephra phase samples are dominated by *Gammaproteobacteria*, *Bacilli* and *Symbiobacteria*, with smaller amounts of *Anaerolineae*. The composition of samples changed following the tephra layer (AD 1886) in the Post-Tephra phase and the range of taxa increased dramatically.

Gammaproteobacteria remained dominant, however, *Bacilli* and *Symbiobacteria* almost disappeared and the proportions of *Campylobacteria*, *Anaerolineae* and *Parcubacteria* increased. In the initial samples in the Post 1930 phase, the proportion of *Campylobacteria* dropped markedly and the proportion of *Anaerolineae* increased. Proportions of *Gammaproteobacteria* also decreased between approximately AD 1930 and 1975 while *Thermodesulfovibrionia* increased. These taxa began to decrease in relation to other taxa post AD 1997. The proportion of *Gammaproteobacteria* and *Campylobacteria* increased in this top section, as the proportion of *Anaerolineae* also increase.

3.6.2 Beta Diversity Analysis

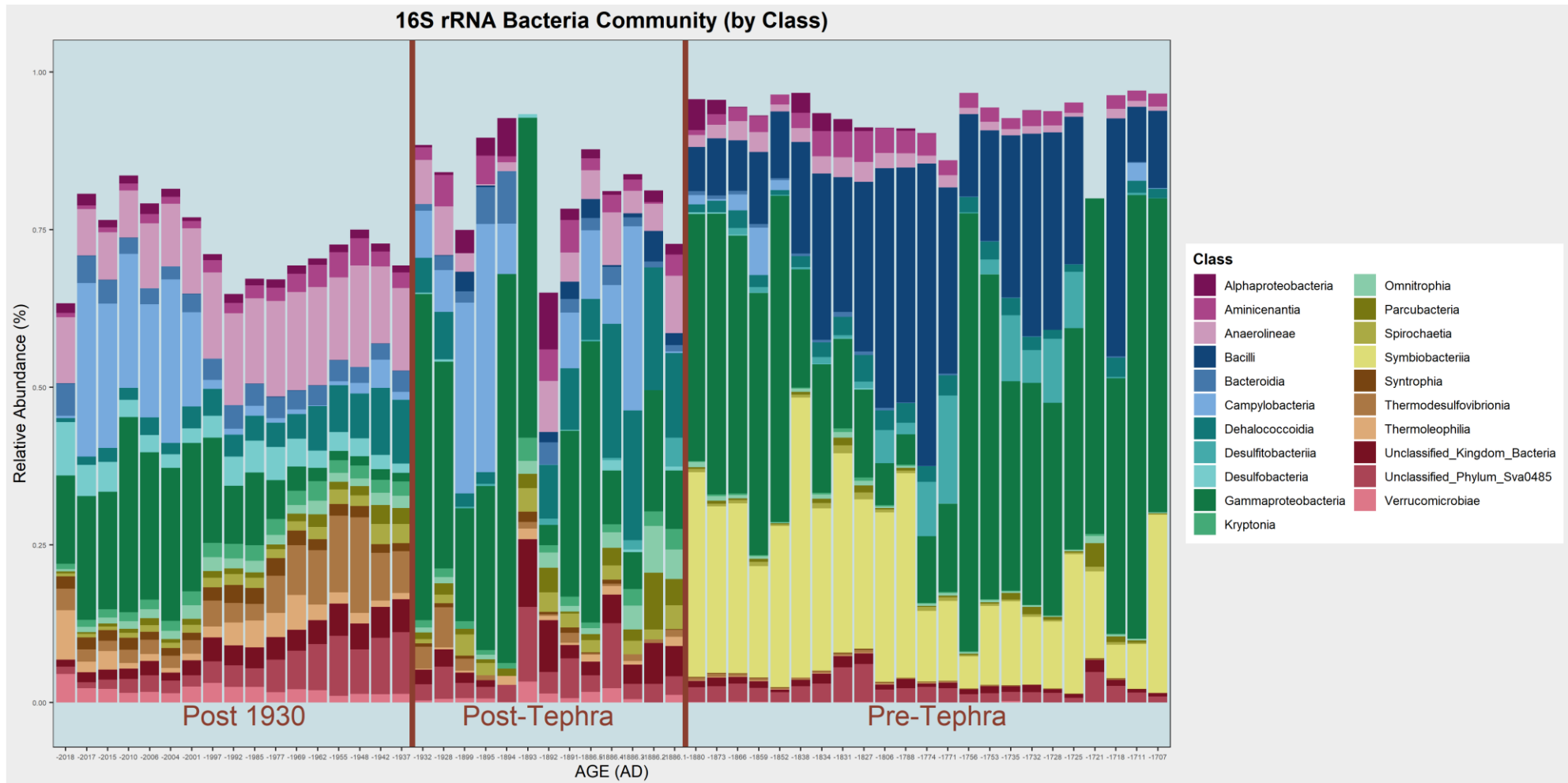


Figure 21: Bar plot of the bacterial community of Lake Okataina (at class level). Note that the sample bars do not equal 100% (as some rare taxa were excluded from the plot for clarity)

Axis 1 of the Principal Coordinates Analysis (PCoA) explained 26.4% of the variation in the dataset and Axis 2, 8.8% (Figure 22). The ordination identified three distinct clusters associated with the three-time phases in the study. The Pre-Tephra cluster (on the right of the plot) is farther from the Post-Tephra (middle) and Post 1930 phases (left), which overlap slightly. The two specific data points in the Post-Tephra phase that sit outside of the cluster are approximately AD 1928 and 1932. The PERMANOVA test showed there was a significant difference among phases ($p < 0.001$), and the pairwise test showed each phase was significantly different from one another ($p < 0.001$).

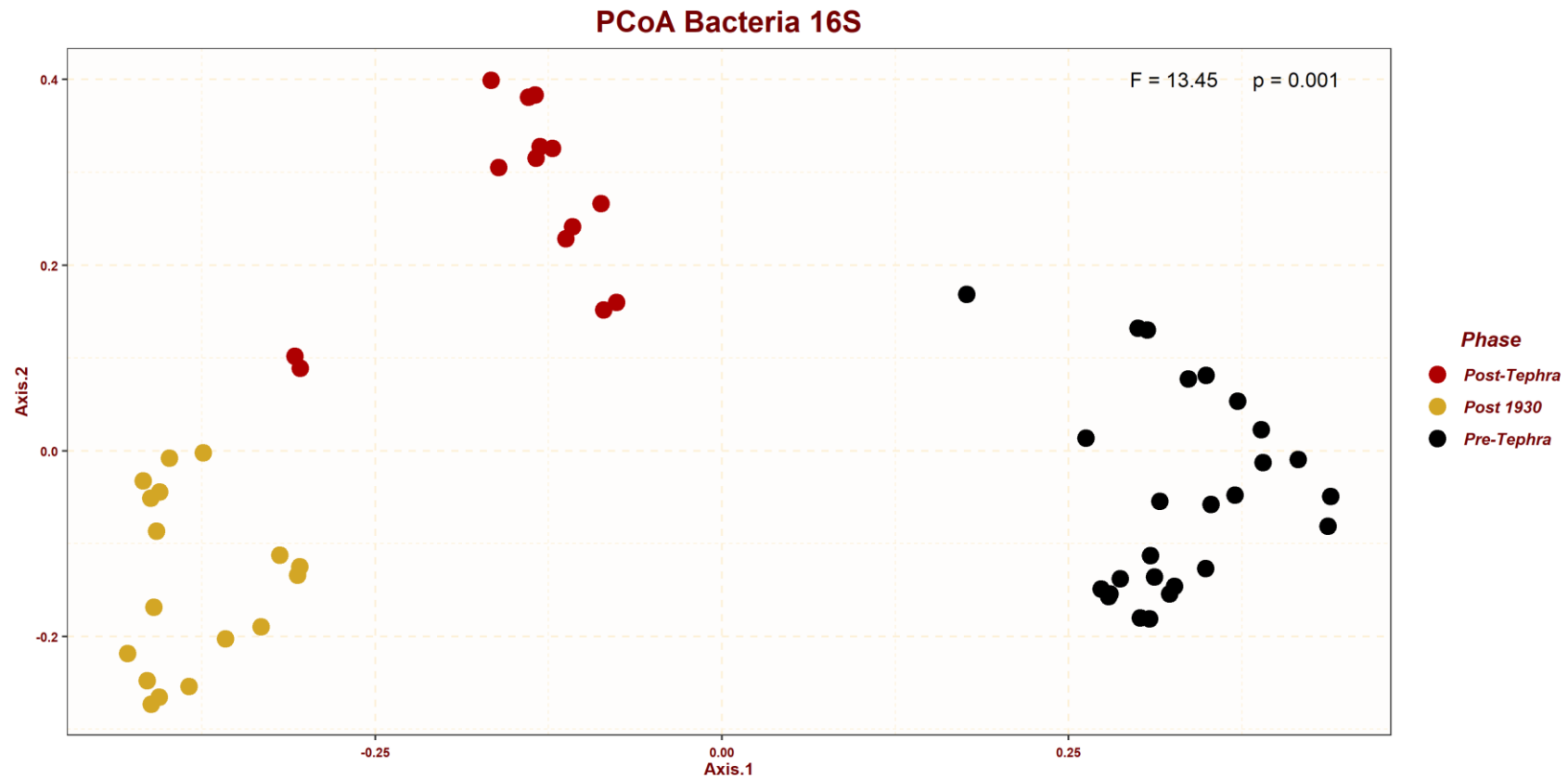


Figure 22: A plot of the PCoA ordination computed from a bray-curtis dissimilarity matrix. Points are coloured by phase (Red = Post-Tephra, Yellow = Post 1930, Black = Pre-Tephra). Results of the PERMANOVA run on this ordination are superimposed (an F statistic of 13.45 and a p-value of 0.001).

