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# The changing water quality of New Zealand's lakes in response to anthropogenic activities

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*Lake Emily (Chapters 4 and 5), Canterbury high country, looking north-east. November 2019 (J Short)*

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## Abstract

Humans have interacted with landscapes for millennia. However, degradation of environmental systems now occurs at unprecedented rates damaging ecosystem functioning and biodiversity. Arguably, freshwater ecosystems, particularly lakes, are the most affected. Continuing anthropogenic pressures have made it necessary to manage and protect lakes effectively, as well as understand their long-term structure and function. New Zealand is in unique location for investigating these matters as it was one of the last substantial landmasses settled by humans, approximately 750–800 years ago. The human-settlement history of New Zealand creates an opportunity to examine changing water quality of lakes while comparing the timing of these shifts with changes in land use.

Lakes in New Zealand are integral to the country's freshwater landscape, and many have elevated nutrient concentrations. There is substantial effort to prevent further enrichment, and understanding past water quality could assist with this process. To provide these insights, the sediment records of five lakes were analysed using diatoms as indicators of past water quality. The primary focus was to examine the responses of these lakes to changes in land use following Māori settlement, and later after European-style agriculture commenced.

Lake Oporoa, a small shallow lake in the Manawatū-Whanganui region of the North Island was the first study site. This lake has significant cultural values to *iwi* (Māori "tribe") Ngāti Hauiti. A high-resolution study provided suggestions for rehabilitating this lake to meet Ngāti Hauiti's cultural aspirations. The diatom assemblages revealed that despite nutrient enrichment from the 1840s, rehabilitating Lake Oporoa using the 1950s as a target, would be sufficient for the cultural wishes of Ngāti Hauiti – this study highlights the importance of working with Indigenous peoples in managing lakes.

The second study location was the Canterbury high country on the South Island of New Zealand. Regional and national governments have focused on conservation of the lakes in this region. Originally covered by native forest, the landscape in the area altered following Māori fires and is now dominated by tussock grasslands. Fossil diatom assemblages from four lakes, Lakes Ōtūroto, Ōpōrea, Kirihonuhonu and Emily, with interpretations aided by analysis of modern diatoms samples, were examined to identify significant points of change in water quality. Before human activity in the catchment, all lakes had extremely low nutrients. After first Māori activity in c. 1400 CE, all lakes experienced aquatic transitions with rapid changes in their diatom assemblages to taxa, *Discostella stelligera*, in particular, indicating cultural nutrient enrichment.

All lake records indicated that European colonial activities triggered marked changes in water quality, albeit at differing times and magnitudes in each lake. There was a two-stage change in the three shallow lakes, Lakes Oporoa, Kirihonuhonu and Emily. They first responded rapidly to pastoral activity (c. 1840–50s) but became further enriched from the 1950s. Diatom assemblages are now dominated by species tolerant of nutrient-enriched conditions. By contrast, Lakes Ōtūroto and Ōpōrea, recorded minimal response to colonial activity and declining water quality occurred from approximately 1990 onwards.

The sedimentary records of the five lakes, over 1000 years in length, clearly captured the legacy of two waves of anthropogenic activity, in addition to the natural pre-human water quality. These lakes, along with others in New Zealand, are of great socio-ecological value, and management of these sites is needed to prevent a further decline in water quality, and to protect the ecosystem services they provide.



## Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

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## Publications from this PhD

### **Journal articles**

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### **Other journal articles contributed to during candidature**

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Francke, A., Dosseto, A., Forbes, M., Cadd, H., Short, J., Sherborne-Higgins, B., Constantine, M., Tyler, J., Tibby, J., Marx, S., Dodson, J., Mooney, S. & Cohen, T.J. (in press). Catchment vegetation and erosion controlled soil carbon cycling in south-eastern Australia during the last two Glacial-Interglacial cycles. *Global and Planetary Change*, 217, <https://doi.org/10.1016/j.gloplacha.2022.103922>

Pearman, J. K., Wood, S. A., Vandergoes, M. J., Atalah, J., Waters, S., Adamson, J., Thomson-Laing, G., Thompson, L., Howarth, J. D., Hamilton, D. P., Pochon, X., Biessy, L., Brasell, K. A., Dahl, J., Ellison, R., Fitzsimons, S. J., Gard, H., Gerrard, T., Gregersen, R., Holloway, M., Li, X., Kelly, D. J., Martin, R., McFarlane, K., McKay, N. P., Moody, A., Moy, C. M., Naeher, S., Newnham, R., Parai, R., Picard, M., Puddick, J., Rees, A. B. H., Reyes, L., Schallenberg, M., Shepherd, C., Short, J., Simon, K. S., Steiner, K., Šunde, C., Terezow, M. & Tibby, J. (2022). A bacterial index to estimate lake trophic level: National scale validation. *Science of the Total Environment*, 812. <https://doi.org/10.1016/j.scitotenv.2021.152385>

# Chapter 1

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Introduction and thesis outline

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# 1 Introduction

## 1.1 Freshwater lakes

For millennia, terrestrial and freshwater ecosystems have been affected by anthropogenic activities which have fundamentally altered biodiversity patterns and the provision of ecosystem services (Newbold et al., 2015; Kennedy et al., 2019; Ellis et al., 2021). The present ecological state and functioning of many ecosystems are inextricably shaped by human activity, and such is the continual pressure and extent of human activities on the environment that a new geological epoch succeeding the Holocene, the Anthropocene, has been proposed (Crutzen, 2002). This term “Anthropocene” recognises that many ecosystems and their function, have been, and will continue to be, shaped by anthropogenic activities (Crutzen, 2002; Steffen et al., 2011). There is now a necessity for effective conservation of biodiversity, and in maintaining the functional capacity of ecosystems (Barnosky et al., 2017). Under these circumstances, freshwater ecosystems, such as lakes, and their biodiversity are some of the world’s most threatened ecosystems (Dudgeon et al., 2006; Reid et al., 2019), with biodiversity of freshwater ecosystems declining faster than in marine and terrestrial environments (Dudgeon et al., 2006; McRae, Deinet & Freeman, 2017; Albert et al., 2021).

Lake systems are an important source of freshwater worldwide (Jenny et al., 2020). Covering approximately 3.7% (Verpoorter et al., 2014) of the Earth’s surface, they play a significant role in the global biogeochemical cycles of carbon, methane and silica (Cole et al., 2007; Tranvik et al., 2009; Bastviken et al., 2011; Frings et al., 2014), while providing a wide range of ecosystems services and values; for example, water supply, recreational activities, habitat for biodiversity and nutrient cycling (Reynaud & Lanzanova, 2017; Jenny et al., 2020). The degradation of freshwater systems increased after the Industrial Revolution (c. 1850) but has accelerated since the mid-20<sup>th</sup> Century (Huang et al., 2022), paralleling the global trend of increasing pressure on environmental systems (Steffen et al., 2015). There are many threats to freshwater biodiversity which include, but are not limited to, habitat degradation, catchment modification, exploitation of resources, chemical and agricultural pollution, invasive species (Dudgeon et al., 2006), algal blooms, microplastic contamination, light and noise pollution, and increasing salinisation (Reid et al., 2019). Furthermore, many of these pressures do not operate in isolation and there are frequently multiple stressors on lake systems (Ormerod et al., 2010; Jackson et al., 2016; Reid et al., 2019), making freshwater management and conservation a complicated and difficult task.

## 1.2 Lakes and landscape changes

Lake ecosystems are highly sensitive to their surrounding environment due to their position in the catchment, and through the linkages and fluxes of energy and organisms they have with the terrestrial

environment (Schindler, 2009; Soininen et al., 2015) and atmosphere (Tranvik et al., 2009). Notwithstanding long-range atmospheric processes and the effects of anthropogenic climate change on lakes (Woolway et al., 2020), human activities in lake catchments can have long-term adverse effects on the ecological health and water quality of lake systems. Land cover, globally, has changed dramatically since the start of the Holocene (Ellis et al., 2021), with land use intensity (encompassing agricultural input, biomass output, and interaction with ecosystems) increasing in the most recent decades (Kastner et al., 2022). Approximately 35% of the ice-free, terrestrial environment is used for some form of agriculture (Goldewijk et al., 2017). Understanding how anthropogenic activities in lake catchments has affected the ecology of lakes, and whether they can recover from these disturbances is a key focus for lake management (*sensu* Heino et al., 2021). However, this becomes difficult when the magnitude of response varies between lakes of different size, and this consequently has driven focus on different ecological theories that encompass the differing effects and magnitude of response, of human activities on lake systems (e.g. Scheffer et al., 1993; Capon et al., 2015). Shallow lakes (< 5 m deep) are especially susceptible to catchment changes (Rabaey et al., 2021) and have long been a focus of research. Studies on shallow lakes provided evidence for the “alternative stable states” and “regime shift” hypotheses (Scheffer et al., 1993; Scheffer et al., 2001) which document the different ecological states in which lakes can exist, i.e. in a clear, macrophyte dominant state (low nutrient), or a turbid state with low, or no submerged macrophytes (enriched). Larger lakes, on the other hand, have greater resilience to anthropogenic perturbations, although observations from around the globe indicate this is rapidly changing (*sensu* Jenny et al., 2020; Seekell et al., 2022).

Combining the anthropogenic and ecosystem values associated with lakes, and the threats to freshwater systems, lake conservation and management are of paramount importance. Water and ecological monitoring of lakes is an essential component of lake management, however are often over too short a time scale for changes in water quality, such as nutrient levels or pH, in the context of historic and natural variability to be placed, and therefore encompass the full signature of anthropogenic effects (Smol, 2019; Svitok et al., 2021). Therefore, to improve the understanding of lake ecosystems and management outcomes, there is a need for long-term records and perspectives of environmental change (Dietl & Flessa, 2011; Boivin & Crowther, 2021) that aim to understand the key processes and functions that drive changes within lakes (Jaiswal et al., 2021). The impacts of anthropogenic activities, including those that have occurred in lake catchments, can be gained through the examination of their sedimentary records.

### 1.3 Palaeolimnological research and methods

Lake sediments are archives of environmental changes and due to continual patterns of deposition, can temporally integrate biological and geochemical signatures of both the lake and its catchment (Anderson, 1995; Williamson et al., 2008; Adrian et al., 2009). Palaeolimnology is the study of these sediments, and with it the historical, ecological conditions of lakes can be inferred. Palaeolimnological studies have become essential for identifying anthropogenic influences, and the extent and scale of anthropogenic pressures on lakes and their catchments. For example, they were instrumental in early research which demonstrated the cause and effects of acid rain on lakes in the Northern Hemisphere (Battarbee, 1984; Renberg, 1990; Hall & Smol, 1996) and have been used widely to examine lake eutrophication (Bennion, Simpson & Goldsmith, 2015; Bunting et al., 2016). Palaeolimnology can also examine anthropogenic effects over a longer time frame (> 1000 years) (Ekdahl et al., 2004; Gąsiorowski et al., 2021).

One of the central foci of palaeolimnological studies that examine the changing water quality in lakes, is the notion of “baseline” or reference conditions (Bennion, Fluin & Simpson, 2004; Abell et al., 2020), as opposed to those which specifically reconstruct historic climate or landscapes. This concept is also used in theories discussing best conservation practice (McNellie et al., 2020) and in general, refers to the ecological condition of a given lake before a significant degradation in its ecological conditions, e.g. change in trophic level or pH. In the “purest” form, reference conditions refer to lake status prior to any discernible human activity. However, concepts of reference conditions now recognise the widespread and long-term interaction of humans with the environment, and therefore, they usually refer to a time when human impact was minimal (Poikane et al., 2010). For example, reference conditions in European lakes are generally considered to be pre-1800–1850 CE (Leira et al., 2006; Bennion et al., 2011), although there is recognition that humans have been influencing the environment for millennia, (e.g. Bradshaw et al., 2005; Rasmussen & Anderson, 2005; Thevenon et al., 2011), and in regions with European colonial histories, sometime before colonisation (e.g. Saunders et al., 2008). Given the disparate nature and timing of human activity, reference conditions will vary from region to region (Hübener et al., 2015; Heino et al., 2021). Additionally, catchment and in-lake variability mean that lakes can have separate “reference” conditions, and therefore the definition of reference conditions should be on a lake-to-lake basis (Carvalho et al., 2009; Abell et al., 2020).

In the context of freshwater degradation, its management, and the extent of human impact, New Zealand is in a unique position for exploring the effects of changes in land use upon its lakes, and to examine the perception of reference conditions. New Zealand has had two waves of human settlement, both of which are relatively recent in comparison with settlement in most other places. Anthropogenic activity on New Zealand’s landscape started approximately 750–800 years ago



(McWethy et al., 2010; Wilmshurst et al., 2011) after the arrival of Polynesians (Māori), from the southern Pacific, while European colonial settlement commenced from the early 1800s (King, 2007).

#### 1.4 New Zealand and New Zealand's lakes

New Zealand has an abundance of freshwater lakes, with over 3800 lakes greater than a hectare in area (Schallenberg et al., 2013). The extensive glaciation on the South Island during the Pleistocene, and geological activity during the Quaternary period, particularly volcanic events in the North Island, have contributed to the development of a diversity of lakes across the country (Lowe & Green, 1987). Most lakes were formed in the last 20,000 years (Brookes & Hamilton, 2009) and glacial lakes, are the most common type (Brookes & Hamilton, 2009). New Zealand's freshwater lakes are of national significance and are valued for their environmental, economic, social, and cultural heritage (Schallenberg et al., 2013; Ministry for the Environment & StatsNZ, 2020b). The ecological state of freshwater is considered one of the country's most pressing environmental issues, with 80% of the country's population thinking the current state of freshwater is a problem (StatsNZ, 2019). In New Zealand despite the high level of endemism of freshwater species (> 85 % fish species are endemic; Joy & Death, 2013), the species diversity of fish and macroinvertebrates in lakes is lower compared with the diversity in flowing waters, but higher in diversity for macrophytes (Schallenberg et al., 2013; Joy & Death, 2013). Thirteen fish species are commonly found in lakes, but there are no species exclusive to lakes (Joy & Death, 2013). Lakes, however, are biodiversity hotspots in New Zealand (Schallenberg et al., 2013) due to their distinct position in the landscape and the disparate populations of species that can exist in them.

The nutrient limiting productivity in New Zealand's lakes varies, with nitrogen and phosphorus and co-limitation occurring (Abell et al., 2010). However, at a national scale, nitrogen is a more suitable indicator of lake productivity (Abell et al., 2010). Consequently, the Trophic Level Index developed to classify the trophic levels of lakes across the country, includes total nitrogen (TN) in its calculations (Burns, Rutherford & Clayton, 1999). Other variables include total phosphorus (TP), Chlorophyll *a* and Secchi depth (Table 1; Burns, Rutherford & Clayton, 1999). Regular monitoring of lakes indicates that their trophic status is generally increasing across New Zealand (Abell et al., 2019, Ministry for the Environment & StatsNZ, 2020) with modelling of lake water finding that 46% of lakes are in poor or very poor ecological health (eutrophic–hypertrophic; Ministry for the Environment & Stats NZ, 2022). Many of these lakes are lowland lakes on the North Island, with the South Island having lakes in better ecological health (microtrophic–oligotrophic; StatsNZ, 2022). A trophic level classification of “oligotrophic” is the desired state for the larger lakes in New Zealand (Drake, Kelly & Schallenberg, 2011). The pressures that New Zealand's lakes face are not dissimilar to pressures elsewhere around

the globe, with the top four issues according to New Zealand’s government being 1) threats to native freshwater species and ecosystems, which is partially a response to New Zealand’s high level of species endemism, 2) water pollution (excess nutrients, chemicals, pathogens) in urban, agricultural and forestry areas, 3) changing hydrology, as a result of hydroelectricity, storage and irrigation projects, and 4) anthropogenic climate change (Ministry for the Environment & Stats NZ, 2020b). Many of these threats are frequently synergistic with each other and other pressures leading to multiple stressors in many sites (Hamilton et al., 2012).