3.6.3 Alpha Diversity Analysis

There were significant differences between the three-time phases (Pre-Tephra, Post-Tephra and Post 1930) with respect to the observed diversity (Kruskal-Wallis test chi square = 34.76, $p < 0.001$; Figure 23). The Post 1930 phase had a richness 3-4 times greater than the Post-Tephra and Pre-Tephra phases.

There were also significant differences among the phases with respect to Shannon diversity (Kruskal-Wallis test chi square = 39.32, $p < 0.001$; Figure 23). The Post 1930 phase had the highest degree of diversity, followed by the Post-Tephra and Pre-Tephra communities.

There was less variation in Simpson diversity among the phases for this dataset compared to the other two measures, however there were still significant differences between the phases (Kruskal-Wallis test chi square = 34.76, $p < 0.001$).

A pairwise, post-hoc, Nemenyi-Kruskal test was also run on all three datasets to identify specifically which groups differed from one another. For observed richness there were significant differences between the Post 1930 and Post-Tephra ($p = < 0.001$) and Post 1930 and Pre-Tephra phases, but there was not sufficient evidence to suggest the Post-Tephra and Pre-Tephra phases were significantly different from one another ($p = 0.74$). Among the Shannon index there were differences between all three groups (Post 1930 vs Post-Tephra, $p = 0.037$, Post 1930 vs Pre-Tephra, $p = < 0.001$, Post-Tephra vs Pre-Tephra, $p = 0.009$), whereas the only identified significant difference, with respect to Simpson diversity was between the Post 1930 and Pre-Tephra ($p = < 0.001$) and Post-Tephra and Pre-Tephra ($p = 0.006$) phases.

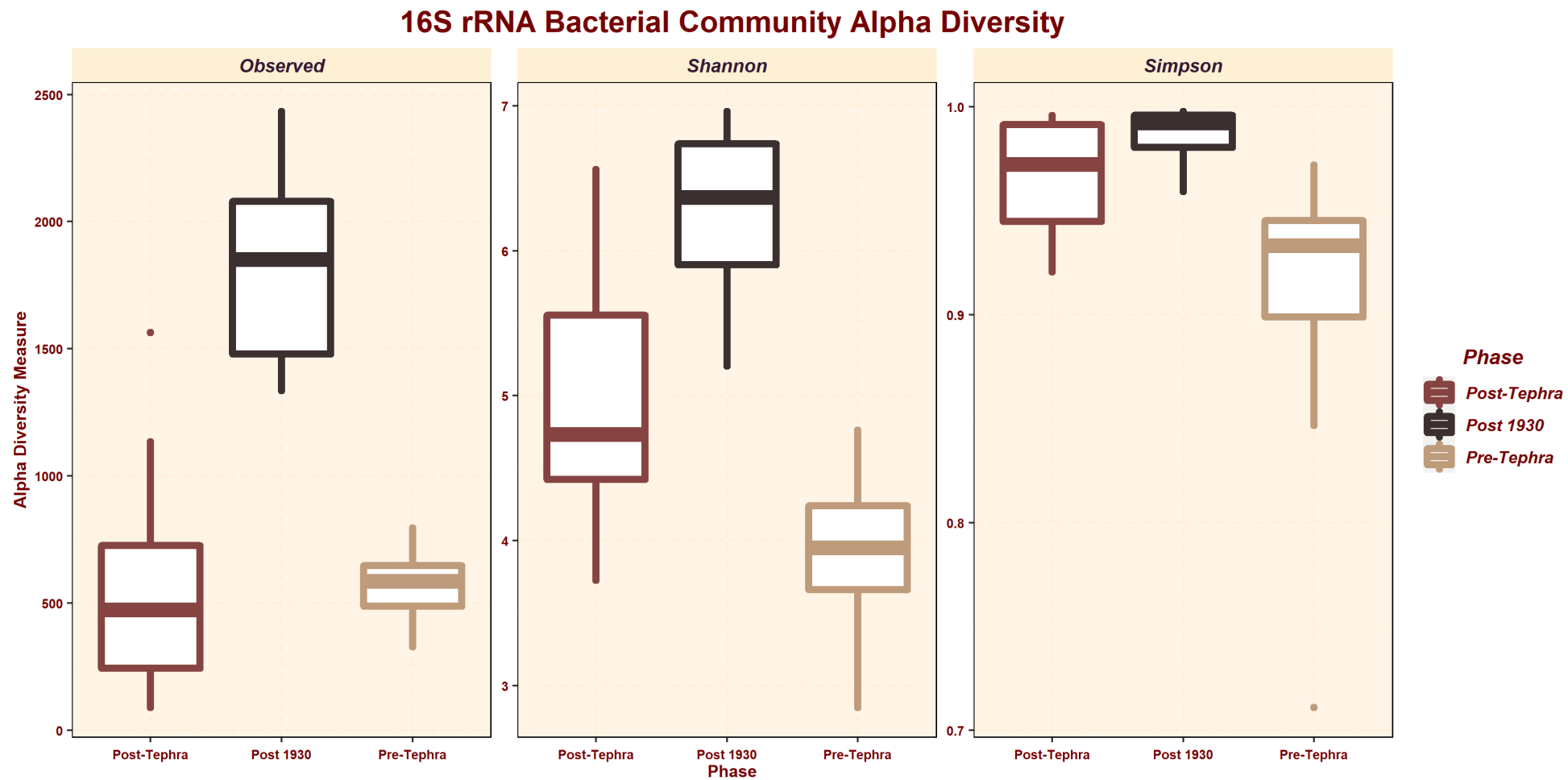


Figure 23: A multi box-plot depicting Observed (actual richness), Shannon and Simpson diversity index values for the 16S rDNA dataset across the three time phases of Post-1930 (Black), Post-Tephra (Brown) and Pre-Tephra (Beige). The y axis labels represent actual number of species (reads) for the observed measure and calculated index values for the Shannon and Diversity measures

3.6.4 Indicator Species Analysis

The results of the multipatt indicator species analysis for the 16S rDNA dataset identified significant classes of bacteria that are associated with different time phases in the history of Lake Okataina.

In the Pre-Tephra phase, four bacteria classes were identified as indicator “species”. These included *Bacilli*, *Symbiobacteriia*, *Desulfitobacteriia* and *Gammaproteobacteria*.

In the combined Post-Tephra and Post 1930 phase (Post-Tephra + Post 1930), three classes were deemed indicator species. These were *Campylobacteria*, *Gammaproteobacteria* and an unclassified organism at class level (*Unclassified Phylum Sva0485*). These phases were combined here as the multipatt analysis only found *Gammaproteobacteria* as an indicator class for the Post-Tephra phase (on its own).

In the Post 1930 phase, six classes of bacteria were identified as indicator species. These classes were *Anaerolineae*, *Desulfobacteria*, *Gracilibacteria*, *Myxococcia*, *Thermodesulfovibrionia* and *Gammaproteobacteria*.

Table 3: Summary of the indicator species (at Class level) for the different phases in the 16S Bacteria dataset

Post 1930	Post-Tephra + Post 1930	Post-Tephra	Pre-Tephra
<i>Anaerolineae</i>			<i>Bacilli</i>
	<i>Campylobacteria</i>		
<i>Desulfobacteria</i>			<i>Desulfitobacteriia</i>
<i>Gammaproteobacteria</i>			
<i>Gracilibacteria</i>	<i>Gammaproteobacteria</i>	<i>Gammaproteobacteria</i>	<i>Gammaproteobacteria</i>
<i>Myxococcia</i>			
<i>Thermodesulfovibrionia</i>	<i>Unclassified_Phylum_Sva0485</i>		<i>Symbiobacteriia</i>

The *Gammaproteobacteria* class appeared an indicator species in the different phases in the multipatt indicator species analysis. *Gammaproteobacteria* were isolated across the different phases to identify significant indicator species (at Genus level). The multipatt analysis identified a number of different species across the phases (Figure 24 and Table 4).

Table 4: Summary of the indicator species, multipatt analysis run on the Gammaproteobacteria class for the different phases in the 16S rRNA Bacteria dataset (species are identified to Genus level, A and B represent different species with the same Genus)

Post 1930	Post-Tephra + Post 1930	Post Tephra	Pre-Tephra
	<i>Pseudomonas</i>	<i>Massilia</i>	Sideroxydans (A)
			Sideroxydans (B)
	<i>Janthinobacterium (A)</i>	<i>Janthinobacterium (B)</i>	
Methylobacter (A)			<i>Ralstonia</i>
			<i>Methylobacter (B)</i>
	<i>Herminiimonas (A)</i>	<i>Herminiimonas (B)</i>	
			<i>Gallionella</i>

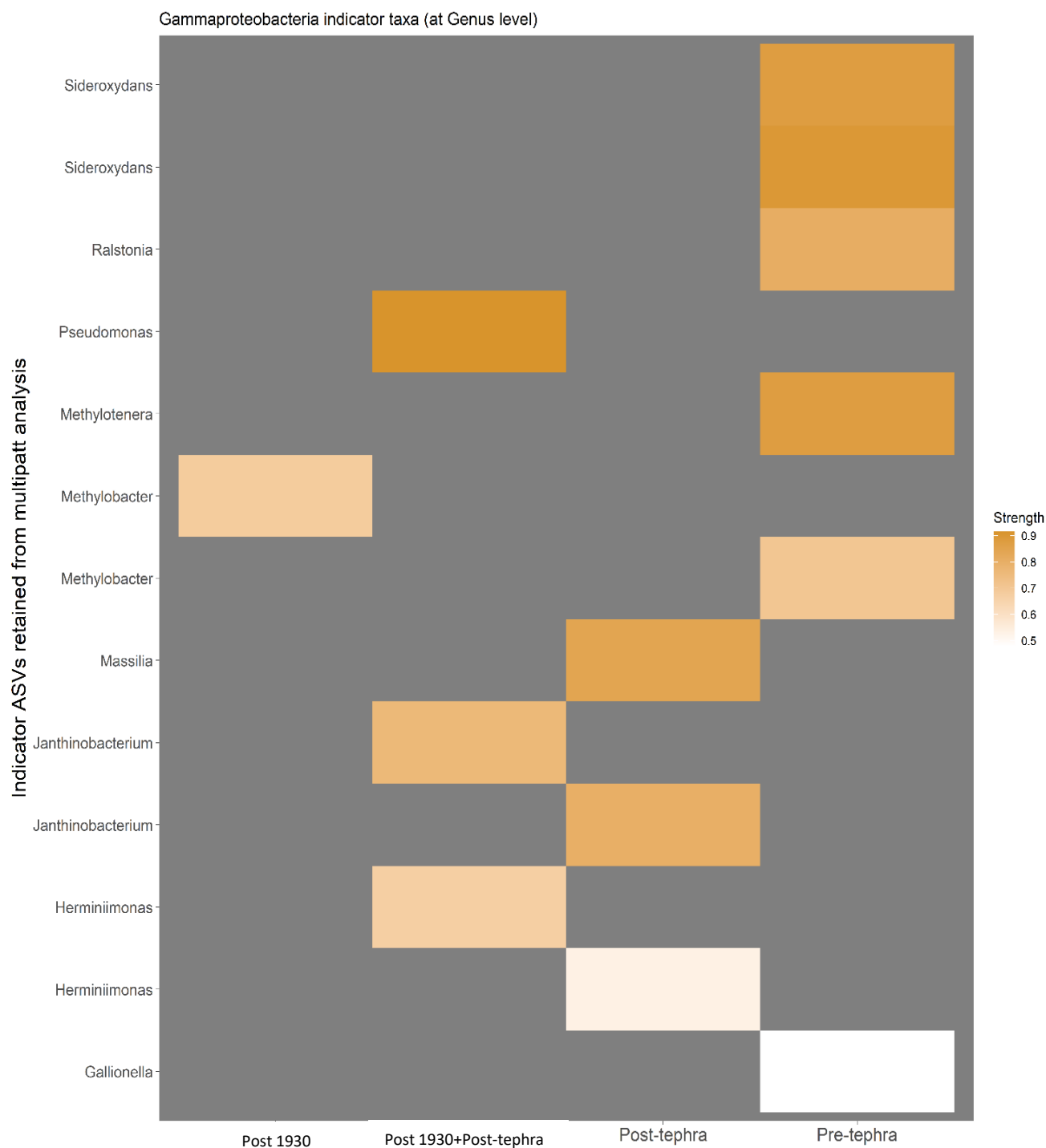


Figure 24: Heatmap from the multipatt, indicator species analysis run on the *Gammaproteobacteria* class across the four different phase “groups” (where ASV = amplicon sequence variant).

3.7 Chironomids

A range of changes were observed in the species of chironomids identified in the Lake Okataina system (Figure 25). Abundances of *Paucispinigera*, *Polypedilum*, *Ablabesmyia*, *Tanytarsus vespertinus* and *Tanytarsus funebris* type C are more abundant before the eruption whilst *Chironomus* abundance is low. The abundances of *Cricotopus aucklandesis* and *Corynocera* appear relatively consistent, before and after the eruption. Abundances of *Paucispinigera* remain high following the eruption, and species of *Chironomus* and *Chironomini* early instar become more abundant. Both species of *Tanytarsus* decrease in abundance sharply following the eruption.

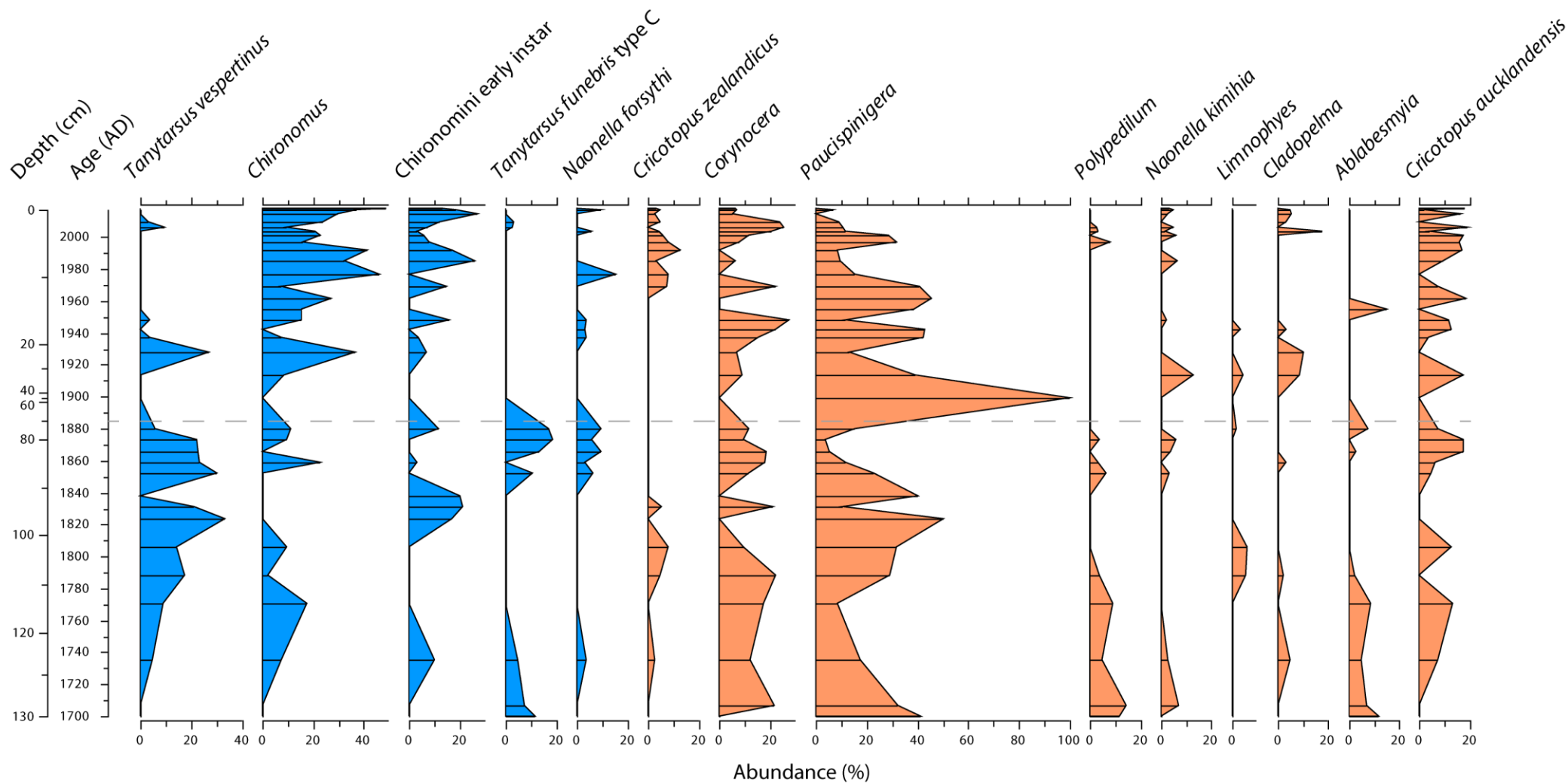


Figure 25: A downcore, stratigraphic plot of relative chironomid abundance (by species). Cool temperature species are coloured blue, warm temperature species red.