**Table 1:** Water quality variables that define the boundaries of each trophic level category in New Zealand. Data sourced from Burns, Rutherford & Clayton (1999). These trophic level categories are referred to throughout the thesis.

Trophic category	TP (µg/L)	TN (µg/L)	Secchi Depth (m)
Ultra-microtrophic	0.84–1.8	16–34	33–25
Microtrophic	1.8–4.1	34–73	25–15
Oligotrophic	4.1–9.0	73–157	15–17
Mesotrophic	9–20	157–337	7–2.8
Eutrophic	20–43	337–725	2.8–1.1
Supertrophic	43–96	725–1558	1.1–0.4
Hypertrophic	> 96	> 1558	< 1.1

In response to these problems in water quality, the National Policy Statement for Freshwater Management (NPS-FM) was introduced in 2014, and requires regional councils, which have primary responsibility for managing freshwater in New Zealand, to provide targets and to outline objectives for improving the ecology and water quality of freshwater systems in their region (Ministry for the Environment, 2020a). Strategies to meet those targets are also required, and irrespective of the freshwater system in question, these targets need to meet a national minimum standard (Stephens et al., 2018; Snelder et al., 2020). Increasingly integral to the NPS-FM (and other freshwater directives in New Zealand) is the Māori concept *Te Mana o te Wai*, which refers to the importance of water itself, in that the health and well-being of water is protected, and the human health requirements of freshwater are given (Ministry for the Environment & Ministry for Primary Industries, 2020c). Part of this process recognises the cultural values placed by Māori on freshwater and is incorporated in reports and policies across New Zealand (Ministry for the Environment & Ministry for Primary Industries, 2020).

Freshwater management is now an essential component of New Zealand’s conservation strategy (Ministry for the Environment & StatsNZ, 2020b), although it is argued that policies and conservation

measures need to be more rigorous and enforced, given the continual declining state of freshwater systems (Weeks et al., 2016; Joy & Canning, 2021). In order to manage ecosystem services, and the broader conservation values, establishing the anthropogenic history of lakes in New Zealand is crucial. Palaeolimnological methods are the principal way of doing so, and can be used to examine the drivers of ecological shifts, and the scale and extent of anthropogenic effects on these systems. New Zealand is one of the very few areas in the world where a combination of remote and low nutrient lakes co-exist with heavily modified lakes, meaning that responses can be compared between sites, especially with regards to understanding baseline conditions and the trajectory of changes in water quality. Diatoms preserved in lake sediments are particularly useful for analysing the history of water quality in lakes and are therefore one of the most frequently used proxies in palaeolimnological studies (Hall & Smol, 2010). An understanding of diatoms' sensitivity to their habitat and the species-specific responses to change in water quality, mean that accurate reconstructions of past water quality and ecology can be made (Smol & Stoermer, 2010).

Diatoms (class Bacillariophyceae) are single-celled, siliceous algae inhabiting most aquatic environments. They are predominantly cosmopolitan in distribution (Soininen & Teittinen, 2019), and are found in many different aquatic conditions and habitats, where their sensitivity and rapid response to numerous variables, including temperature, light, turbidity, pH, nutrient concentrations, salinity and dissolved organic carbon, can influence the relative abundances of specific taxa (Battarbee et al., 2002; Smol & Stoermer, 2010). In addition, some diatom taxa have very specific habitat requirements, and these can be used to infer changes in lake environments, i.e. planktonic species live in the water column, and benthic species live around the edges of lakes and near, or in, the sediment, while epiphytic diatoms grow attached to plants (Battarbee et al., 2002). Recent estimates suggest that there are at least 30,000 species of diatoms, although this number could be upward of 100,000 (Mann & Vanormelingen, 2013). Under a variety of aquatic conditions, with some exceptions (Ryves et al., 2001), the siliceous cell wall of diatoms have been preserved well in lake sediments for millennia, e.g. Rioual & Mackay (2005). This is particularly relevant for examining the changes in the water quality of lakes in response to changes in the surrounding landscape, such as those which have occurred extensively in New Zealand. As an example, native forests comprise approximately 25% of total land cover (Ministry for the Environment & Stats, 2022), which is a reduction from approximately 40% native forest cover before 1800 CE (McWethy et al., 2010), and 80% prior to human settlement (Ministry for the Environment & Stats, 2022).

## 1.5 Palaeolimnological studies in New Zealand

Palaeolimnological studies, although extensive across New Zealand have primarily focused on palaeoclimate reconstruction, (e.g. Jara et al., 2015; Anderson et al., 2018; van den Bos et al., 2018; Evans et al., 2022), and identifying the time of human settlement of the country, and the subsequent landscape changes (Wilmshurst, McGlone & Partridge, 1997; McGlone, 2002; Chester & Prior, 2004; Newnham et al., 2018). There are few studies that purely address the water quality and ecological response of lakes to anthropogenic activities. Those that focus on anthropogenic activities show eutrophication of lakes following European colonisation (Woodward & Shulmeister, 2005; Schallenberg, Goff & Harper, 2012; Schallenberg & Saulnier-Talbot, 2016; Stephens et al., 2018), which mirrors the results found in other lakes with histories of recent European colonisation, e.g. Velez et al., (2021), Reid & Ogden (2009). Similarly, studies examining the response by lakes to Māori activities show that some nutrient enrichment occurred, along with changes in sedimentation rates (McWethy et al., 2010; Woodward et al., 2014). There are comparatively few studies, however, that cover this time period of first Māori activity and the subsequent effect on lakes (McWethy et al., 2010; Woodward et al., 2014). The extensive number of lakes across New Zealand, and the diversity of landscapes has contributed to this limited understanding of the extent of historical lake response to anthropogenic activities.

## 2 Thesis aims and objectives

The broad aim of this thesis was to examine the changing water quality of a suite of five lakes as they responded to anthropogenic activities.<sup>1</sup> Diatoms were the primary proxy used in this study, although data were complemented by pollen, sediment geochemistry, chronology, microbial sedDNA, and  $\mu$ -XRF elemental data. The specific aims of this thesis were to:

1. Identify periods of significant changes in water quality in a selection of New Zealand's lakes through the last ~1000 years, a period which includes, and is just before the first human (Māori) arrival in New Zealand,
2. Analyse the differences in response of lakes to first Māori and European activities, and
3. To examine how palaeolimnology can be used to contribute to future lake management, using examples from lakes that are of i) cultural significance to *iwi* (which loosely translates to "tribe"), and ii) are important for national and local governments.

This study will contribute to understanding the scale and magnitude of anthropogenic impacts on New Zealand's freshwater lakes, which despite monitoring and awareness of the degradation of freshwater, are still comparatively understudied. Furthermore, the information derived from this

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<sup>1</sup> The sediment record of six lakes was analysed in this thesis. However, as the sixth lake (Lake Te Puna a Taka) had poor stratigraphy in both the diatom and pollen records, it is only discussed in Chapter 2. The data from this lake site were not used to assist with answering the aims of this thesis.

study can contribute to the knowledge of freshwater ecosystems worldwide. This study was an opportunity to examine the first response of lakes to human activities, as the relatively short settlement timescale means that the quality of water before human activity can be well-defined. Palaeolimnological techniques are suited for a shorter time scale, especially when the main area of focus for anthropogenic changes is less than a thousand years in the sedimentary records. This information can subsequently be applied to understanding the geochemical trajectory of lake systems as they first respond to human activity, and towards the present where they are shaped by multiple anthropogenic pressures. Finally, the use of diatoms as palaeolimnological indicators in New Zealand is underutilised and hence this study highlights their value.

### 3 Study regions

Two regions were studied for this thesis – both of which were chosen for the interest shown by stakeholders and *iwi* in the history of the study lakes. For many lakes in New Zealand, there is a gazetted name and a Te Reo Māori name. For this thesis, the lakes are discussed using their Te Reo Māori name where available, but their gazetted name is also listed for reference.

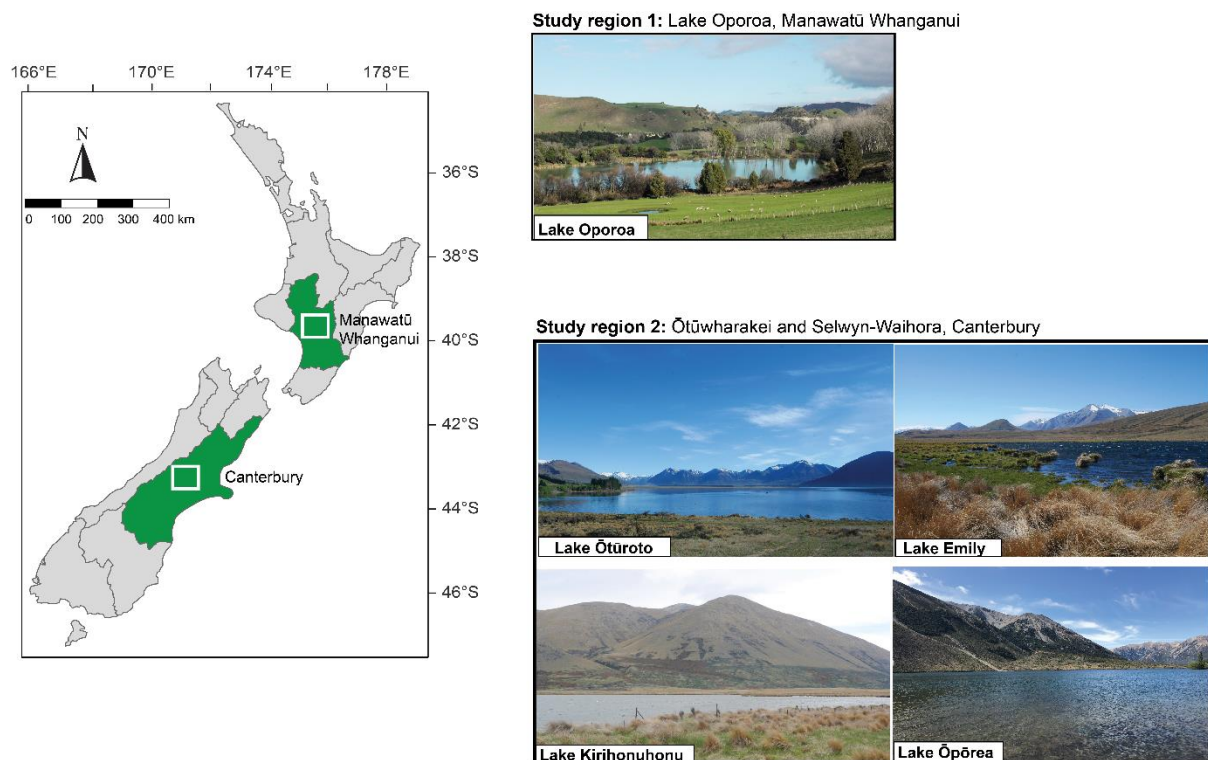


Figure 1: Location in New Zealand of the two study regions (white boxes) with each of the lakes shown. Further details of each lake and their catchment are mapped in Chapters 3–5.

#### Study region 1: Lake Oporoa, Manawātū-Whanganui

Lake Oporoa is a small and shallow, lowland lake located in the Manawatu-Wanganui region of the North Island, in the upper Rangitīkei River catchment. It is situated in one of the drier areas of the region receiving less than 900 mm of rain per year while weather is predominantly controlled by migratory anti cyclones and low pressure systems (Chappell, 2015). The lake has an area of 7.1 ha (2019) and a maximum depth of 3 m (2019) and was formed by a landslide. The riparian zone is semi-vegetated with both native and non-native trees and shrubs (e.g. native: *Dacrydium cupressinum*, *Podocarpus toatara*, *Prymnopterys ferruginea* and *Coprosma* spp., non-native: *Populus* spp. and *Salix* spp.). The landscape is primarily under agricultural use and is classified as high-productivity grassland meaning that it is used for crop rotation and animal production (Thompson, Grüner & Gapare, 2003). Lake Oporoa is of significant cultural importance to Ngāti Hauiti *iwi*, and due to its present degraded state has been a recent focus of rehabilitation, by the *iwi*, together with local government (Horizons Regional Council). Lake Oporoa is among a selection of lakes and waterways in the Rangitīkei region that are being rehabilitated with a focus on engaging with *iwi* and supporting cultural and ecological wellbeing (NPRR, 2019).

**Study region 2:** Ōtūwharekai and Selwyn Waihora, Canterbury high country, Canterbury.

The Canterbury high country is a region located on the eastern side of the Southern Alps on the South Island of New Zealand, at an altitude of 600–800 m above sea level. The area is subject to the orographic effects of the Southern Alps, which block the prevailing westerly winds, causing a distinct weather gradient between the western and eastern sides of the range (Salinger & Mullan, 1999; Lorrey & Bostock, 2017; Lachniet et al., 2021). Consequently, the region experiences hot and dry summers, with cold winters (Macara, 2016). The study sites are located in two adjacent inter-montane basins: Lakes Ōtūroto (Heron), Kirihonuhonu (Emma) and Emily are in the Ōtūwharekai (Ashburton) region and Lake Ōpōrea (Pearson) is in the Selwyn-Waihora region approximately 60 km east of Ōtūwharekai. The Ōtūwharekai region is bounded by glacial-fed, braided river systems with the Rakaia River to the east, and upper Rangitata River in the west, while Lake Ōpōrea is in the upper Waimakariri River Catchment.

Glacial activity was extensive in the regions during the local Last Glacial Maximum in New Zealand (29–18 kya; Alloway et al., 2007). Glacial recession in the Ōtūwharekai and Selwyn-Waihora regions began about 18 kya (Barrell, Putnam & Denton, 2019) and 17.5 kya (Rother et al., 2015) respectively. As glaciers receded, the landscape was shaped through erosional and depositional processes leaving outwash fans, kettle holes, lakes and braided rivers (*sensu* Mabin, 1984; Sullivan et al., 2012; Borsellino, Shulmeister & Winkler, 2017). Many lakes in this region were formed by deposited terminal moraines (Pugh, 2008; Sutherland et al., 2019). Lake Ōtūroto formed approximately ~18.6 kya (Pugh,

2008; Rother et al., 2014) in a terminal moraine system (Sutherland et al., 2019). Lake Emily was similarly formed as ice retreated from the moraine (Pugh, 2008) and while a moraine has not been discussed with reference to the formation of Lake Kirihonuhonu, there is indication that it is associated with a moraine complex (Cromarty & Scott, 1995; Rother et al., 2014). Palaeo-shorelines (lake benches) indicate that both Lakes Ōtūroto and Emily were once larger (Pugh, 2008). Lake Ōpōrea, however, was formed by post-glacial alluvial fans, blocking a stream channel (Gage, 1958; Cromarty & Scott, 1995).

In the Ōtūwharekai region, land use in the catchments of Lakes Ōtūroto, Kirihonuhonu and Emily, is mixed low intensity pastoral and grazing activities. The region is recognised for its conservation value given the unique landscape (Sullivan et al., 2012). The region's vegetation is open, dominated by tussock grassland comprising native (*Chionochloa* spp.) and non-native species. There are also some non-native trees (*Pinus* spp. and *Salix* spp.) to be found planted on pastoral land. Conservation measures in the region aim to protect endemic and rare fauna, e.g. *Anarhynchus frontalis* wrybill; *Porzana pusilla affinis*, Baillon's crane; *Oligosoma waimatense* scree skink and threatened plant species such as *Iphigenia novae-zelandiae* native lily and *Myosotis minutiflora* pygmy forget-me-knot (Robertson & Suggate, 2011).

Lake Ōtūroto is the largest of these three lakes in the upper Rakaia River catchment with an area of 695 ha, and a maximum depth of 36.2 m (Bayer & Meredith, 2020), and is shaped by alluvial fans along its margin (Sutherland et al., 2019). Lake Emily is in the same basin as Lake Ōtūroto and is approximately 7.5 km away to the south-east. It is a small and shallow lake, at 19 ha and 2.3 m depth, but is connected to a 50 ha swamp to the north-west, with a large wetland margin (Bayer & Meredith, 2020). Finally, Lake Kirihonuhonu is approximately 16 km south-west of Lake Ōtūroto and is medium-sized and shallow, 167 ha in area, and a maximum of 2.7 m in depth (Bayer & Meredith, 2020). Similar to Lake Emily, it has a connected wetland margin.

Lake Ōpōrea is approximately 60 km east of the Ōtūwharekai lakes. It has two distinct basins, which are permanently connected, and together form a surface area of 202 ha; the lake's maximum depth is 17 m (Bayer & Meredith, 2020). The development of the two different basins is due to a debris fan extending from its western and eastern margins (Cromarty & Scott, 1995). Lake Ōpōrea is located adjacent to a national highway and is fringed by both native (*Fuscospora* spp.) and non-native (*Salix* spp.) trees. The catchment is protected as a wildlife refuge for rare birds, as the Moana Rua Wildlife Refuge. Only non-motorised recreational activities are permitted, including fishing and camping. Water quality monitoring by Environment Canterbury (Bayer & Meredith, 2020), shows similar water quality in both basins.

## 4 Thesis outline

### Chapter 2: The ecology of diatoms in New Zealand, with a focus on *Discostella stelligera*

This chapter investigates and discusses the autecology of selected New Zealand diatoms from a combination of 26 surface sediment samples, 49 habitat samples from plant, rock and mud scrapes, and six sediment cores, along with a literature survey. Lake Oporoa's was the first sedimentary record analysed in the study (Chapter 3; Short et al., 2022) and additional habitat information would have been valuable in interpreting the palaeolimnological record (Short et al., 2022). Therefore, on a sediment coring field trip to the Canterbury region in November 2019, habitat samples were collected at each lake site. Following analysis of these samples, a more systematic approach was applied in a separate field trip in January 2020 where different plant samples were analysed to determine whether different diatom assemblages could be found growing on different plant species. Further planned sampling was prevented by the international border closures associated with the COVID-19 pandemic.

The habitat samples and the surface samples assisted with interpreting the longer diatom records from all Canterbury lakes. The diatom assemblages from the habitat samples were important in reconstructing the habitat of the Canterbury lakes, especially the macrophyte communities of shallow Lakes Kirihonuhonu and Emily. Species common to each data set, and how their interpretation can be applied to these long-term records are discussed in this chapter. Species abundance and allied water chemistry data were also used to estimate total nitrogen and total phosphorus optima using weighted averaging.

Finally, Chapter 2 discusses the ecology of *Discostella stelligera* in New Zealand's lakes. *Discostella stelligera* is an abundant diatom taxon found in all five records studied. It was also in the diatom record of a sixth study lake, Lake Te Puna a Taka. This record is only analysed in Chapter 2 given its poor chronology. *Discostella stelligera* was an historically abundant taxon in all lakes, except for Lake Kirihonuhonu. Following evidence of first Māori activity in each lake's catchment, the taxon always fluctuated in abundance. Many palaeolimnological and limnological studies have been conducted in the Northern Hemisphere to establish the ecology of this species, while at the same time, the taxon is frequently associated with anthropogenic climate warming (Rühland et al., 2008). The aim, therefore, was to discuss the driver of its presence in New Zealand's lakes and whether climate warming contributes to any of its present abundance.

This chapter is formatted for future submission to *New Zealand Journal of Marine and Freshwater Research*.

### Chapter 3: The rehabilitation of a culturally significant lake in New Zealand



In Chapter 3, a 1200-year high-resolution diatom record from Lake Oporoa is discussed. This lake site is culturally significant to Ngāti Hauiti *iwi*. Diatom data are presented in conjunction with pollen, pigment, elemental and sedDNA analyses, to reconstruct the ecological history of Lake Oporoa and its catchment, from before Māori settlement of the country, until the present. The aim was to provide rehabilitation options for the lake, using palaeolimnological methods, while incorporating some oral histories, and desires from traditional owners. The results indicated that a suitable rehabilitation target would be the 1950s, before the acceleration in degradation of water quality (inferred from the diatom data). This time frame also supports Ngāti Hauiti cultural activities, such as *tuna* (*Anguilla* spp., eel) harvesting. This study highlights the benefit of using Māori knowledge together with Western scientific techniques in palaeolimnology, that could be similarly used with other indigenous groups.

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#### Chapter 4: Initial human impact on landscape vegetation drove nutrient change and aquatic transitions in lake ecosystems

The primary aim of this chapter was to address how lake ecosystems respond to first human impacts, and whether any lakes experienced aquatic transitions. An aquatic transition is defined as a significant change in the biogeochemical structure or function of a lake system (Dubois et al., 2018). New Zealand is in a unique position to explore whether aquatic transitions have occurred as it has only been recently settled by humans (in the last approximately 750–800 years). In this study the long-term (> 1000 year) diatom records from four lakes; Lake Ōtūroto (Heron), Lake Kiriuhonuhonu (Emma), Lake Emily and Lake Ōpōrea (Pearson) were analysed. These lakes are all located in the Canterbury high country region, in an area in which native forests declined and were replaced by native tussock grassland, following Māori activity. Lakes Ōtūroto and Ōpōrea are deep lakes (> 15 m) relative to the shallow lakes of Lakes Kiriuhonuhonu and Emily (< 5 m). Pollen and sediment geochemistry ( $\delta^{13}\text{C}$ , C:N) data were used in conjunction with the diatom record to reconstruct the water quality history of the lakes.

Each lake experienced a significant change in diatom assemblages just preceding, or at the same time as the complete shift to tussock grassland from native forest. This signified that nutrient enrichment had occurred in these systems. It is likely that before human activity, all lakes could be classified as microtrophic (extremely low nutrients), and following Māori vegetation clearance, the lakes became oligotrophic-mesotrophic (low to moderate nutrients). No lakes reverted to their pre-human water

quality. This study is one of the few studies globally, that shows evidence for aquatic transitions in response to first human activity in the region.

In this chapter the palaeolimnological data analysed are from the pre-human and the Māori section of the sedimentary record. The changes in water quality following European colonisation and subsequent agricultural practices are discussed in the next chapter.

This chapter is formatted for future submission to *Global Change Biology*.

The Supplementary Information for both Chapters 4 and 5 is located at the end of Chapter 4.

#### Chapter 5: The legacy of anthropogenic activities in New Zealand's high country lakes

Chapter 5 discusses the water quality history of the four Canterbury lakes: Lakes Ōtūroto, Lake Kiriuhonuhonu, Lake Emily and Lake Ōpōrea since the start of European pastoral activities in the Canterbury high country (c. 1850). This completes the discussion of the full sedimentary record first presented in Chapter 4. There was specific interest, however, in identifying whether all the lakes recorded changes in water quality at the same time, as they did after evidence of first Māori activity. The same proxies, namely diatoms, sediment geochemistry and pollen, were used. In addition, monitoring data were used to complement the results in the palaeolimnological records which have a relatively low resolution, especially with identifying periods of recent nutrient enrichment. While the focus was to analyse the changes in the lakes after European activities commenced, reference is also made to the longer sedimentary record to assess how the effects of European activities in the landscape compared with the effects of Māori activities. Data from the diatom assemblages indicated that these lakes continued to respond to human activities in the landscape. Lakes Kiriuhonuhonu and Emily responded rapidly to European pastoral activity, becoming more eutrophic towards the present, while Lakes Ōtūroto and Ōpōrea have only become nutrient rich in recent decades and are now mesotrophic.

This study builds on existing palaeolimnological studies in New Zealand that specifically address the response of lake systems to European activities. It further supports the colonial histories of lakes that occur elsewhere, in that major ecological changes of lakes, and other freshwater systems occurred following European colonisation, especially in the Southern Hemisphere.

References to the supplementary figures and tables in this chapter, are referring to the Supplementary Information found after Chapter 4.

This chapter is formatted for future submission to *Journal of Paleolimnology*.

#### Chapter 6: Conclusions and future work

This chapter discusses the findings in context of the research aims and the broader application beyond New Zealand. The limitations of this study as well as avenues of future work are also addressed.

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Contribution to the Paper	Conceptual design, field work and sample preparation, diatom data collection and analyses, interpretation and statistical analyses (diatoms), producing figures, Manuscript production, writing and editing		
Overall percentage (%)	85%		
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Signature		Date	19/7/22

### Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the thesis; and
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Contribution to the Paper	Conceptual design, data interpretation (diatoms), manuscript editing and reviewing

Signature		Date	19/7/22
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## Chapter 2

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The ecology of diatoms in New Zealand's high country lakes, with a focus on *Discostella stelligera*

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## Abstract

Understanding diatom taxa and their ecological niches is necessary for interpreting palaeolimnological records. Useful ecological data can be obtained by sampling substrates and identifying associated diatom communities and calculating water quality optima for species. These data are derived by multivariate analyses of the relationship between ecological variables and diatom assemblage data, and experimental studies. Subsequently, quantitative analyses are made and can be used to reconstruct long-term water quality. As has been noted worldwide, local factors are an important control in determining taxon presence and abundance in lakes. However, there are few investigations of diatom ecology in New Zealand, meaning that abiotic control on diatoms is not well understood. To assist with the reconstruction of historic water quality from palaeolimnological records, surface sediment samples were analysed from 26 lakes in the Canterbury high country region. The diatom assemblage data were analysed in relation to a limited number of water quality variables collected by regional government, and their optima and tolerances to total nitrogen and total phosphorus were derived. The diatom assemblages from in-lake habitats; plants, rocks and sediments were also analysed from the littoral zone from seven lakes ( $n = 49$ ). Redundancy analysis revealed total nitrogen had greater explanatory power on diatom assemblages from these lakes, while similarly performing better in weighted averaging regression ( $R^2 = 0.39$ , RMSEP  $139 \mu\text{g l}^{-1}$  TN, measured vs diatom inferred TN). One of the most common taxa in the surface samples and palaeolimnological records was *Discostella stelligera*. From the habitat samples, there were no taxa specific to one substrate, although there were distinct substrate preferences for some taxa, e.g. Fragilariaceae preferred plants and mud or sand habitats, over rocks. PERMANOVA analyses demonstrated habitat type was more significant (F-statistic 5.06,  $p < 0.001$ ) than the lake sampled (F-statistic 4.36,  $p < 0.001$ ) in explaining diatom composition. This highlights the importance of changes in habitat in interpreting palaeolimnological records. The results from this study can be used to refine understanding diatom ecology from the Canterbury high country, especially when examining historical water quality from diatom records. Additionally, this study contributed to understanding of cosmopolitan diatom taxa, in particular *Discostella stelligera*, and their ecology in New Zealand's lakes.

## 1 Introduction

Diatoms (Bacillariophyceae) are a class of siliceous algae found in a wide range of aquatic conditions and trophic status (Hall & Smol, 2010). They are known for their sensitivity to differing biogeochemical factors often with distinctive species' responses occurring along environmental gradients. In many freshwater lakes, diatoms can be the dominant primary producer (Rühland et al., 2015), growing in distinct communities found in benthic, epiphytic and planktonic habitats (Julius & Theriot, 2010). Diatoms have been used in palaeolimnological studies to assess water quality degradation in lakes as a direct result of anthropogenic activities. Diatoms have, for example, been used to assess lake acidification, particularly in the Northern Hemisphere (Renberg, 1990; Battarbee et al., 2008), track nutrient enrichment and heavy metal or chemical pollution (e.g. Fong, Leng & Taylor, 2020; Beck et al., 2020), and to examine the response of lakes to landscape changes (Reinhardt et al., 2022). Palaeolimnological techniques have also been used to assess the extent and effect of anthropogenic climate change (Rühland et al., 2008; Streib et al., 2021; Benito et al., 2022) and nutrient enrichment from atmospheric nitrogen deposition on lake systems (Wolfe, Van Gorp & Baron, 2003; Hobbs et al., 2010; Oleksy et al., 2020).

Fundamental to diatom palaeolimnology is understanding the modern ecology of diatoms, especially the specific controls of taxon abundances. Examination of the relationship between species and environmental variables, for example, water quality, sometimes accompanies palaeolimnological methods, while experimental studies looking at specific taxa and their environmental gradient are becoming more common (e.g. Shatwell, Köhler & Nicklisch, 2013; Saros et al., 2014). Transfer functions have become a method to understand diatom ecology, allowing for a quantitative reconstruction of historic water quality in a palaeoecological record based on the distribution and habitat of modern biota. However, they have been criticised, essentially for their simplicity and disregard for considering the full suite of environmental variables that drive species distribution (Sayer, 2001; Juggins, 2013). Optima for, and tolerances to, ecological variables are developed for taxa, and these methods have been instrumental in assessing historic trends in, for example, pH (Dixit et al., 1999; Battarbee et al., 2008), total phosphorus (Cumming et al., 2015), and nitrogen (Arnett, Saros & Mast, 2012). They remain a common feature in many studies, e.g. Tammelin et al. (2019), primarily because quantitative reconstructions of historic water quality are frequently desired as a component of lake management or understanding deviation away from "natural" conditions (Bennion & Battarbee, 2007). Yet, techniques that capture further ecological information, such as substrate preference, are of benefit to palaeolimnological studies. This information can assist down-core inferences in past lake ecology and an understanding of benthic diatom communities (Michelutti et al., 2003; McGowan et al., 2018; Pla-Rabés & Catalan, 2018). Despite the value of understanding



substrate preference of diatom assemblages, this information is rarely analysed alongside palaeolimnological data.