The ordination identified two distinct clusters associated with two of the phases in this study (Pre-Tephra and Post 1930), while a third cluster of points was less obvious (Post-Tephra; Figure 26A). The PCA bi-plot (Figure 26B), highlights important species driving the clusters. The arrows suggest that species of *Chironomus* (Ch), *Cricotopus Zealandus* (CZ), as well as *Chironomini* early instar (Che) shape the Post 1930 community while *Tanytarsus vespertinus* (Tvs) and *Tanytarsus funebris* (TC) appear to drive the Pre-Tephra community.

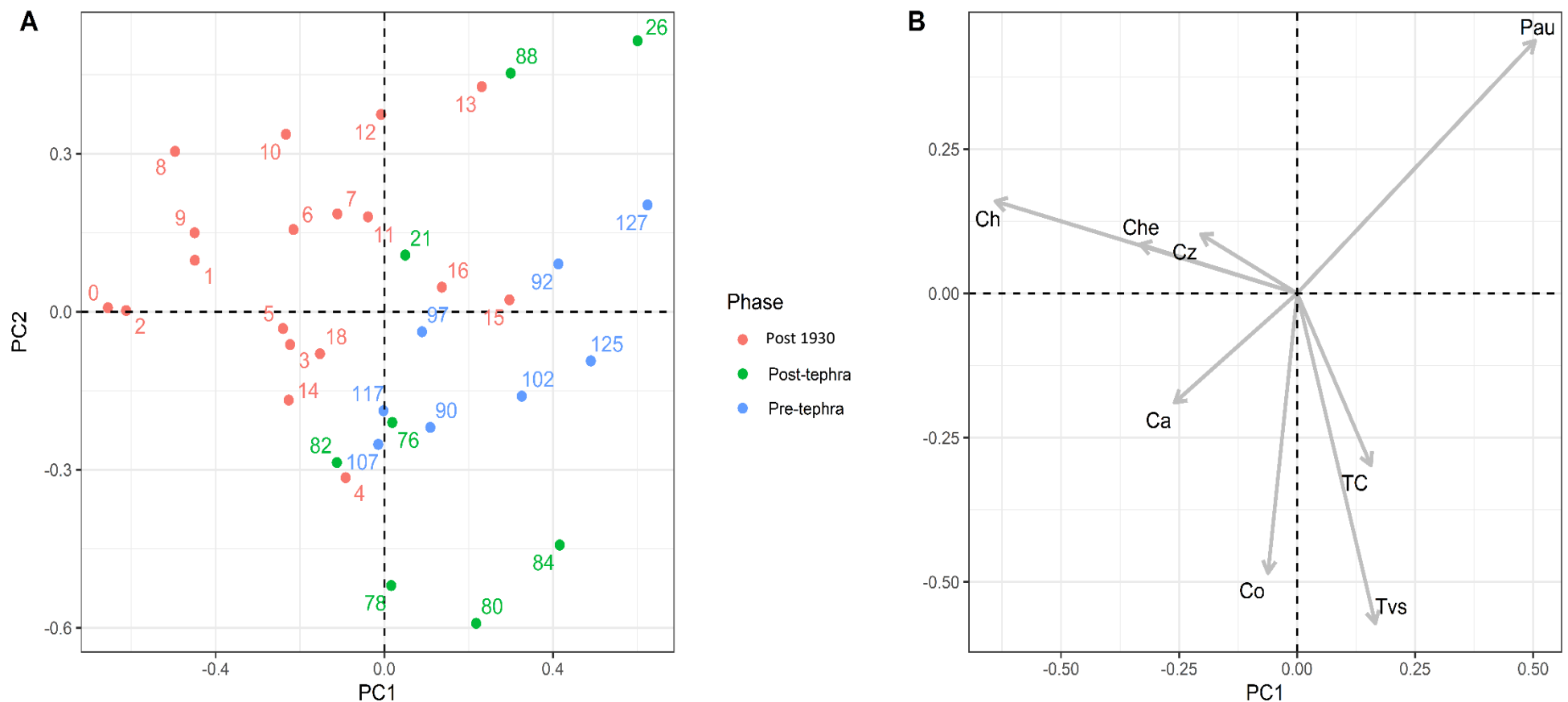


Figure 26: A PCA plot (A) depicting different clusters of chironomid samples across different phases in the study and a PCA bi-plot (B) highlighting significant species that drive these observed differences

Chapter 4: Discussion

4.1 Prelude

Understanding the current health of a lake system and the triggers that control their biophysical processes is challenging and can require long term monitoring. The following sections discuss the possible mechanisms and environmental drivers responsible for the system changes observed in Lake Okataina over a period of approximately 300 years. The sections are split into the three main time phases described for this study; the Pre-Tephra phase, the Post-Tephra phase and the Post 1930 phase and are described chronologically.

Regime shifts occur when a disturbance perturbs a system enough to force a widescale change to the characteristics and properties of that system, resulting in a change of state (Folke et al., 2004; Scheffer et al., 2012). Geochemical and palynological evidence outlines the extent to which the 1886 Mt Tarawera eruption impacted the catchment and system of Lake Okataina. This event initiated both instantaneous, and long-lasting, multi-trophic level responses in the ecosystem of Lake Okataina. These phases are framed as different stages in the regime shift model shown below in Figure 27.

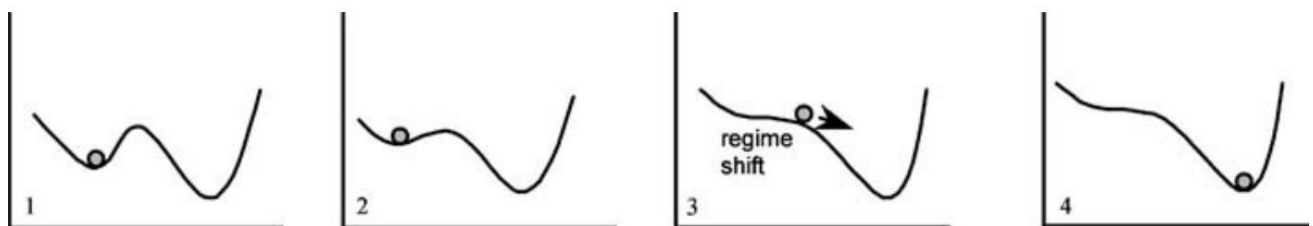


Figure 27: The transition of a “steady state” ecosystem (1) into a period of transition (2) and a complete “regime shift” (3) into a “new state” (4), (Folke et al., 2004)

4.2 Pre-Tephra phase – The “steady-state”

For approximately 180 years prior to the Mt Tarawera eruption, Lake Okataina was a stable and relatively undisturbed environment. Despite the previous volcanic disturbances many centuries before (– the most recent notable event being the Kaharoa eruption in AD 1314), Lake Okataina was largely in a steady state. The surrounding vegetation in the catchment was relatively pristine and was dominated by large, native species of trees such as *Dacrydium cupressinum*. Within the lake, green algae (*Botryococcus*) were abundant. Primary productivity within the lake was high, as indicated by elevated RABD chlorophyll-a levels during this phase. The Si/Ti ratio from the ITRAX dataset is also relatively high, indicating that there is likely a higher abundance of biogenic silica in the system (a proxy for diatoms). Caution must be exercised here, as the effects of detrital elements may be affected by grain size, diagenesis or other volcanic processes (Croudace and Rothwell, 2015). The depositional environment is thus an important control on the specific proxy selection. For this thesis, I interpret Si/Ti as a genuine indicator of diatom productivity, but this needs to be confirmed by future analyses (e.g., smear slides, diatom counts).

Levels of P were also high and the ratio of Fe/Mn was low during this phase, indicating aerobic conditions. The community composition of bacteria was dominated by species of *Bacilli* and *Symbiocateriia*, together with *Gammaproteobacteria* and measures of alpha diversity were low.

Community stability is defined as a combination of ecological resilience and resistance to change (Pimm, 1984). The driving mechanisms behind community structure can be environment, species or situation specific, which makes their interpretation and understanding complex and often difficult. Microbial communities are one of the key lower-order contributors to flows of energy and a range of biogeochemical cycles in aquatic ecosystems. Understanding of their structure and functioning is key in assessing wider scale system changes. Bacteria freely interact with other groups in their associated food web systems and often engage in symbiotic and synergistic relationships with other organisms as a result. In the Pre-Tephra phase, the degree of primary productivity and the abundance of diatoms and algae is high.