In concert with understanding taxon-specific environmental variables, spatial ecology principles are also used to guide the interpretation of stratigraphic changes in diatom assemblages, the most common of which is the evaluation, and application, of niche conservatism. In theory a species grows under the same ecological conditions across time and space (Wiens et al., 2010). Therefore, the ecological knowledge of taxa from North America, e.g. Reavie & Kireta (2015), can be applied to taxa that are found, for example, in New Zealand or Australia. By contrast, recent work has demonstrated that regional (local) abiotic factors have greater influence over the pattern of diatom distributions (Benito et al., 2018a; Soininen & Teittinen, 2019; Heikkinen et al., 2022). Diatom species distribution is also influenced by historic continental dispersion and dispersal limitation (Kociolek, 2018; Verleyen et al., 2021). Despite the variety of biogeographical effects that shape diatom distribution, these are frequently ignored when reconstructing historic water quality, from down-core data, as there is often an absence of accurate and reliable diatom ecology for a given region (*sensu* Oeding & Taffs, 2017; Van de Vyver et al., 2022).

*Discostella stelligera* is a key taxon with which to examine diatom biogeography and niche conservatism (Soininen & Teittinen, 2019) due to its cosmopolitan distribution and differing ecological interpretation worldwide. In the Northern Hemisphere, *Discostella stelligera* has become associated with anthropogenic climate change (Ruhland et al., 2005). It is frequently argued that anthropogenic climate change has driven changes in water such as increasing thermal stratification, shallower mixing depths and longer ice-free periods (Michelutti et al., 2015; Saros et al., 2016; Reavie et al., 2017), thus causing the unprecedented abundance of this taxon. Conversely other limnological variables, such as nutrient concentrations and light ability, also influence the abundance of *Discostella stelligera* (Saros & Anderson, 2015; Boeff et al., 2016; Reavie et al., 2017) which further varies between lakes, meaning the interpreting the presence of the taxon, or the driver of its abundance, is often confounded by the diversity of ecological variables that can influence its presence (*sensu* Saros et al., 2015).

New Zealand is a useful location for examining these ecological theories, as despite the diversity of freshwater systems, diatom records and an understanding of diatom ecology is relatively scarce, and interpretation of diatom data relies on external studies. There are, however, some exceptions, e.g. Foged (1979), Reid (2005), Li et al. (2014) and Kilroy et al. (2017). *Discostella stelligera* is also a common taxon, found in both sedimentary records and modern samples (e.g. Reid, 2005; Augustinus et al., 2006; McWethy et al., 2010; Stephens et al., 2018). New Zealand's diatom flora has been subject to the influences of isolation as a landmass (Vyverman et al., 2007; Vanormelingen, Verleyen &

Vyverman, 2008) resulting in a unique diversity of diatom taxa and some diatom endemism (e.g. Vyverman et al., 1998; Kilroy et al., 2003). Endemic species are frequently found alongside cosmopolitan taxa, although it is thought that low nutrient water bodies, especially high-altitude tarns and bogs have a higher rate of endemism (Kilroy, Biggs & Vyverman, 2007). Additionally, there are some regional similarities between diatom assemblages from New Zealand and low-nutrient lakes in Tasmania (Australia) (Vyverman et al., 1998; Vanhoutte et al., 2006; Kilroy, Biggs & Vyverman, 2007).

Diatom samples were analysed from a suite of lakes in the Canterbury high country. The lakes selected are all located in this region to minimise the biogeographical effects on diatom distribution by ensuring the differences in diatoms assemblages between lakes is not due to biogeography. The analyses include surface sediment samples, habitat scrape samples, and five sedimentary records from lakes (the foci for Chapters 4 and 5) in the Canterbury region. While the diatom species from the surface samples reflect water quality and ecology from approximately the past 5–10 years, they nevertheless can provide a snapshot of the water quality of lakes in the region, in absence of long-term palaeolimnological records for each lake. Using these data, this study therefore aimed to, 1) contribute to the understanding of the water quality preferences of specific diatom taxa, 2) to learn whether habitat preferences exist for key benthic diatom taxa, and 3) given that *Discostella stelligera* was a key taxon in all lake records, provide a discussion on its ecology in the Canterbury high country.

## 2 Methods

### 2.1 Study area

The Canterbury high country region is located on the eastern side of the Southern Alps, of New Zealand's South Island, covering an altitude of 600–800 metres above sea level. Many lakes in this region were formed following glacial retreat. Land use is mixed with agriculture, conservation uses and native forests remnants. Vegetation is predominantly grassland with both native tussock (*Chionochloa* spp., *Festuca* spp. and *Poa* spp.) and non-native species (*Trifolium* spp., *Lolium perenne* and *Dactylis glomerata*; Thompson, Grüner & Gapare, 2003; Hewitt et al., 2012). Grassland vegetation use is usually classified as either “low producing grassland” or “high producing grassland”. The former is a combination of native and non-native grasses without regular use of fertiliser, that can also include native tussock species (Hewitt et al., 2012), while the latter is usually non-native grasses with regular fertiliser application and used for livestock and grazing (Thompson, Grüner & Gapar, 2003). The lakes in this study cover a broad range of nutrient conditions from microtrophic to supertrophic. Trophic level categories discussed herein are from New Zealand's Trophic Level categorisation (Burns, Rutherford & Clayton, 1999; Table 1). Unless specified water quality values are a five-year average from the austral spring–autumn (December–May) sampling period.

In the past two decades, there has been a general trend of decreasing water quality in the region particularly in shallow and smaller lakes, which are experiencing N enrichment (Chapter 5; Bayer & Meredith, 2020), while some of the larger and deeper lakes have excellent water quality (microtrophic–oligotrophic). Surface samples were analysed from 26 lakes in this region, while sediment cores were analysed from five of these lakes: Lakes Ōtūroto (Heron), Ōpōrea (Pearson), Kirihonuhonu (Emma), Emily and Te Puna a Taka (Clearwater). Full site selection and the latest available water quality data are listed in Table 2.

**Table 1:** Water quality variables that define the boundaries of each trophic level category. Data sourced from Burns, Rutherford & Clayton (1999).

Trophic category	TP (µg/L)	TN (µg/L)	Secchi Depth (m)
Ultra-microtrophic	0.84–1.8	16–34	33–25
Microtrophic	1.8–4.1	34–73	25–15
Oligotrophic	4.1–9.0	73–157	15–17
Mesotrophic	9–20	157–337	7–2.8
Eutrophic	20–43	337–725	2.8–1.1
Supertrophic	43–96	725–1558	1.1–0.4
Hypertrophic	> 96	> 1558	< 1.1

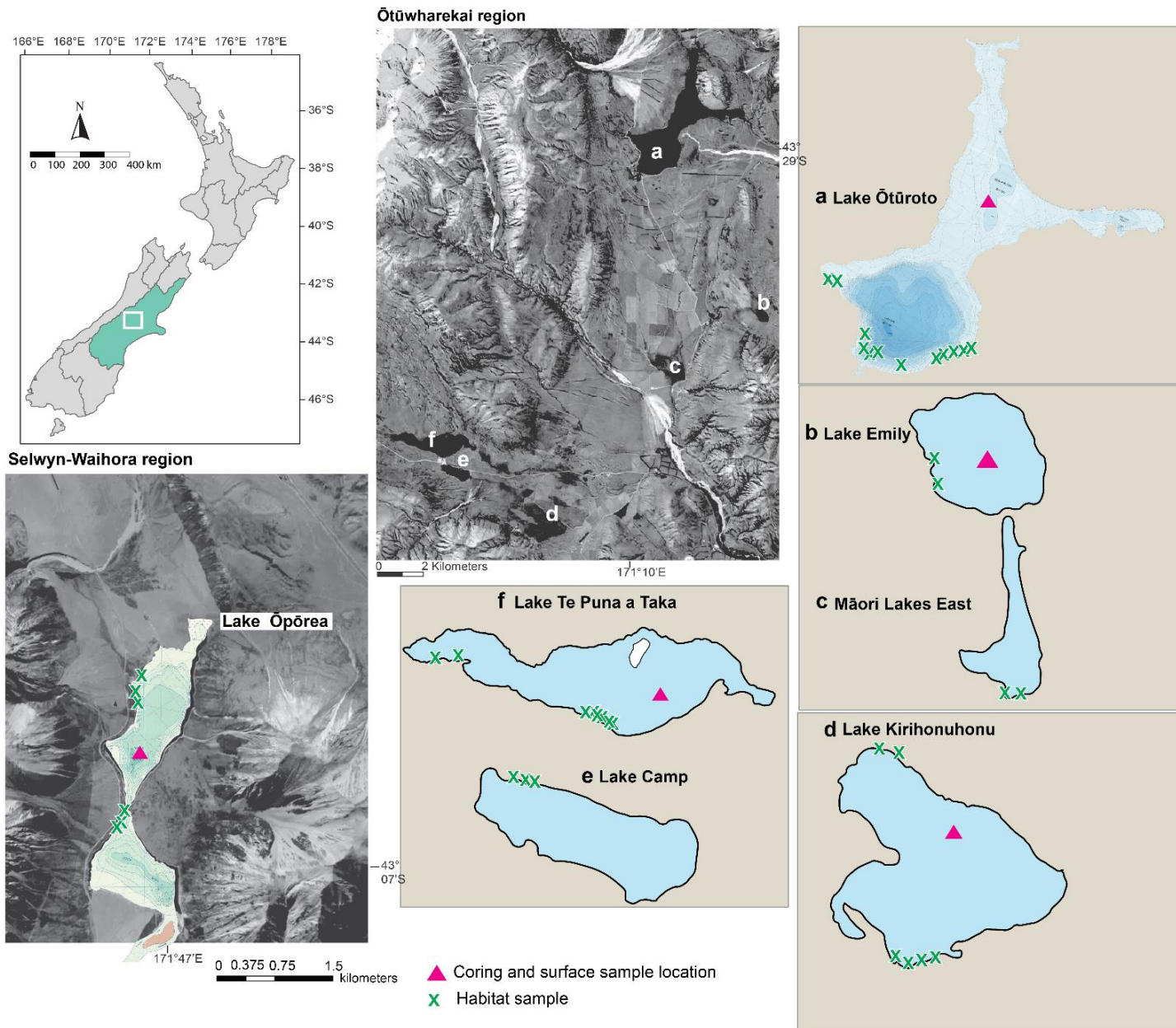
## 2.2 Surface and habitat samples

Surface samples were collected using a grab sampler (Ponar) in November 2019. The top two centimetres were collected and integrated as one sediment sample. This was to ensure the average water quality in recent years of each lake was reflected in the diatom assemblages, and it minimised the risk of samples being biased by annual bloom events (*sensu* Winegardner et al., 2015). The age models presented in Chapters 4 and 5, suggests the upper two centimetres of sediments Lakes Ōtūroto, Ōpōrea, Kirihonuhonu and Emily span 10–15 years. However, this is likely an overestimation of the sediment collected using the grab sampler, as much of it was flocculent material (pers. obs.).

**Table 2:** The physical and chemical characteristics of each lake sampled. Data sourced from Bayer & Meredith (2020).

Lake	Size (ha)	max. depth (m)	Catchment Land use	Trophic Level Index	TP µg/L (5 year average)	TN µg/L (5 year average)
Sumner	1180	134.5	Forest	Oligotrophic	2	55
Mason*	73	38.5	Tussock grassland, beech forest	Oligotrophic	NA	95
Katrine	75	28	Beech forest, low producing grassland, shacks	Oligotrophic	3.6	117
Taylor	185	40.5	High and low producing grassland, and forests	Oligotrophic	4.8	100
Sheppard*	115	21	grassland	Mesotrophic	10	198
Marion	10	~19	Native forest	Mesotrophic	13	300
Sarah	20	6.7	Pastoral, grassland	Mesotrophic	9.2	258
Grasmere	63	14	Conservation, pastoral/cropping, grassland	Mesotrophic	11.4	154
Ōpōrea (Pearson)	202	17	Grassland, pastoral	Mesotrophic	14.8	268
Hawdon	35	4	Pastoral, grassland	Mesotrophic	5.4	479
Lyndon	88	19	Native shrubs and tussock grassland	Mesotrophic	6	173
Georgina	17	10	Pastoral, tussock grassland	Eutrophic	14.4	604
Ida	10	9	Grassland, native vegetation	Mesotrophic	5.2	187
Selfe	65	30	Grassland	Mesotrophic	5	154
Henrietta**	4	5	Wetland, swamp	Mesotrophic	8	290
Evelyn**	17	3.2	Low producing grassland, native vegetation	Mesotrophic	4	191
Catherine**	18	6	High producing grassland, tussock grassland	Oligotrophic	2	181
Marymere	24	9.2	Low productivity grassland	Mesotrophic	NA	NA
Ōtūroto (Heron)	395	36.2	Native grassland, rock/gravel, pastoral	Mesotrophic	5.6	156
Horseshoe	4	10	Low producing grassland	Mesotrophic	NA	NA
Te Puna a Taka (Clearwater)	197	18	Pastoral, cropping, tussock grassland, small shacks	Mesotrophic	12.8	512
Māori Lakes East	9	~1.3	100 ha wetland, high producing grassland	Mesotrophic	8.2	564
Ōtautari (Camp)	44	13	Low producing grassland	Mesotrophic	6.2	354
Kirihonuhonu (Emma)	167	2.7	Conservation, wetland, Low producing grassland, tussock	Eutrophic	26.4	632
Emily	19	2.3	Low producing grassland, conservation, wetland	Eutrophic	21	430
Denny	NA	2.1	High producing exotic grassland	Super	83.8	950

\*most recent data are from 2017. \*\*Uses data from 2019 as a 5-year average is not available.



**Figure 1:** Location of the lakes and two regions from which the sediment cores and habitat samples were taken. The lakes are not to scale and the Selwyn-Waihora region is approximately 60 km east of Ōtūwharekai. The lettering of each inset corresponds to each lake's location on the map. Lake Ōpōrea bathymetry by Irwin (1970)

In November 2019, littoral zone substrates (rocks, submerged and emergent macrophytes, sand and sediment) were samples for diatoms at a selection of lakes in the Ōtūwharekai (Ashburton) region: Lakes Ōtūroto, Kirihonuhonu, Emily, Camp, Te Puna a Taka, Māori Lakes East (Figure 1, Table 3). The samples were collected by scraping the surface of five sub samples, from a one metre radius of the same substrate. Samples were collected with a toothbrush and preserved with Lugol's Iodine. The substrates were selected opportunistically as there were time constraints. Substrate sampling was repeated at Lakes Ōtūroto, Te Puna a Taka, Camp, Kirihonuhonu and in the Selwyn-Waihora region, Lake Ōpōrea, on a separate field trip in January 2020. This time, a variety of specific plants were also sampled to analyse whether diatoms assemblages varied between different plants (Rojas & Hassan, 2017). The plants sampled were: *Myriophyllum* spp., *Potamogeton* spp., *Carex* spp., *Ranunculus tricophyllus*, *Isoetes alpinus* and *Apodasmia similis* and each sample was comprised of five smaller sub-samples. In all lakes, samples were only collected from substrates in the littoral zone at 0.5–1 m depth, with light availability appearing greater for rock and pebble samples. The trophic categories were different in each lake and ranged from oligotrophic to eutrophic (Table 1, 2). There were no samples taken from planktonic habitats on either fieldtrip.

Phytoplankton samples were also collected from Lakes Lyndon, Ōpōrea, Grasmere and Ōtūroto in February, March, May and June 2020, as part of the monitoring programme by Environment Canterbury Regional Council (Table 3; see Bayer & Meredith (2020) for full description). A 500 mL water sample was retrieved (by helicopter) from the mixed layer of these lakes and preserved with Lugol's Iodine, settled and transferred to smaller containers and shipped to the University of Adelaide for processing and analysis. The aim was to regularly sample for phytoplankton and water quality, but the COVID-19 Pandemic prevented this.

### 2.3 Sediment coring

Sediment cores from Lakes Ōtūroto, Ōpōrea, Kirihonuhonu, Emily and Te Puna a Taka were collected in November 2019 using a UWITEC Percussion corer with a 95 mm diameter core barrel (Figure 1). Diatom samples were collected for the first 10 cm at centimetre resolution, and then every second centimetre thereafter. For full methods see Chapter 4 and 5. Lake Te Puna a Taka is only discussed in this chapter. The diatom records from Lakes Ōtūroto, Ōpōrea, Kirihonuhonu and Emily are discussed in detail in Chapters 4 and 5.



**Table 3:** The number of habitat samples taken at each lake, and their corresponding substrate

Lake	Substrate				Total
	Plant (epiphytic)	Rock or pebble (epipelagic)	Sand or mud (benthic)		
Ōtūroto	9	6	2		17
Kirihonuhonu	3	2	4		9
Emily	-	-	2		2
Camp	-	2	1		3
Te Puna a Taka	6	2	2		10
Māori Lakes East	-	-	2		2
Ōpōrea	3	3	-		6
	<b>Planktonic</b>				
Lake	February 2020	March 2020	May 2020	June 2020	Total
Ōtūroto	1	1	1	-	3
Ōpōrea	1	1	-	1	3
Grasmere	1	1	-	1	3
Lyndon	1	1	-	1	3

#### 2.4 Diatom sample preparation and identification

The core and surface sediment samples were treated following Battarbee et al. (2002), using 15% hydrochloric acid to remove carbonates and 25% hydrogen peroxide to remove organic matter. The habitat samples were only treated with hydrogen peroxide. For each chemical step, samples were heated in a water bath at 70°C for three hours, with three rinses, using reverse osmosis treated water, between each process (Battarbee et al., 2002). Diatom slurries were permanently mounted on microscope slides using Naphrax (Brunel Microscopes). Diatoms valves ( $300 \pm 10$ ) were counted at x1000 magnification under oil immersion, on a Zeiss Axio A1 microscope with Differential Imaging Contrast. Identifications were made using: Krammer & Lange-Bertalot (1986), Krammer & Lange-Bertalot (1988), Krammer & Lange-Bertalot (1991a), Krammer & Lange-Bertalot (1991b), Vyverman, et al. (1995), Sonneman et al. (1999), Morales (2001), Knapp, Furey & Lowe (2006), Van de Vijver et al. (2008), Delgado et al. (2015), Reavie & Kireta (2015), John (2018), Rusanov et al. (2018), Wetzel & Ector (2021).

#### 2.5 Statistical analyses

Diatom assemblage data were converted to relative abundances before statistical analysis. A two factor PERMANOVA analysis (Anderson, 2001) was conducted on the habitat samples to test whether

substrate type (i.e. a fixed factor: plant, rock, mud) or lake (i.e. a fixed factor: Ōtūroto, Kirihonuhonu, Emily, Māori Lakes East, Camp, Te Puna a Taka and Ōpōrea) was a stronger explanatory variable on the diatom assemblage data. Samples from the same type of substrate were kept separate. A PERMANOVA is a permutational calculation used to assess the difference between group centroids of a cluster of samples, from a dissimilarity matrix (Anderson, 2001). This analysis was completed the *vegan 2.6-2* package (Oksanen et al., 2022) in R (R Core Team, 2021).

To examine the relationship between diatoms species and the environmental data, the surface sediment data set, was analysed together with the data from water quality monitoring in Bayer & Meredith (2020). Lakes Marymere and Horseshoe were not included any statistical analyses as there were no available monitoring data. The environmental variables use were TN, TP, maximum lake depth, and chlorophyll *a*. There was no other water quality data available. A redundancy analysis (RDA) was undertaken using the *vegan 2.6-2* package (Oksanen et al., 2022) in R (R Core Team, 2021) to ascertain the water quality variable that explains the most variance in the diatom data. Data were square-root transformed prior to PERMANOVA and RDA analyses to reduce the influence of dominant taxa (such as those belonging to the Fragilariaceae family), and diatom taxa appearing at least once at 5% abundance were included.

To characterise the ecology of *Discostella stelligera* in Canterbury lakes, simple weighted averaging optima and tolerances (Birks et al., 1990; ter Braak & Juggins, 1993) for TN were derived in C2 Version 1.7.7 (Juggins, 2007). There were diatom assemblage data for 26 lakes, but four lakes were excluded from the analysis: Lakes Marymere and Horseshoe did not have any associated water quality data and Lake Denny and Māori Lakes East were extreme outliers (> 250 µg TN residuals between measured and diatom inferred TN). These lakes are situated in catchments with high agriculture use. The optima and tolerances were therefore developed from a data set of 22 lakes. The surface data set is discussed in the context of the N2 value (Hill, 1973) of each taxon from the weighted averaging model of the 22 lakes, which is analogous to the effective number of occurrences in the data set (Sienkiewicz et al., 2021). However, due to the small number of samples which renders more complex models (e.g. Generalise additive models) inappropriate, this approach is likely to provide some insights into the ecology of select taxa, including *Discostella stelligera*. COVID travel restrictions meant the field sites could not be accessed and consequently this is a small data set, yet, these statistical analyses provide some indication of water quality variables that drive diatom species distribution.

### 3 Results

#### 3.1 Surface samples



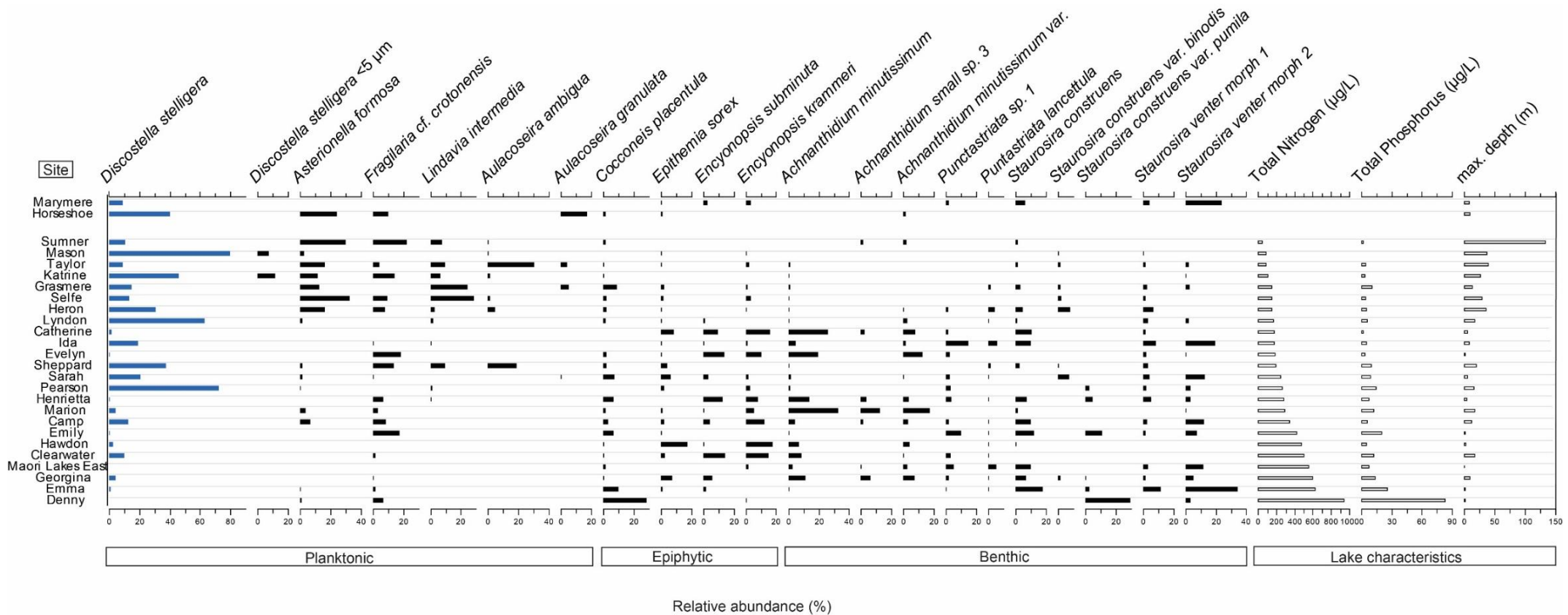
The most common diatom taxon in the surface data set (26 lakes) was *Discostella stelligera*, occurring in 16 of 26 lakes at 5% or more (N2 = 9.4) (Figure 2). The next most common taxa found in abundances of 5% or more, were: *Achnantheidium minutissimum* (N2 = 7.2), *Asterionella formosa* (N2 = 6.7), *Cocconeis* cf. *placentula* (N2 = 9.7), *Encyonopsis krammeri* (N2 = 8.1), *Encyonopsis subminuta* (N2 = 6.4) *Fragilaria* cf. *crotonensis* (N2 = 9.2), *Lindavia intermedia* (N2 = 4.9), *Punctastriata* sp. 1 (N2 = 6.0), *Staurosira construens* (N2 = 8.9), *Staurosira venter* morph 1 (N2 = 10.4), *Staurosira venter* morph 2 (N2 = 5.5), *Staurosira* cf. *ovata* (N2 = 5.5) (Figure 2).

### 3.2 Habitat samples

There were 49 habitat samples analysed from seven lakes. From the Ōtūwharekai region, Lakes Ōtūroto ( $n = 17$ ), Kirihonuhonu ( $n = 9$ ), Emily ( $n = 2$ ), Camp ( $n = 3$ ), Te Puna a Taka ( $n = 10$ ), Māori Lakes East ( $n = 2$ ), and the Selwyn-Waihora region, Ōpōrea ( $n = 6$ ) were analysed. This included 13 benthic samples collected from the lakebed, either sand or mud, 21 plant samples from four lakes and 15 rock scrapes from shoreline pebbles or rocks (Figure 3). From these samples the most common taxa occurring in abundances of 5% or more were: *Achnantheidium minutissimum* ( $n = 28$ ), *Cocconeis* spp. ( $n = 10$ ), *Encyonopsis krammeri* ( $n = 24$ ), *Epithemia sorex* ( $n = 9$ ), *Nitzschia perminuta* ( $n = 10$ ), *Punctastriata lancetulla* ( $n = 8$ ), *Staurosira binodis* ( $n = 9$ ), *Staurosira construens* cf. *var pumila* ( $n = 10$ ), *Staurosira venter* morph 1 ( $n = 17$ ), *Staurosirella* cf. *ovata* ( $n = 9$ ) and *Tabellaria* spp. ( $n = 9$ ). Several species, belonging to the benthic family Fragilariaceae (*Staurosirella* cf. *ovata*, *Punctastriata* sp. 1, *Pseudostaurosira* sp. 1), in this study were unable to be identified (Morales, pers. comm.), and are likely new to science (Supplementary Figure S4–S7). There were no taxa growing on just one type of substrate, although some taxa appeared to prefer specific substrates. *Cocconeis* cf. *placentula* was found mostly on plant samples, *Encyonopsis krammeri*, *Tabellaria flocculosa* and *Achnantheidium minutissimum* all preferred plant and rock habitats (Figure 3), while taxa belonging to the Fragilariaceae family: *Staurosira construens*, *S. construens* cf. *var. pumila*, *S. venter* morph 1 and morph 2, *S. binodis*, *Staurosirella* cf. *ovata*, *Punctastriata lancetulla* were mostly found in plant, mud or sand habitats with only a small abundance from rock samples. *Encyonopsis krammeri*, *Cocconeis* spp., *Epithemia sorex* and *Achnantheidium minutissimum* were found in reasonable abundance (> 15%) on *Myriophyllum* spp., *Potamogeton tricophyllus* and *Isoetes alpines* (Figure 4). *Tabellaria* spp. was found growing on *Apodasmia similis* at > 70% abundance, as was *Staurosira binodis* at 30%. The taxa belonging to Fragilariaceae were uncommon on *Myriophyllum* spp. and *Isoetes alpines*.

PERMANOVA showed distinct diatom assemblages between different habitat groups: F-statistic 5.06,  $p < 0.001$ . The PERMANOVA results for diatom assemblages according to lake were: F-statistic 4.36,  $p < 0.001$ . In the RDA, TN and TP together explained 24% of variance in the data, while TN by itself

explained 15%, and TP explained 9% of the variance (Figure 5). The TN transfer function performed only moderately well with a leave one out correlation coefficient of  $r^2=0.39$  and a Root Mean Squared Error of Prediction (RMSEP) of  $139 \mu\text{g l}^{-1}$  TN. Nevertheless, *Discostella stelligera*, which has an approximately unimodal distribution along the TN gradient (Figure 6), had an optimum of  $189 \mu\text{g l}^{-1}$  and a tolerance of  $105 \mu\text{g l}^{-1}$ . Notably a TP model performed much more poorly ( $r^2=0.06$ , RMSEP of  $5.5 \mu\text{g l}^{-1}$  TP), even with the two largest outliers (Lakes Denny and Kirihonuhonu excluded).



**Figure 2:** Diatom assemblage data in surface samples from 26 high country lakes. Taxa found at  $\leq 5\%$  abundance in at least two samples are shown. Lakes are plotted according to Total Nitrogen concentration (lowest to highest). Note: There were no water quality data available for Lakes Marymere and Horseshoe.