Planktonic bacterial and algal communities share a similar substrate (and thus niche) in lakes and their close proximity can lead to interspecies relationships between the two (Gleason et al., 2008; Wurzbacher et al., 2010). Importantly, algae can provide resources that bacteria are unable to acquire on their own. These predominantly physiological-nutritional relationships help to shape microbial communities in Lake Okataina. In this study, the relative abundance of algae is highest in

the Pre-Tephra phase and this mirrors the relative abundance and presence of two classes of bacteria (*Bacilli* and *Symbiobacteriia* – both of the phyla *Firmicutes*).

These classes, particularly *Symbiobacteriia*, are believed to prosper in relatively undisturbed environmental conditions, where they are free to engage in symbiotic relationships with other organisms – such as algae (Callieri, 2008).

The chironomid community was largely dominated by species of *Paucispinigera* and *Tanytarsus vespertinus*. There is limited literature on these species of chironomids and it is thus difficult to infer anything about the characteristics of the lake environment in this phase, based purely off their presence. Of the little that is known, *Paucispinigera* are believed to favour relatively warm, organic and productive lake systems, whereas *T. vespertinus* are known to favour cooler and clearer lakes (Dieffenbacher-Krall et al., 2007).

4.3 Post-Tephra phase – The “regime shift”

Lake Okataina drastically shifted following the eruption of Mt Tarawera becoming markedly different from the stable, Pre-Tephra environment described above.

The ITRAX data demonstrates that Lake Okataina experienced significant geochemical disturbance after the eruption. K, S, Ca and Ti all increased immediately following the eruption with the deposition of tephra and the resulting in-wash. This likely altered the limnetic properties in the lake water column. These types of elements commonly settle on the lake-bed and can alter benthic and diagenetic processes such as nutrient cycling of N and P (Ayris and Delmelle, 2012). The deposition of tephra on the lake-bed can in some cases, create an impermeable barrier that severely impedes the exchange of nutrients across the sediment-water interface (Barker et al., 2000). Other soluble elements commonly present in tephra (and shown to peak following the eruption in this study), such as As and Mn, also play a role in ecosystem functioning in aquatic systems as increased concentrations can inhibit rates of biological growth (Bruland et al., 1991; Chakraborty et al., 2010).

The observed changes in the Fe/Mn and Ti/Mn ratios, indicate changes in the oxygenation of the water column (Naeher et al., 2013; Żarczyński et al., 2019). Oxic conditions are indicated by lower Fe/Mn or Ti/Mn values (as seen in the Pre-Tephra phase) and anoxic conditions relate to higher values (as seen in the Post Tephra- Post 1930 phases). Lake Okataina thus appears to undergo a significant transition from a relatively oxygen rich environment to one that is comparably oxygen limited.

This change marks a regime shift, commonly defined as an abrupt, large and persistent change to the structure and function of ecosystems, driven by either gradual “press” or sudden “pulse” disturbances to the system (Folke et al., 2004; Scheffer and Carpenter, 2003; Scheffer et al., 2012). In lake systems, like Lake Okataina, this transition can be hard to reverse, and a return to oxygen-rich conditions can take time.

The palynological record further highlighted a shift in the characteristics of Lake Okataina’s wider catchment, by outlining an increased abundance of *Cyathea smithi* and *Cyathea dealbata*. Both these plants are species of ferns which are highly resistant to disturbances and often colonise freshly perturbed environments where other types of vegetation struggle to grow and survive (Richardson et al., 2014). The increased amount of fern spores also likely reflects an increase in the degree of terrestrial in-wash following the eruption, as fern spores are relatively hardy and resistant to mechanical wear.

Following the eruption, the RABD index values decreased markedly representing a fall in the production of chlorophyll-a within the water column; the Si/Ti ratio also falls, indicating a decreased abundance of diatoms. There was also a notable decrease in the abundance of *Botryococcus*. Using all these values as a proxy for primary productivity and phytoplanktonic biomass, there is evidently a major disturbance to this community.

Phytoplanktonic communities are reliant on the availability of light and nutrients for growth and survival (Eilers and Peeters, 1988; Kurenkov, 1966; Modenutti et al., 2013). The increased supply of terrestrial and geochemical material to the lake following the eruption, may have been expected to increase the availability of nutrients and thus promote greater rates of nutrient cycling and nutrient uptake by phytoplankton. As highlighted by the response of P to the eruption, this is not the case in Lake Okataina. Contrary to this, the addition of tephra appears to have increased the concentration of total dissolved solids within Lake Okataina.

The influx of material potentially diluted the amount of chlorophyll-a in the system and may have initiated a reduction in the availability of light to the system. This appears to have driven a significant shift in primary productivity within Lake Okataina.

This type of disruption to a key, base component of the lake food-web system, likely exerted significant bottom-up pressure on other organisms in Lake Okataina, driving a major change in the entire biological system.

The bacterial community composition of Lake Okataina changed dramatically following the eruption of Mt Tarawera. This pulse disturbance perturbed the bacterial community and initiated a series of interesting shifts in its structure and composition. The reduced abundance of algae, as indicated by the relative decreases in the RABD and Si/Ti indexes and the abundance of *Botryococcus*, initiated a shift away from symbiotic bacteria (such as *Bacilli* and *Symbiobacteriia*) towards a new microbial community, dominated by bacteria that are suited to reduced oxygen environments. Populations of *Bacilli* and *Symbiobacteriia* disappeared completely and failed to return to their pre-eruption levels. Contrastingly, populations of *Campylobacteria*, *Anaerolineae* and *Thermodesulfovibrionia* increased. The results from the PCoA analysis reaffirm that the bacterial communities in the Pre-Tephra and Post-Tephra phases are significantly different from one another. These shifts in the bacterial community, help to regulate and maintain the shift to an anoxic state.

In the anoxic Post-Tephra system, sulphur reducing bacteria play an important role in the decomposition and remineralisation of the living, organic biomass. *Thermodesulfovibronia* are one of the key anaerobic bacteria that reduce sulphate to sulphide in lake systems (Jørgensen, 1982). These bacteria begin to appear in Lake Okataina following the eruption, after the in-wash period that triggers a flux in available sulphur. They have significant importance for element and nutrient cycles within ecosystems and for other organisms that rely on these processes for growth and survival (Holmer and Storkholm, 2001; Peiffer, 1998; Rudd et al., 1986). In limnetic systems, the mineralisation of organic matter on the lakebed is controlled by a number of microorganisms, including bacteria. If this sediment is oxic in nature, oxidation processes occur through aerobic processes. Oxygen, however, is often consumed rapidly (as it appears to be in Lake Okataina following the deposition of tephra) and it is here that the anaerobically driven process of sulphur reduction takes over. The rates of sulphur cycling are controlled by a range of factors that can be hard to isolate. The supply of organic material to a lake and the actual concentration of available sulphur within the water column, appear to exert leading controls on rates of sulphur cycling processes (Holmer and Storkholm, 2001; Urban et al., 1994).

Species of *Paucispinigera* remain relatively high following the eruption, however the abundance of *T. vespertinus*, *Polypedilum* and *T. funebris* drops markedly. The abundance of *Chironomus* increases substantially in this Post-Tephra environment, further highlighting the shift towards a more deoxygenated system. Previous studies have suggested that species of *Chironomus* thrive in lower-oxygen environments, where the overall quality of the water is also lower (i.e. mesotrophic and eutrophic lakes), (Schakau, 1993; Woodward and Shulmeister, 2006).

Following the addition of tephra and the subsequent in-wash to the system, a new series of oxide forming elements (e.g. Ca, Fe and Mn) are added to the water column. These elements may have scrubbed the system of available oxygen, favouring a reducing environment. Furthermore, sulphur reducing bacteria (in the sediment), capture electrons to produce chemical energy, further driving a shift towards reducing conditions. The large and instantaneous removal of phytoplankton from Lake Okataina following the eruption (highlighted by the hyperspectral results) would also eliminate oxygen added to the system via photosynthesis carried out by algae and macro-phytic plant communities (Hilt et al., 2011). Finally, the addition of Ca and other elements could create a more alkaline system than in the Pre-Tephra environment, further prompting a shift to a reducing environment (Casas et al., 1998).

4.4 Post 1930 phase – The “new state”

After the initial disturbance caused by the eruption, the resulting deposition of tephra and the in-wash period, the biophysical system of Lake Okataina still remains significantly different from the original environment observed in the Pre-Tephra phase.

The system still appears to be largely devoid of oxygen, as the Fe/Mn and Ti/Mn ratios remain low. Influences from the wider catchment appear to exert more pressure on the system than previously. The abundance of As begins to increase, as does the abundance of P right at the top of the core. This could signify a return to a Pre-Tephra environment. Similarly, the RABD index values begin to dramatically increase here in this phase too, even surpassing levels observed in the initial Pre-Tephra phase. Interestingly though, the Si/Ti ratio (proxy for diatoms/algae) remains relatively stable and low during this phase, which implies that the changes in the RABD and P indices are not driven by changes in these communities but rather by something else in the system. The dominant form of algae in the system is no longer diatoms, however further work targeting specific genes together with the analysis of pigments would assist in understanding the observed shifts here.

The appearance of *Campylobacteria* in the bacterial community in this phase, suggests that the catchment is no longer completely pristine, as this class of bacteria are commonly found in the intestinal gut systems of large, domesticated animals such as cattle (Horrocks et al., 2009). This is to be expected as although the catchment of Lake Okataina is relatively undisturbed and pristine, there is a small amount of agriculture and pastoral farming that occurs in the catchment and this has trickle down effects for the lake system.

The introduction of *Pinus* to the catchment and the clearance of native forest around the lake margins (Figure 28), also signifies a shift away from a natural, pristine catchment. Additionally, there are now also numerous wild mammals in the catchment such as goat, deer, pig and wallaby (Kpodonu et al., 2016). The increase in P, also seen in the Post 1930 phase in the study is likely fuelled by increased runoff and inputs from increased erosional processes as a result of these catchment changes too.



Figure 28: An aerial photograph from 1945 depicting extensive land clearance along the southern shores of Lake Okataina, highlighting a move away from a natural, pristine catchment

The bacterial community also appears to increase in diversity, as many new classes of bacteria appear for the first time in the record. This is outlined by the key measures of alpha diversity for the bacterial community being highest during this Post 1930 phase. The theory of functional equivalency or redundancy could apply here, that is, the phenomena that multiple different species (or classes) can share very similar or identical roles in the ecosystem functionality in their given environments (Allison and Martiny, 2008).

The post disturbance, semi-settled environment that we see in this Post 1930 phase has a host of new available niches and ecosystem functions that can be taken up by a range of new bacterial classes. Many of these roles are similar however, and by applying the concept of functional redundancy, instead of one bacterial class filling this niche, we see multiple classes do so, in turn promoting an increase in diversity. Sulphur reducing bacteria (*Thermodesulfovibronia* and *Desulfobacteria*) make up an even greater proportion of the bacterial community in this phase, as the system remains in an anoxic state. In the chironomid community, the abundance of *Chironomus* species during this phase, again signifies a shift to an oxygen depleted environment as they can tolerate low oxygen conditions (Dieffenbacher-Krall et al., 2007).

Increased microbial diversity in the Post 1930 phase of this study could also be driven by the introduction of predatory species of fish such as Rainbow Trout (*Oncorhynchus mykiss*). Trout have been shown to have significant implications for limnetic processes such as nutrient cycling in established lake systems (Liu et al., 2009; Perez-Fuentetaja et al., 1996). The predatory grazing behaviours of fish play an important role in determining the structure of lower trophic level organisms such as phytoplankton and zooplankton. The impacts of these fish compound the changes and pressures exerted by the already disturbed environment and create further new niches and opportunities for new classes of bacteria. Given the close temporal association of the introduction of trout and the eruption, it is very difficult to disentangle the impacts of the fish introduction from the impacts from the eruption. Further work is therefore required here to better understand this relationship.

4.5 Comparing to previous literature on Lake Okataina

Previous work by Kpodonu et al. (2016) on the system of Lake Okataina, supplements the understanding of the regime shift identified in this thesis. Kpodonu et al. (2016), focused on changing water quality within Lake Okataina following the 1886 eruption and the role introduced species within the catchment, play in moderating and regulating the system following disturbance. The results of their study supported the idea of a regime shift following the eruption, driven by changes to nutrient pathways and the reduced availability of oxygen in the system. They suggest that diatom abundance and primary productivity has decreased in the last 150 years following the eruption and that changes to other proxies (such as P speciation) are driven by nutrient and sediment fluxes in the system. They posit that the changes and state of the new system (post regime shift), following the disturbance caused by the eruption, can also be explained by the role of mammalian predators and introduced species of trout (Kpodonu et al., 2019).

Lake Okataina has been subject to extensive volcanism in its relatively short history and despite this, pre the Tarawera eruption, the lake appears to be in a relatively steady state. Kpodonu et al. (2019), indicated that the effects of the eruption appear to have been more transient and temporary on the system and the true driver of the regime shift is the increased influence of introduced species in the catchment. They link introduced terrestrial species to increased rates of erosion within the catchment and hypothesise that species of trout alter rates of primary productivity through stimulating algal production via the regeneration of benthic and terrestrial nutrients (Kpodonu et al., 2019).

The results of this thesis highlight that initial concentrations of P (prior to the eruption) were actually relatively high, which suggests that perhaps mammalian predators and trout are not the main or only controls on concentration of P, as suggested by Kpodonu et al. (2016).

Other previous literature also suggests that there are a variety of mechanisms through which inputs of tephra into lakes may cause changes in ecological systems and functioning. Telford et al. (2004) present evidence to suggest that despite the influx of material to a system following the deposition of tephra, stronger ecological changes follow when the P cycle is disrupted, irrespective of the source of any potentially new nutrients. Responses of diatom communities to changes in P (Telford et al., 2004), support this theory and highlight the role P cycling plays in the functioning of these systems.

4.6 Limitations

4.6.1 DNA variability and fragility

The use of environmental DNA as a paleoenvironmental indicator is still largely in its infancy and consequently, there remain a series of questions about its reliability downcore. There is currently limited understanding of the fragility of DNA compounds in sediments, particularly in older sediments (such as in the Pre-Tephra phase of this study). It can also be hard to associate genetic species with specific environments (particularly for bacteria) when compared with more conventional proxies such as the study of diatoms or chironomids (Harper et al., 2019). The implications for the interpretation of the resulting data can be significant. For instance, the observed lack of diversity in the Pre – Tephra samples could be more an artefact of degradation, compared to the much younger Post – Tephra and Post 1930 samples.

4.6.2 Classic paleo uncertainties

As with all paleoenvironmental research, the ability to actually prove the existence of “cause and effect” relationships is difficult. Paleolimnological studies that reconstruct lake system characteristics and community responses can be particularly problematic, as lake systems are highly complex. In most cases there are many environmental, ecological or bio-physical mechanisms responsible for the different changes observed in lake systems through time (Payne and Egan, 2019). The use of a multi-proxy approach goes some way to mitigating the risk posed here, but caution must still be exercised.

In the present study, there is clear evidence of changes to the geochemistry and shifts in the limnetic system of the lake; however, the ecological response is harder to interpret. There is little doubt that there are a series of significant shifts in the array of ecological proxies used in this study, but the causes of these shifts (as suggested in the discussion), should be treated as hypotheses rather than definitive explanations. Additionally, it is difficult to isolate eruption specific changes from wider catchment changes, especially in the upper sections of the paleo record.

4.6.3 Greater breadth of system

To further this study and better disentangle the response of the lake system to the eruption of Mt Tarawera, a greater range of ecological proxies could be used. Understanding of zooplankton community response to this event would help to piece together the ecological history of Lake Okataina. This could help to provide more context for the bacteria and chironomid community changes outlined in this thesis. An analysis of higher order organisms such as introduced species of fish, could also provide context for the observed changes we see in the Post 1930 and Post-Tephra phases of this study. Rainbow trout were introduced into the system following the eruption and understanding of their impact on rates of primary productivity and bacterial and chironomid community composition may prove interesting.

4.6.4 Ground truth hyperspectral data with eDNA to show aquatic plant changes/diatoms

Whilst the hyperspectral data provides some evidence for changes in primary productivity, further study is needed to fully understand which species are responsible for these shifts. Whilst the Si/Ti ratio provided by the ITRAX results appears to suggest that the changes observed in the hyperspectral index are within-lake related, specific understanding still remains limited. To improve knowledge here, targeted plant or eukaryotic algal genes could be analysed using eDNA metabarcoding to try and ascertain whether the fluctuations in the hyperspectral indices are driven primarily by changes to algal or aquatic macrophyte communities, or even changes to terrestrial vegetation in the catchment. This could then potentially provide a greater context for the other biological shifts we observe in the system.

Information on the origin of other extraneous material deposited in the lake system could also help to provide context for some of the ecological changes observed. The analysis of C/N ratios, for instance, could highlight whether material is sourced from a terrestrial or within-lake setting. This again could help with the interpretation of the data from the different ecological proxies used in this study.

Pigment analysis, another common method use in paleo reconstructions (Leavitt and Hodgson, 2002), would also help in determining which type of algae are responsible for the most recent increases in the chlorophyll-a observed in the hyperspectral data.

4.6.5 Chronology

The age-depth model for Lake Okataina has many constraints following the eruption of Mt Tarawera in 1886 with 25 ^{210}Pb and 2 radiocarbon samples (between 1886 and 2018). Below the tephra layer, there are no constraints and thus for the depths below this mark, the model is extrapolating using linear modelling, based off the CRS model (outlined in Section 2.1.4). Further work should attempt to find chronological constraints in this period of Lake Okataina's history to build a more accurate and well-informed age-depth model.