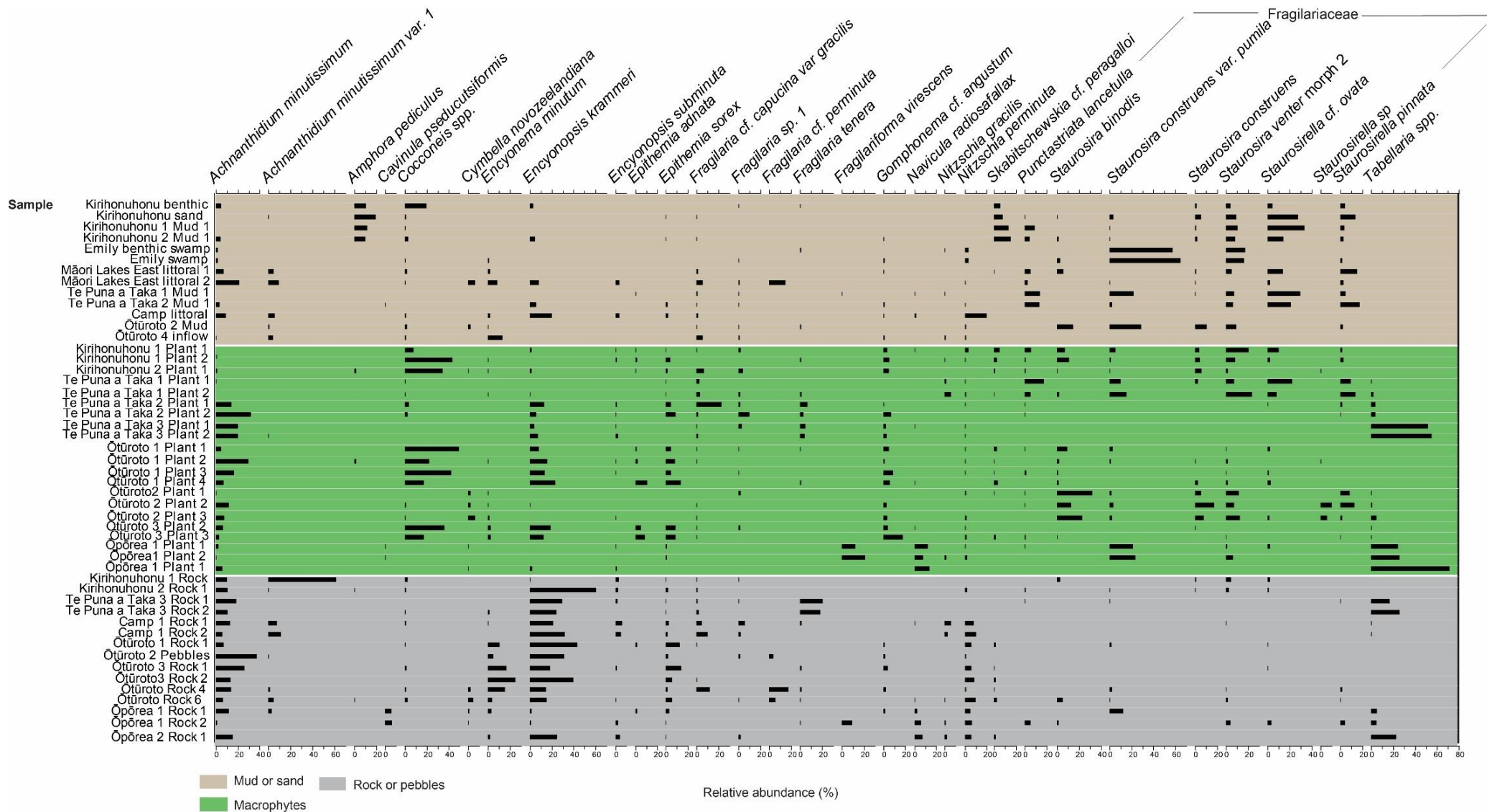
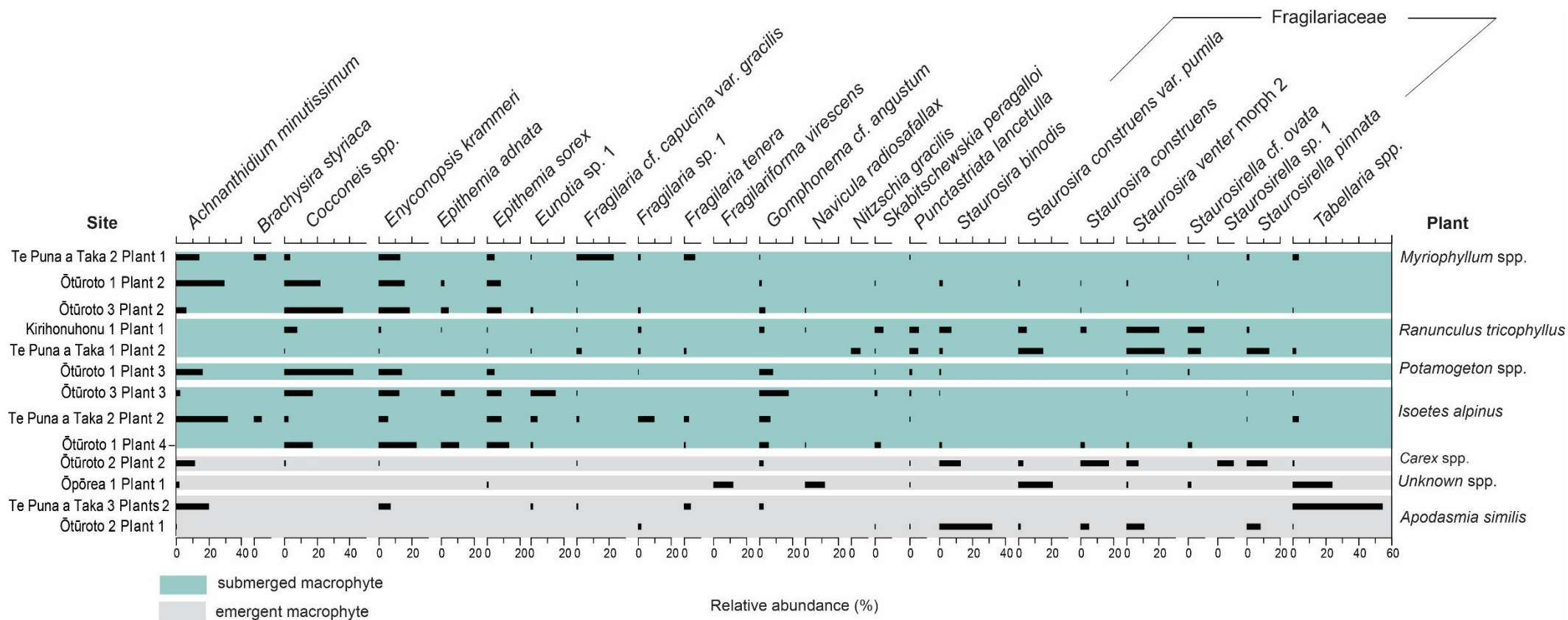
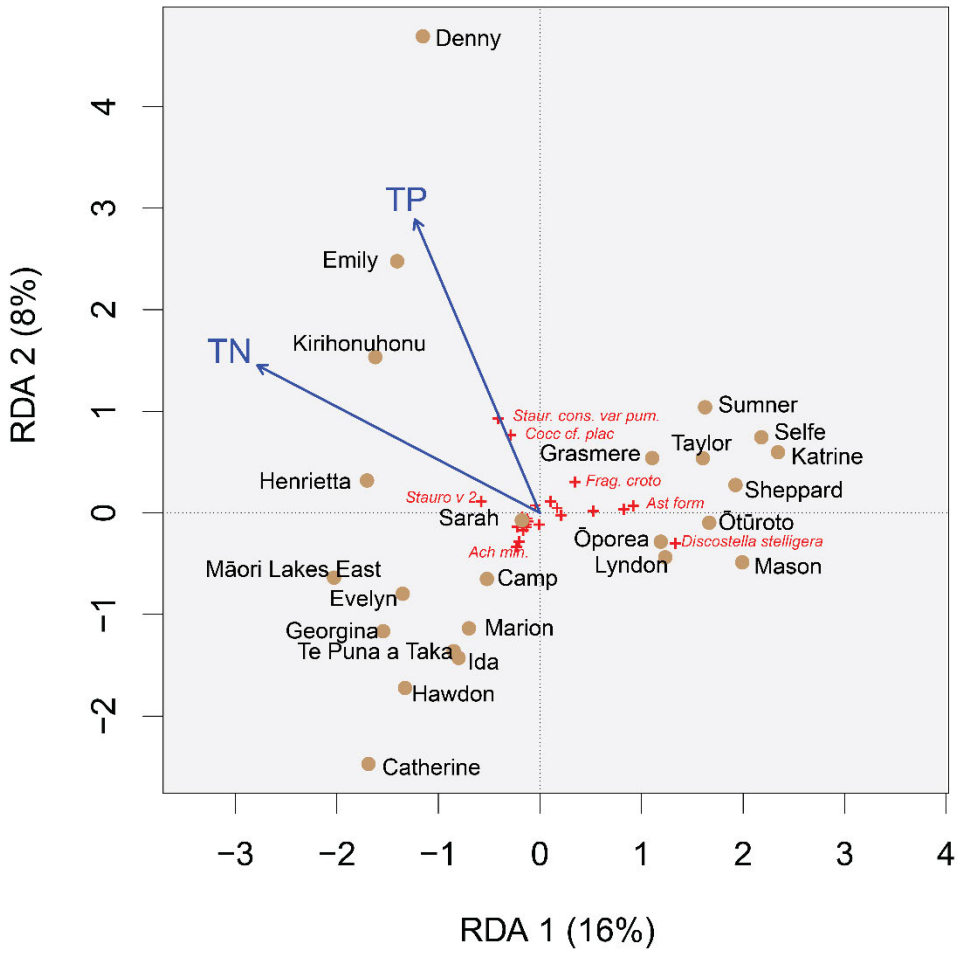


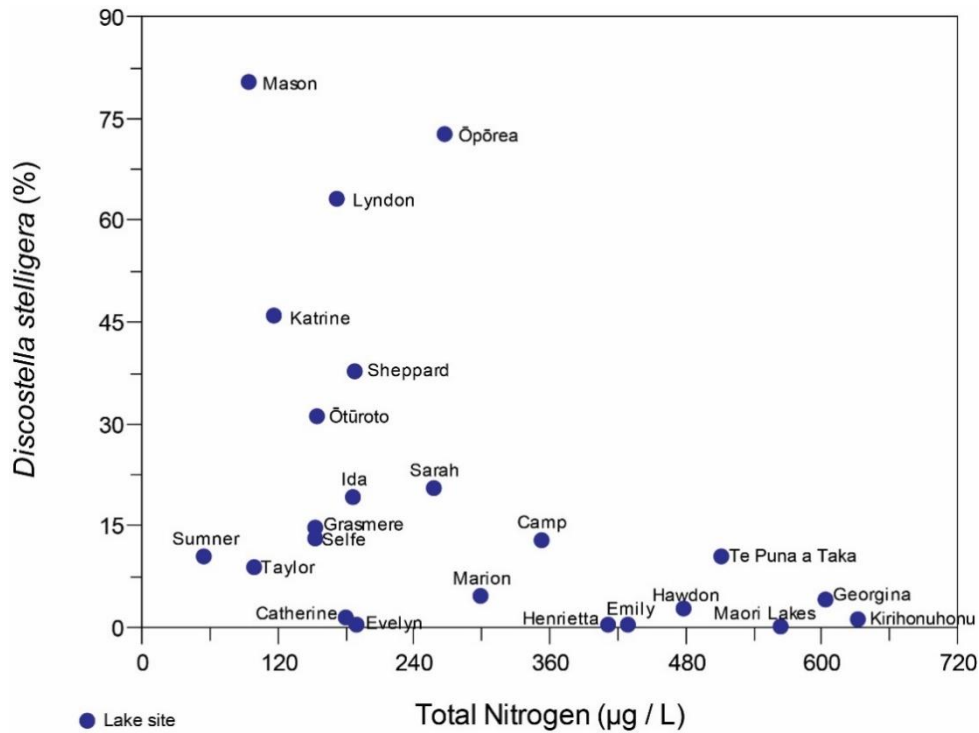
Figure 3: Diatom assemblage data from habitat samples in the Ōtūwharekai and Selwyn-Waihora (Lake Ōpōrea) regions. Taxa at ≤ 5% in at least two samples are shown



**Figure 4:** Diatom assemblage data from the different macrophytes. The macrophyte species is listed on the left-hand side. These data are a subset of the data presented in Figure 3.



**Figure 5:** Results from the RDA ordination of the surface samples. The red crosses mark diatom taxa, while select taxa are labelled. *Staur. v 2* = *Stauosira venter* morph 2, *Staur. cons. var. pum.* = *Stauosira construens* var. *pumila*, *Frag. croto* = *Fragilaria* cf. *crotonensis*, *Ast. form.* = *Asterionella formosa*

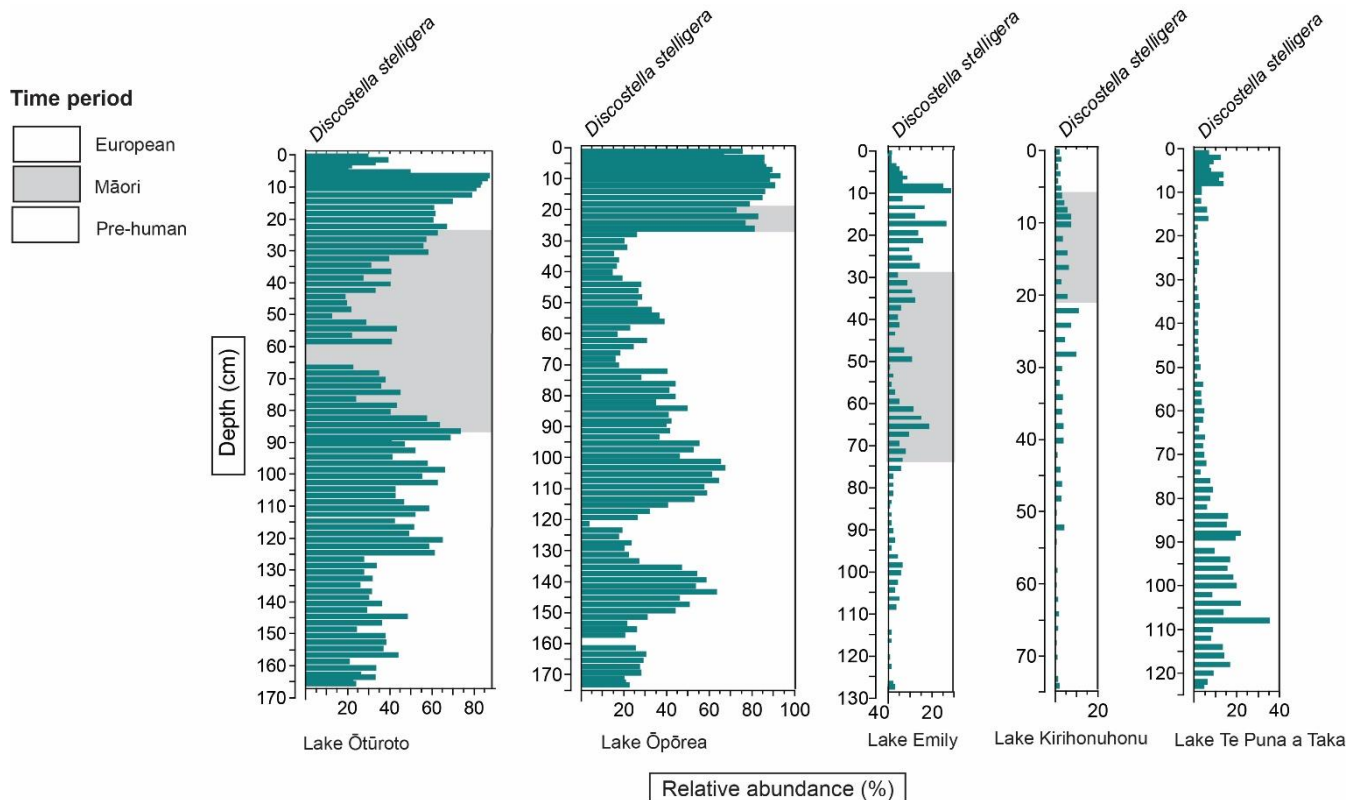


**Figure 6:** The relative abundance of *Discostella stelligera* in surface samples vs TN concentration in the Canterbury lakes. Lake Denny was removed from this plot as it is an outlier in its TN concentration 950 µg/L and there was no *D. stelligera*.