Chapter 5: Conclusion

The results of this research clearly highlight a substantial shift in the system of Lake Okataina following the eruption of Mt Tarawera. This change affected many different components of the geochemical, biophysical and ecological systems in Lake Okataina. Initiated by nutrient driven processes, this regime shift led to a move to a relatively deoxygenated environment and this appeared to persist for many years following the eruption. The lake itself is still considered oligotrophic in nature with a much higher water quality than other lakes in the region; however, the degree of deoxygenation still appears more severe in Lake Okataina than in other neighbouring lakes and a regional council report concluded that the lake experienced prolonged periods of anoxia in summer (B.O.P Regional Council, 2012).

The present-day system of Lake Okataina appears different to the environment characterised in the Pre-Tephra phase of this study and therefore appears to have adopted a new, independent stable state, unique from the previous, pre-eruption stable state. Levels of primary productivity appear similar to pre-eruption conditions and some of the geochemical proxies appear to be returning to their former states too, although, the community compositions of bacteria and chironomids appear markedly different. The summary multi proxy figure (Figure 29), highlights the simultaneous shifts that ecological communities faced in response to the eruption. Fluctuations in primary productivity (A), bacterial community composition (B) and two key species of chironomid (C and D) clearly outline how the regime shift in Lake Okataina, impact multiple trophic levels. More research, addressing many of the points detailed in the limitations (above) is required to fully understand these changes and create a more holistic record of environmental change in Lake Okataina.

Additionally, many other lakes in this region were impacted to varying degrees by the Mt Tarawera eruption. The depth and consistency of the tephra varies markedly in these systems. Future research could focus on undertaking a similar study in some of these other lakes and explore whether the impact of the eruption and recovery rates are similar to that of Lake Okataina.

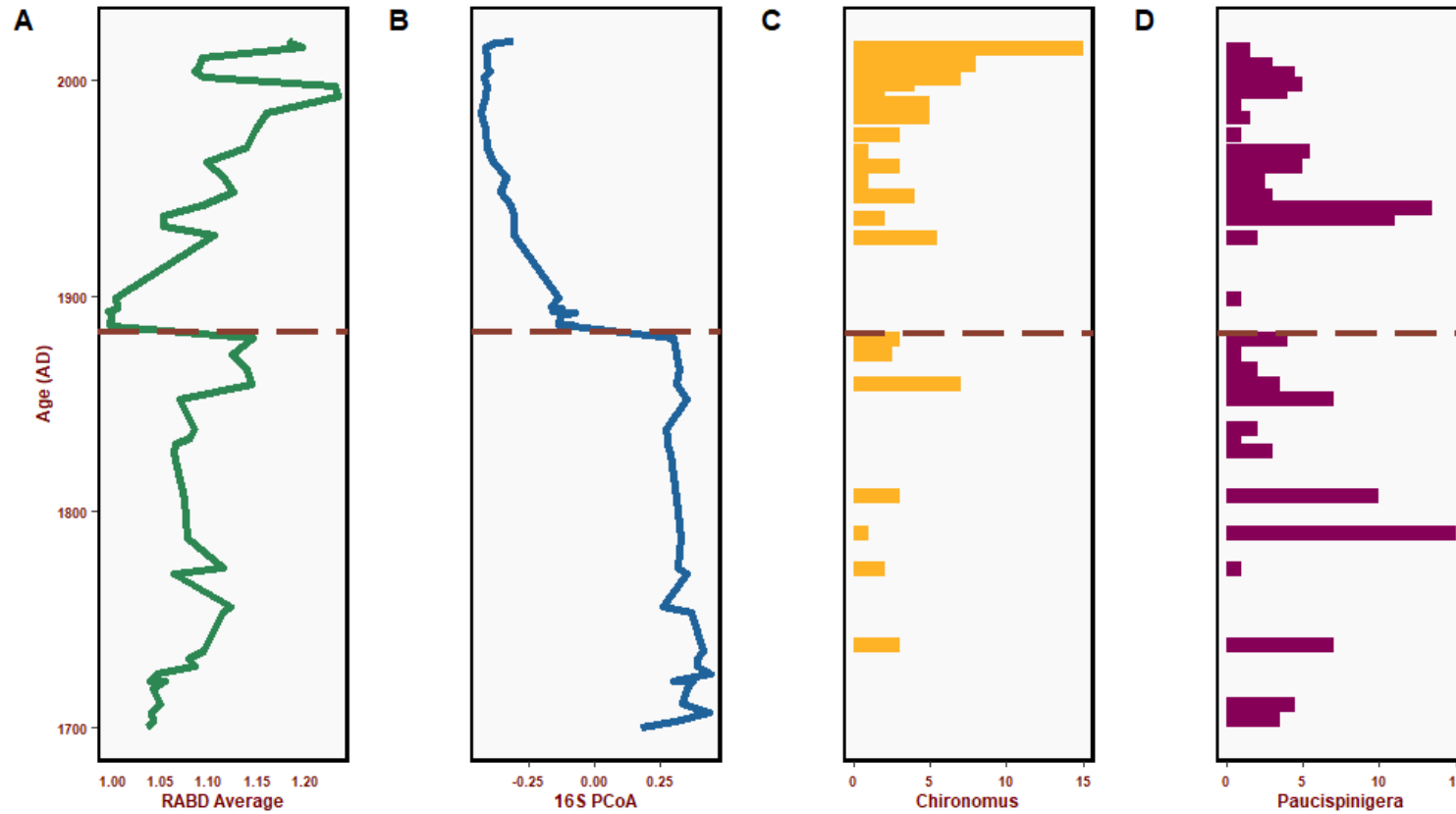


Figure 29: Multi-proxy summary of ecological change in Lake Okataina. A depicts changes in primary productivity, B depicts changes to the community composition of bacteria (variation explained by axis 1 in the PCoA ordination) and C and D depict changes to the abundance of two important species of chironomid

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Appendices

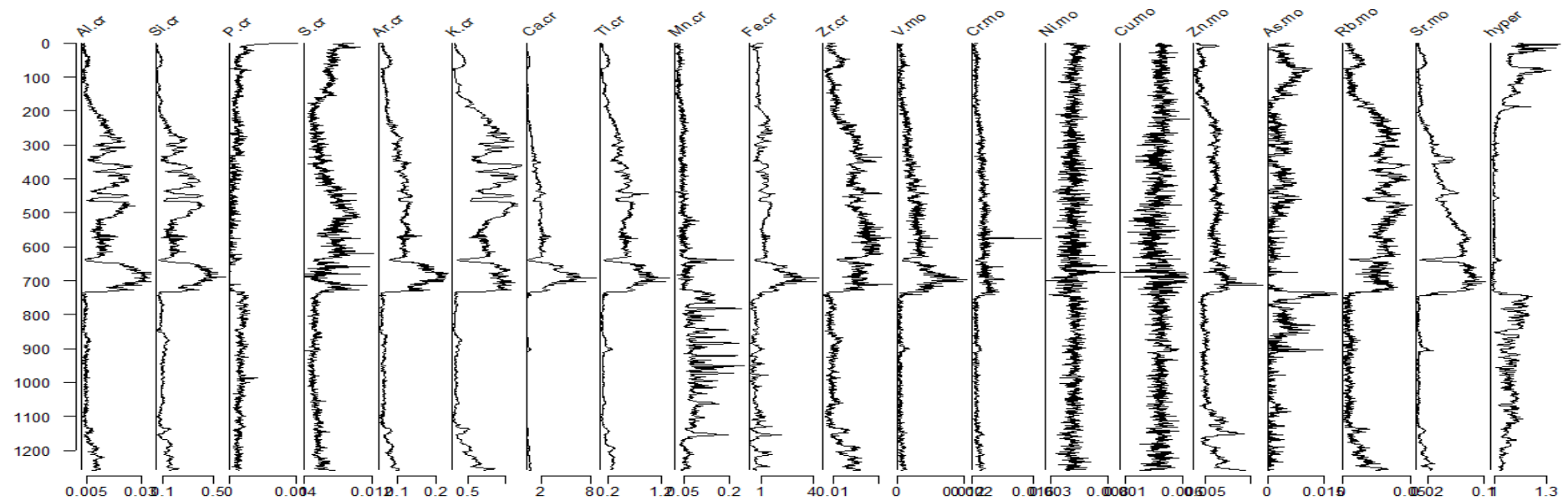


Figure 30: Full set of downcore elements picked up by the ITRAX analysis (plotted by depth from 0 – 1200mm)

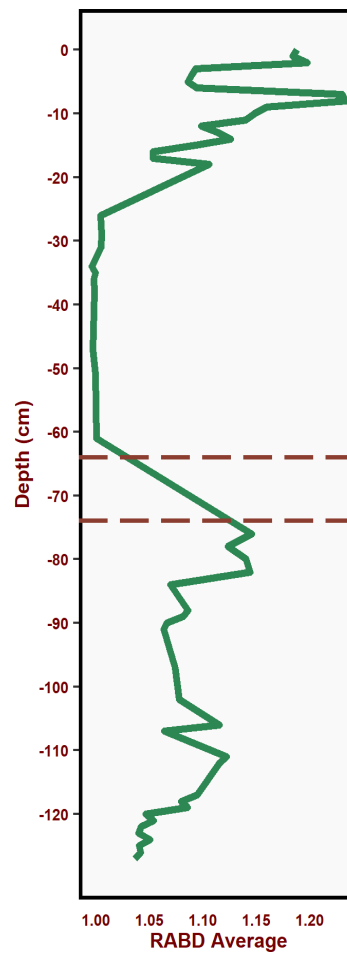


Figure 31: Downcore plot of RABD (660-670 nm) index values from the hyperspectral imaging analysis