### 3.3 Sediment core assemblage data

Lake Te Puna a Taka is only considered in this chapter as the diatom (and pollen) record indicated accelerated deposition and mixing had occurred in the core, suggesting the record only spanned a few years (Supplementary Figure S1–3). The trend for *Discostella stelligera* in Lakes Emily and Ōpōrea shows broad increases in the taxon following evidence of first Māori activity in the landscape (Figure 7), while the taxon declines in Lakes Ōtūroto and Kirihonuhonu (Chapter 4, Figure 5). Towards the present, the taxon declines in all lake records. There is some trend in Lake Te Puna a Taka but due to the irregular depositional profile and lack of analysis, its interpretation is uncertain.





**Figure 7:** *Discostella stelligera* abundance in five Canterbury high country lakes palaeolimnological records. The shaded area represents the time of Māori settlement in the catchment, determined by pollen stratigraphy in Chapters 4 and 5. This information was not available for Lake Te Puna a Taka where it is likely that the entire stratigraphy is post-European.

## 4 Discussion

There is a fundamental difference in the drivers of planktonic and benthic taxa in lakes. Planktonic diatoms are those that inhabit the water column and are often dominant in open water conditions (Wolin & Stone, 2010) and are an important component of pelagic food webs (*sensu* Vadeboncoeur et al., 2003; Berger et al., 2010). While, like littoral zone taxa they are also influenced by light availability and nutrient concentrations, additional variables that determine their abundance include water column stability, thermal structure (temperature), turbulence and lake level, e.g. Stone & Fritz (2004), Rioual et al. (2007), Hobbs et al. (2010), Rimet, Bouchez & Montuelle (2015), Streib et al. (2021). Compared to benthic (attached) taxa, planktonic taxa are generally thought to be more influenced by their surrounding water chemistry (Siver, 1999; Winegardner et al., 2015; Benito et al., 2018b). In this data set the planktonic taxa belonging to genera *Fragilaria*, *Asterionella*, *Lindavia*, *Aulacoseira* and *Discostella*, while the benthic data set was diverse comprising species from *Staurosira*, *Staurosirella*, *Punctastriata*, *Encyonopsis* and *Achnanthisidium*.

### 4.1 Habitat samples



In the habitat samples, there was a diversity of diatom taxa, many of which were found in both the surface samples and the longer sedimentary records described in Chapters 4 and 5. Attached algae in shallow lakes, or the littoral zone of larger lakes, are an important component of whole lake primary productivity contributing significantly to in-lake biogeochemical cycles (Vadeboncoeur et al., 2008). These lake areas often have high light availability favouring the growth of algae, which can become part of the periphyton growing attached on substrates (Vadeboncoeur & Power, 2017). In New Zealand, periphyton are comprised of a broad range of diatom taxa and other algae (Biggs & Kilroy, 2000). Apart from nutrient concentrations, there is a wide range of environmental variables that influence presence or absence of taxa in the littoral zones of lakes, including light availability as a function of depth (Kingsbury, Laird & Cumming, 2012; Gushulak & Cumming, 2020) or dissolved organic matter (Ask et al., 2009), or greater physical disturbance (Rimet, Bouchez & Montuelle, 2015). The microhabitat, or microtopography, of specific substrates, e.g. plants and rocks, can also influence the composition of algal species and the structure of the assemblage (Murdock & Dodds, 2007; Woller-Skar et al., 2021). This in turn, affects how algae respond to resource availability, e.g. light, or physical disturbance, e.g. wave action. Consequently, there is a complexity in determining the dominant abiotic or resource control upon algal growth in littoral zones. Nevertheless, despite the diversity in variables that influence species composition in littoral zones PERMANOVA analyses revealed that substrate type was a more significant explanatory variable for diatom species than the lake in which the assemblage was found.

Despite the bias in different sample size for each lake, it is interesting that substrate type had greater explanatory power than the lake in which the samples was taken, as there is clear difference in trophic level for each lake, especially comparing the water quality variables between Lake Ōtūroto and Lake Kirihonuhonu. Lake Ōtūroto has reasonably good water quality (mesotrophic) and is considered the “ideal” lake in the region (Bayer, pers. comm.), while in contrast Lake Kirihonuhonu is well known for its eutrophic conditions and subsequent variability in its macrophyte population (Schallenberg & Sorrell, 2009; Bayer & Meredith, 2020). It has been found that chemical characteristics of lakes are less likely to influence epiphytic (or epilithic) diatom assemblages when compared to pelagic zone (planktonic) diatoms (Rimet, Bouchez & Montuelle, 2015; Riato & Leira, 2020). It is likely that disturbance and light availability have greater contribution, or control, over diatom species distribution on substrates, possibly irrespective of the substrate sampled (Cantonati & Lowe, 2014; Rimet, Bouchez & Montuelle, 2015). A good example of the relationship between light availability and the presence of diatom taxa in this suite of lakes and samples, is in relation to the two dominant taxa: *Staurosira construens* cf. *var pumila* and *Staurosirella* cf. *ovata*. Both were reasonably abundant in the habitat scrapes and the sedimentary record. *Staurosirella* cf. *ovata* is abundant in Lakes Emily and

Ōpōrea (Chapter 5), and to a lesser extent Lake Kirihonuhonu. *Stausirella cf. ovata* was also abundant in Lake Oporoa (Chapter 3) and was inferred as an indicator of high light penetration and low nutrients. However, the taxon is found in Kirihonuhonu, Emily and Te Puna a Taka which are all eutrophic lakes. While this suggests a broad tolerance to nutrient concentrations it is likely that light availability has greater control over the presence or absence of *Stausirella cf. ovata*, which is subsequently “replaced” by *Stausira construens cf. var pumila* in Lake Emily, while disappearing in Lake Ōpōrea. In these eutrophic lakes *Stausirella cf. ovata* was abundant from samples collected under higher light levels (shallow water depth) and was only prevalent in all sedimentary records prior to human activity, likely a reflection of higher light availability. Conversely, *Stausira construens cf. var pumila* is likely to have a higher tolerance to light attenuation than *Stausirella cf. ovata* as it is abundant in the records of Lakes Emily (and Kirihonuhonu) where turbidity is higher. Additionally, with respect to their tolerances for disturbances, both taxa were abundant on aquatic macrophytes or benthic (sand or mud grains) samples, in comparison to rocks and pebbles. These substrates are more influenced (i.e. through movement) during disturbance events.

In this study, although some taxa had specific substrate preferences taxa, i.e. *Cocconeis* spp., mostly exclusive to plants and *Stausirella cf. ovata* preferring plants and mud, the study revealed that some species were common across all substrates despite the PERMANOVA results. Interestingly, there was no diatom taxon that was exclusively found on one substrate type (Figure 3). This has been reported elsewhere, e.g. Lim, Kwan & Douglas (2001), and demonstrates the care with which autecological preferences should be assigned to diatom taxa, especially when reconstructing past habitats. The habitat samples contribute to further understanding of Fragilariaceae taxa (Figures 3, 4). These species were found in primarily benthic and epiphytic habitats, with only small representation in epilithic samples. While, this confirms the habitat attribution frequently given to these genera, as taxa that grow abundantly in shallow lake systems, and littoral zones by extension (e.g. Bennion, Fluin & Simpson, 2004), in this study region these taxa prefer plants and sandy or muddy substrates. This is irrespective of nutrient level as the sample lakes covered a range of trophic categories. Furthermore, while these species are abundant in many shallow lake systems, globally, hindering their interpretation in quantitative reconstructions, e.g. Bennion, Appleby & Phillips (2001), these studies have occurred in lakes where TP values are well in excess of those recorded in these Canterbury lakes. Despite the eutrophic (or higher) classification for some Canterbury lakes the full range of TP (2–84 µg/L) is still low, compared to other lakes globally. Indeed, two of these lakes are classified as oligotrophic in Vadeboncoeur et al. (2021). This would also create problems if studies from outside New Zealand were used to reconstruct water quality history with the same taxon, as values would be over-represented, e.g. in Whitmore et al. (2018), TP optima for *Stausira construens* and *Stausira*

venter are 39 µg/L and 90 µg/L respectively which exceeds the TP range of all sampled lakes in Canterbury (TP from 2–84 µg/L). Gregeresen & Simon (2022) observed a similar issue for select taxa (*Fragilaria crotonensis*, *Fragilaria capucina* and *Nitzschia palea*) when using data sets from outside the North Island dune lakes. This problem highlights the necessity to develop regional data sets if there is interest in establishing quantitative reconstructions from longer sedimentary records or when establishing baseline conditions from an ecological understanding of the sedimentary record.

There was some evidence for diatom assemblages preferring specific plants. *Achnantheidium minutissimum* and *Encyonopsis krammeri* were more abundant on submerged macrophytes *Myriophyllum* spp., *Isoetes* spp. and *Potamogeton* spp. but not *Ranunculus* spp. (Figure 4). Meanwhile Fragilariaceae were common on *Ranunculus* spp., *Carex* spp. and *Apodasmia similis*. Host plant specificity can occur in epiphytic diatom assemblages (Rojas & Hassan, 2017) but the driving mechanism is thought to be more related to the microtopography (surface structure) of the substrate, rather than surrounding water chemistry (Letáková et al., 2016). In the Canterbury region, analysing additional plant samples would be useful in deciding whether there were significant patterns (e.g. genus or species' preferences) in diatoms assemblages growing on New Zealand's aquatic macrophytes (including submerged, emergent or sprawling macrophytes). The diatom taxa found in the habitat samples of this study, should be considered alongside the more "traditional" epiphytic genera like *Epithemia* and *Cocconeis* when aiming to understand historic macrophyte abundance from diatom records.

*Achnantheidium minutissimum* and *Encyonopsis krammeri* were both abundant in epilithic, and to a lesser extent epiphytic samples, and together they sometimes mirrored the abundance of *Tabellaria* spp. This epilithic habitat preference is consistent with other *Encyonopsis* taxa especially those in the *Encyonopsis microcephala* group in which *E. krammeri* sits (Bahls, 2013; Kennedy, Buckley & Allott, 2019; Kennedy & Buckley, 2021). *A. minutissimum* is also found in epilithic samples (Pla-Rabés & Catalan, 2018) but can grow upon multiple substrates (Michelutti et al., 2003). Both taxa were abundant in rock samples taken from the shoreline, where there was high light availability and disturbance from wave action indicating their tolerance to such conditions; a trait of *A. minutissimum* (Biggs & Thomsen, 1995; Pla-Rabés & Catalan, 2018). Even though no water quality samples were taken at the exact location of the sample, the lakes themselves were alkaline with pH > 8 at the time of coring, which supports the broad alkaline preference of *E. krammeri* (Bahls, 2013; Kennedy & Buckley, 2021). The TN optimum (N2 = 8.1) was 335 µg/L which fits in the mesotrophic category of New Zealand's lakes, which is important to consider in the longer sedimentary records due to the abundance of *Encyonopsis krammeri*. It is also likely *Encyonopsis krammeri* species can become

abundant on plants as other taxa in the genus do (Sonneman et al., 1999) especially in shallow lake environments if light conditions are favourable.

A comparison between the habitat samples with the downcore data revealed that some taxa appeared underrepresented especially in Lakes Ōtūroto and Ōpōrea. These two lakes had greater abundances of planktonic taxa in their longer records. For example, in Lake Ōpōrea, epiphytic samples had an abundance of *Tabellaria* spp. but this was rarely seen in the record and Lake Ōtūroto had an abundance of *Encyonopsis krammeri*, which was only found in small amounts in the most recent (~10 years) diatom stratigraphy. *Didymosphenia geminata* (an invasive diatom) is also present in Lake Ōtūroto (Bayer, pers. comm.) but was not found in the sedimentary record. Lake bathymetry plays an important role in the depositional profile of sediments (Blais & Kalff, 1995; Stone & Fritz, 2004) and the complex bathymetries of Lakes Ōtūroto and Ōpōrea, in that there are separate basins in each lake (Figure 1) will have influenced the depositional profile likely preferencing planktonic diatoms. Despite this, other epilithic and epiphytic taxa from this data set, e.g. *Encyonopsis krammeri*, *Achnanthydium minutissimum sensu lato*, *Epithemia*, *Gomphonema*, *Encyonema* and *Nitzschia* (not including colonial Fragilariaceae which have multiple substrate preferences) were still present in both lakes and therefore the sedimentary records from Lakes Ōtūroto and Ōpōrea broadly reflect the array of habitat and ecological conditions of their lake.

In addition to understanding diatom habitats, and their interpretation in the sedimentary record, it may be possible to use this sampling strategy and their corresponding diatom assemblages, to detect early changes in water quality. There is increasing emphasis in using littoral zone diatom taxa as part of routine ecological monitoring (Kelly, Snell & Surridge, 2018; Kennedy & Buckley, 2021). This is due to the ability of diatoms to rapidly respond to their surroundings and as such, they can act as an early indication of the effects of anthropogenic activity in catchments (Snell & Irvine, 2013; Rimet, Bouchez & Montuelle, 2015; Kelly, Snell & Surridge, 2018) prior to their sedimentation in the pelagic zone of lakes. There is evidence to suggest that epiphytic diatoms in New Zealand from wetlands, are useful for assessing wetland condition (Kilroy et al., 2017). Landscape-lake interactions have a different suite of abiotic factors that influence littoral zone taxa in comparison to the variables controlling diatom taxa inhabiting deeper areas of lakes (Cantonati & Lowe, 2014; Gushulak & Cumming, 2020). Regular monitoring of periphyton in the littoral zone may detect seasonal trends that occur in these communities and build up a profile of the environmental variables that could influence diatom species composition (Cantonati & Lowe, 2014). Using *Didymosphenia geminata* as an example, even though it was not recorded in any of these samples, this species has been found in the littoral zone of Lakes Ōtūroto (Bayer & Meredith, 2020), and prefers freshwater systems under nutrient limiting conditions (Bray et al., 2016). There is the possibility, therefore, that some of the taxa from the habitat samples

could be a direct result of catchment activity that is not yet observed in the sedimentary record and cannot be explained through routine water quality monitoring (which currently takes samples from the lake's surface, or epilimnion).

#### 4.2 *Discostella stelligera* and its presence in New Zealand

*Discostella stelligera* is one of the most common diatom taxa in the Canterbury high country lakes, and was found in 16 of the 26 lakes, at an abundance of at least 5%. It is dominant in the sediment records of Lakes Ōtūroto and Ōpōrea, and to a lesser extent, Lakes Kirihonuhonu, Emily and Te Puna a Taka (Figure 7 and Chapter 4). It was also abundant in Lake Oporoa, a North Island site (Chapter 3), and has been found in other lakes on both the North (Augustinus et al., 2006; Stephens et al., 2018) and South (McWethy et al., 2010) islands. The taxon is also common in New Zealand's lakes with a preference for low nutrient lakes (Reid, 2005) which is broadly consistent with it being used as a global indicator of oligotrophic conditions (Saros & Anderson, 2015). It was abundant in Lakes Ōtūroto and Ōpōrea before human arrival while having a fluctuating presence in Lakes Kirihonuhonu and Emily.