Lake Okataina_LC4U_1A&2A

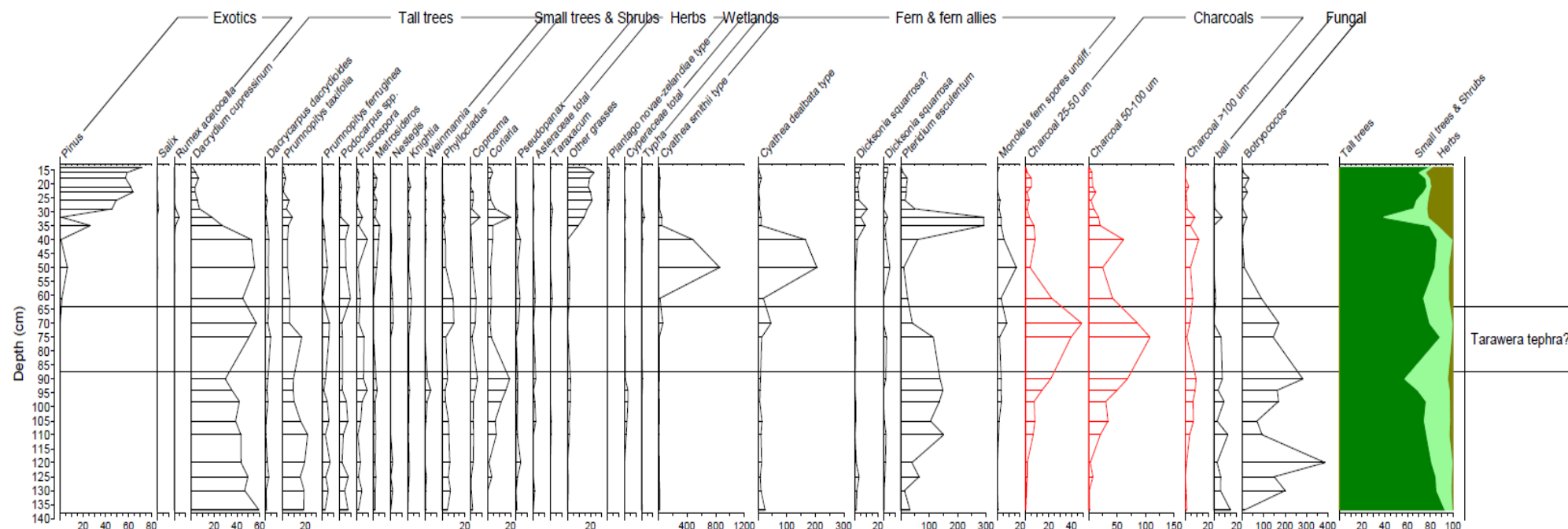


Figure 32: Full pollen summary from the LC4U core for Lake Okataina (produced by Xun Li – GNS Science)

Table 5: Results from the ^{210}Pb analysis, depicting sample depths, calculated ages (AD) and their associated errors

^{210}Pb Sample Depth	Age (AD)	^{210}Pb Error (Sigma) +/-
25 cm	1877	5.0
24 cm	1891	4.0
23 cm	1901	3.3
22 cm	1908	2.8
21 cm	1914	2.5
20 cm	1919	2.3
19 cm	1924	2.0
18 cm	1928	1.9
17 cm	1932	1.8
16 cm	1937	1.6
15 cm	1942	1.5
14 cm	1948	1.3
13 cm	1955	1.1
12 cm	1962	1.0
11 cm	1969	0.9
10 cm	1977	0.8
9 cm	1985	0.7
8 cm	1992	0.6
7 cm	1997	0.5
6 cm	2001	0.4
5 cm	2004	0.4
4 cm	2006	0.4
3 cm	2010	0.3
2 cm	2015	0.2
1 cm	2017	0.1

Table 6: Results from the radiocarbon analysis, depicting sample depths, calculated ages (AD) and the 95% confidence interval (CI)

RC Sample Depths	Age (AD)	RC 95% CI
30 - 31 cm	1890	1875 - 1905
39 – 40 cm	1895	1880 - 1910

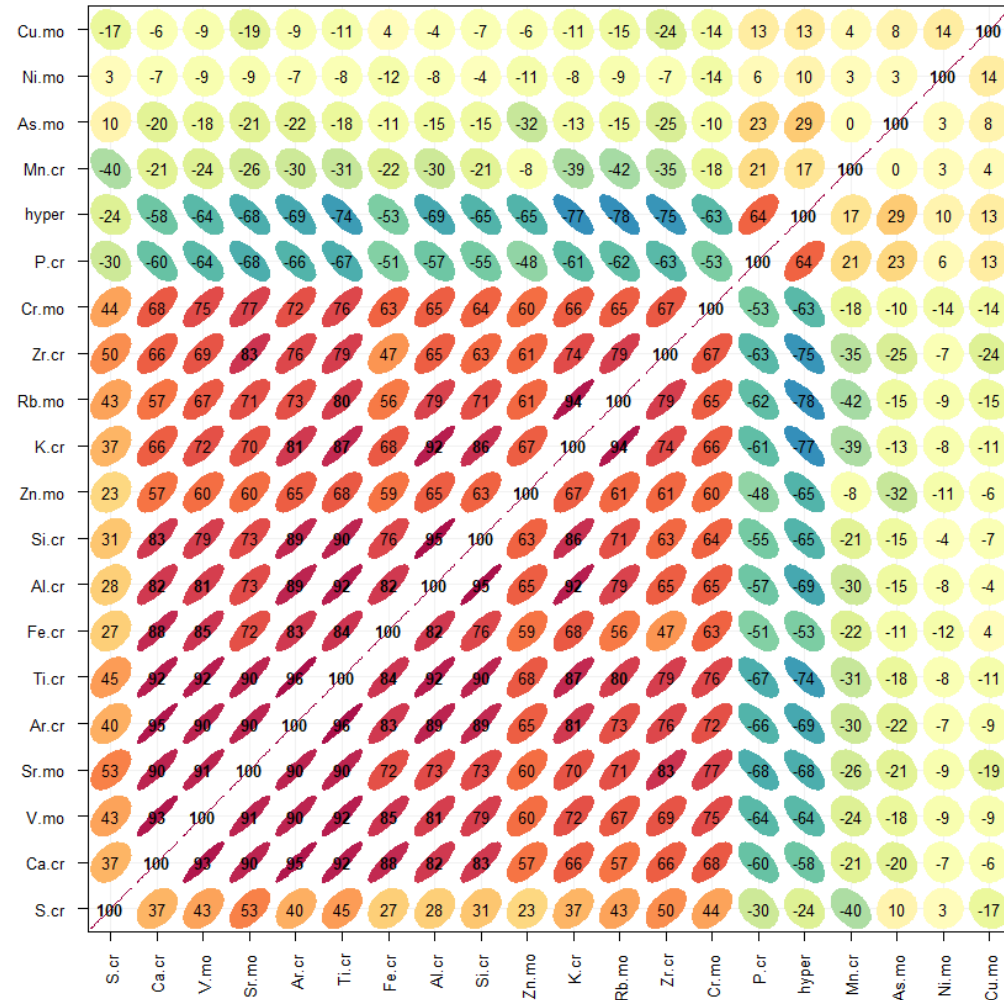


Figure 33: Correlation matrix for the ITRAX dataset

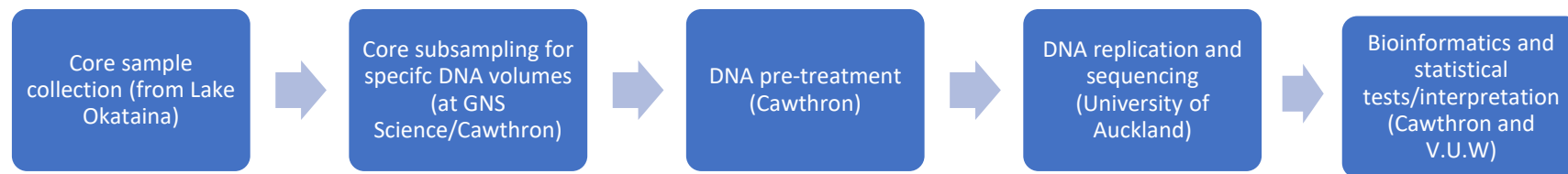


Figure 34: Flow diagram depicting the eDNA sampling and analysis process