Both the RDA and weighted averaging calibration show that TN has greater explanatory power, than TP in this data set, therefore indicating the suitability of deriving TN optima for the surface sample data. Results indicating that for *Discostella stelligera* the optimum for TN is 180 µg/L. This sits in the mesotrophic category for New Zealand's lakes. In the four lakes, Lakes Mason, Katrine, Lyndon and Ōpōrea where *D. stelligera* comprised 50% or more of the sample, the range for TN was 95–268 µg/L. While the model performance, was low ( $R^2=0.39$  for TN) and does not account for other abiotic variables that can determine a species' abundance (*sensu* Juggins, 2013) the data from this study indicate that *Discostella stelligera* is suited to both oligotrophic (and likely microtrophic) and mesotrophic categories for New Zealand's lakes (Table 2). The taxon is known to respond favourably to nutrient enrichment (Saros & Anderson, 2015) and therefore mesotrophic conditions are within the taxon's ecological range, a key factor when considering its historic and present abundance in Canterbury's lakes. In the Canterbury high country, nutrient concentrations, as a response to catchment activities, are likely to be the dominant control over the abundance of *Discostella stelligera* in lakes given the taxon's concomitant response to any inferences of change in nutrient status. The sedimentary records of Lakes Ōpōrea and Emily (Figure 7) indicate that *Discostella stelligera* increased after evidence of Māori settlement, a result of the nutrient loading that occurred following sediment erosion driven by catchment landscape clearance (Chapter 4), while declining in Lake Ōtūroto as the increasing nutrients likely favoured other taxa. Furthermore, in the recent decades, *Discostella stelligera* concomitantly declines (Chapter 5) with increasing nutrients (TN and TP) in Lakes Ōtūroto and Ōpōrea.

Fluctuations in the abundance of *Discostella stelligera* (and other planktonic taxa especially those belonging to *Discostella*, *Cyclotella* and *Lindavia*), however, have been used in other lakes, as a reflection of the effects of anthropogenic climate warming, e.g. Winder, Reuter & Schladow (2009), Rühland, Paterson & Smol, (2015), Michelutti et al. (2015), Streib et al. (2021). In lakes in the Arctic, North and South America, the unprecedented abundance of *Discostella stelligera* has been attributed to increases in temperature driving factors such as enhanced thermal stratification, shallower mixing depths and longer ice-free periods (Winder, Reuter & Schladow, 2009; Rühland, Paterson & Smol, 2015; Michelutti et al., 2015; Saros et al., 2016; Sivarajah et al., 2020; Wiltse et al., 2022). The exact driver behind its shifts, however, is complex as it involves interactions between different physical and chemical structures of lakes (Saros & Anderson, 2015; Boeff et al., 2016; Reavie et al., 2017) which further varies between lakes. For example, as the climate warms, intensified stratification can reduce the concentration of nutrients (nitrogen) in the photic zone, as there is limited re-supply of nutrients from mixing (Winder, Reuter & Schladow, 2009), while deeper mixing (from temperature increases) can contribute to altered light exposure and reduce the abundance of *Discostella stelligera* (Saros et al., 2016).

In New Zealand, there is some indication that *Discostella stelligera* and *Cyclotella* have responded to climate warming. In Lake Wanaka, a larger (max. 311 m depth, 18 000 ha) microtrophic lake on the South Island these taxa have become more dominant compared to their historic abundance, and this shift has been attributed to the warming of surface waters (Bayer, Schallenberg & Burns, 2016). However, in Canterbury diatom blooms occur in autumn and winter (Bayer, pers. comm.), and therefore, the effects of climate change presented as an earlier onset of a spring phytoplankton bloom (Peeters et al., 2007) is not necessarily applicable. There are also differences in mixing and stratification patterns in the Canterbury lakes (polymictic and seasonal stratification, Bayer & Meredith, 2020) and so there is difficulty in predicting the effects of climate change in these lakes, although it is likely the trends in phytoplankton will change (Bayer & Meredith, 2020). However, a winter phytoplankton bloom could occur earlier if the bloom itself is a result of the eroding hypolimnion and subsequent internal supply of nutrients (Bayer, Schallenberg & Burns, 2016). The patterns in *Discostella stelligera* abundance of the lakes in Canterbury, therefore, need to be assessed in context of their longer record and their historic response to external factors (Rühland et al., 2015) and given the aforementioned fluctuations of the taxa with changing nutrient concentrations the interpretation of the taxon's abundance in the high country lakes, especially, Lakes Ōtūroto and Ōpōrea from the time of first Māori activity to present (Chapters 4 and 5) is associated with changing nutrient concentrations, and with caution, this can be applied to the interpretation of the taxon's abundance in other Canterbury lakes, instead of a mechanism of climate change. Regular

phytoplankton monitoring and water quality monitoring is required to understand the effects of climate change on *Discostella stelligera* (and other planktonic taxa) in New Zealand's lakes (*sensu* Li et al., 2014). This would also provide insight into the dominant nutrient control on the taxon.

#### 4.3 Other planktonic taxa and their nutrient optima

In the Canterbury lakes, the other abundant planktonic taxa in both the sedimentary diatom records (Chapters 4 and 5), and surface samples, were *Aulacoseira ambigua*, *Asterionella formosa*, *Fragilaria crotonensis* and *Lindavia intermedia*. These taxa are generally associated with greater nitrogen availability, in particular *Asterionella formosa* (Wolfe, Van Gorp & Baron, 2003; Arnett, Saros & Mast, 2012). *Asterionella formosa* is a planktonic taxon which is frequently inferred to be an indicator of N enrichment, particularly atmospheric N deposition in low nutrient Northern Hemisphere lakes (Wolfe, Baron & Cornett, 2001; Saros et al., 2005). *Fragilaria crotonensis* is similarly an N enrichment indicator (Saros et al., 2011; Arnett, Saros & Mast, 2012; Klamt et al., 2021) but in New Zealand is more likely an indicator of P limitation and responds to N if P is no longer limiting (Gregersen & Simon, 2022). In the plankton samples taken over several months from Lakes Ōtūroto and Grasmere, there are higher abundances of *F. crotonensis* and *Asterionella formosa* when *Lindavia intermedia* and *Aulacoseira ambigua* are low, and vice versa (Supplementary Table S1, S3). This indicates complexity in resource availability and limitation for these diatom taxa. Regular monitoring of planktonic diatoms and water chemistry may be able to detect the dominant control.

*Asterionella formosa* was abundant in the surface sediment samples of a selection of lakes ( $N_2 = 6.7$ ) with a TN optimum of 140  $\mu\text{g/L}$ . Applying niche conservatism theory *Asterionella formosa* should be an indicator of N enrichment given its ability to respond to these conditions (Saros et al., 2005). However, the TN optimum of the taxon in this data set, is lower than *Discostella stelligera*, despite the fact that in Lake Ōtūroto increasing *Asterionella formosa* (Chapter 5) is concomitant with increasing N concentrations. This in turn, coincides with greater fertiliser application and agricultural activities occurring in New Zealand (Ministry for the Environment & StatsNZ, 2020). The small number of samples, low  $N_2$  and poor model performance prevents *Asterionella formosa* from being used as an indicator of TN in this data set. Furthermore, while the changing land-uses in the region indicate increasing N availability in these lakes, there is emerging evidence that like *Discostella stelligera*, *Asterionella formosa* may also be an indicator of anthropogenic climate warming. This has been one of the suggestions for its presence (along with *Lindavia intermedia*) in low-nutrient lakes where instead of declining with nutrient levels, the taxon continues to remain abundant (Sivarajah et al., 2016). Instead, it is thought that warming temperatures have contributed to longer ice-free periods and changes in the timing (earlier) of stratification, and mixing depth, thus favouring *Asterionella*

*formosa* abundance (Interlandi, Kilham & Theriot, 1999; Enache et al., 2011; Berthon et al., 2014; Rühland et al., 2015; Sivarajah et al., 2016; Gushulak et al., 2021). However, for this data set there is strong evidence that the taxon reflects nutrient concentrations, although the regular monitoring of Canterbury lakes will assist with determining whether anthropogenic climate warming becomes a dominant driver of its (and *Discostella stelligera*) presence in the future.

The ecology of *Lindavia intermedia* in New Zealand's lakes has received considerable attention as it is one of two invasive and nuisance diatoms species in New Zealand – the other being *Didymosphenia geminata* (Kilroy et al., 2021). The species was accidentally introduced in the early 2000s (Novis et al., 2017; Kilroy et al., 2021), and was first detected in abundance in microtrophic Lake Wanaka further south on the South Island. The taxon produces extracellular polymeric substances, forming mats, and giving appearance of large algal biomass in these lakes, commonly termed 'lake snow' (Novis et al., 2017). Despite the nuisance taxon being widespread, there is still limited understanding of its specific ecology even though its occurrence and production of extracellular polymeric substances occurs in oligotrophic (low nutrient) lakes (Novis et al., 2021). Lake snow is thought to be more abundant in the summer and autumn (Novis et al., 2021), while cell counts of the taxon shows greater abundance in winter, however the relationship between cell concentration and lake snow abundance is poor (Novis et al., 2021). Diatom counts from Lakes Lyndon and Grasmere from February, March and June 2020, show high cell counts in February and March for both lakes and in June for Grasmere. Lake Ōtūroto data from the same sampling period also has a similar trend as Lyndon, but other planktonic taxa are more abundant (Supplementary Table S1). Kilroy et al. (2021) suggested that the presence of *Lindavia intermedia* is strongly associated with cool, low nutrient systems where TP is < 0.011 mg/L. The TP values for Lakes Ōtūroto and Ōpōrea are lower than the threshold listed in Kilroy et al. (2021), while the TP levels in Lakes Kirihonuhonu and Emily have been higher than the threshold since water monitoring commenced (Bayer & Meredith, 2020). Lastly, as there are reliable data indicating it is introduced, *Lindavia intermedia* was included in the age models for Lakes Ōtūroto and Ōpōrea in Chapters 4 and 5.

*Aulacoseira ambigua* is interpreted in the Canterbury lakes as an indication of nutrient enrichment (N, P and Si) given its established affinity for mesotrophic-eutrophic conditions and higher Si requirements (Rioual et al., 2007; Poister et al., 2012). In Lake Ōtūroto's sedimentary record, *Aulacoseira ambigua* clearly marked a response to landscape vegetation change following Māori settlement (Chapter 4), with the idea that catchment erosion drove an influx of nutrients into the lake causing decline in oligotrophic species *Discostella stelligera*. A low N2 for a species in a model (*Aulacoseira ambigua*, N2 = 2.5) means inferred nutrient optima are unreliable, even more so when combined with the low performance of the model. In the modern samples *Aulacoseira ambigua* was found in Lake Taylor



(oligotrophic) and Lake Sheppard (mesotrophic) meaning that in comparison to global records of meso-eutrophic preference, the water quality preferences of this species are not well defined for lakes in the Canterbury high country. *Aulacoseira ambigua* was present in the phytoplankton samples from Lake Ōtūroto (February, March and May 2020), however, only comprised 5–12% of the sample (Supplementary Information Table S1). Instead, *Fragilaria crotonensis* and *Asterionella formosa* were the dominant planktonic species, possibly indicating N enriched conditions, and limited Si conditions, given the high Si requirement for *Aulacoseira ambigua* (Wolin & Stoermer, 2005).

## 5 Conclusion

The diatom assemblages in the Canterbury high country today are representative of lakes that have been substantially shaped by anthropogenic activity. These lakes harbour at least two invasive diatom taxa in addition to species that appear unknown to science (*Staurosirella cf. ovata*, *Pseudostaurosira* sp. 1, *Punctastriata* sp. 1). The water quality and substrate preferences of the diatoms in this study provides ecological information valuable to the interpretation of palaeolimnological records from this region, presented in Chapters 4 and 5. This study also shows that despite a relatively small number of sites and samples, the abiotic variables influencing the diatom composition of freshwater sites, differ to the variables found to be important in other geographical locations. This observation is likely to be applicable in other lakes in New Zealand due to the unique geomorphology of many of the country's freshwater systems, and the longevity of New Zealand's isolation from other landmasses.

Therefore, further experimental analyses and compilation of diatom data sets, adding to Foged, (1979), Reid (2005), Kilroy et al., (2007) and Li et al., (2014) and are essential in unravelling the environmental controls on New Zealand's diatom species. In the absence, however, of comprehensive, regional data sets, this thesis uses a combination of global diatom records, and the environmental data presented in this chapter.

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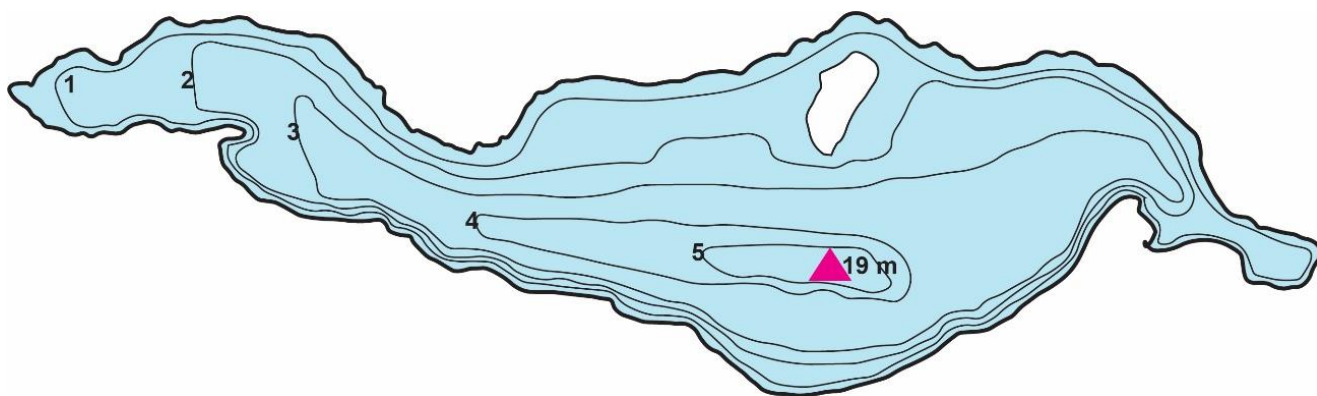
## 8 Supplementary Information

**Chapter 2:** The ecology of diatoms in New Zealand's high country lakes, with a focus on *Discostella stelligera*

### 1 Results

#### Lake Te Puna a Taka (Clearwater)

The pollen and diatom stratigraphy suggest rapid sedimentation or continual mixing of sediments (Figure S2 and S3). The sediment core was taken from a kettle hole in the lake which has a maximum depth of 19 m. Except for this deep hole the bathymetry of Lake Te Puna a Taka covers a depth of 0–5 m (Figure S1). There was no introduced *Pinus* spp., *Salix* spp., or *Rumex acetosella* pollen, nor was any *Pteridium esculentum*. This prevented the occupation phases of the catchment from being identified and further contributed to the decision to not further analyse this sedimentary record.



**Figure S1:** The bathymetry of Lake Te Puna a Taka. This figure is adapted from Woodward et al. (2014) and is not to scale. Contours are at 1 m intervals.

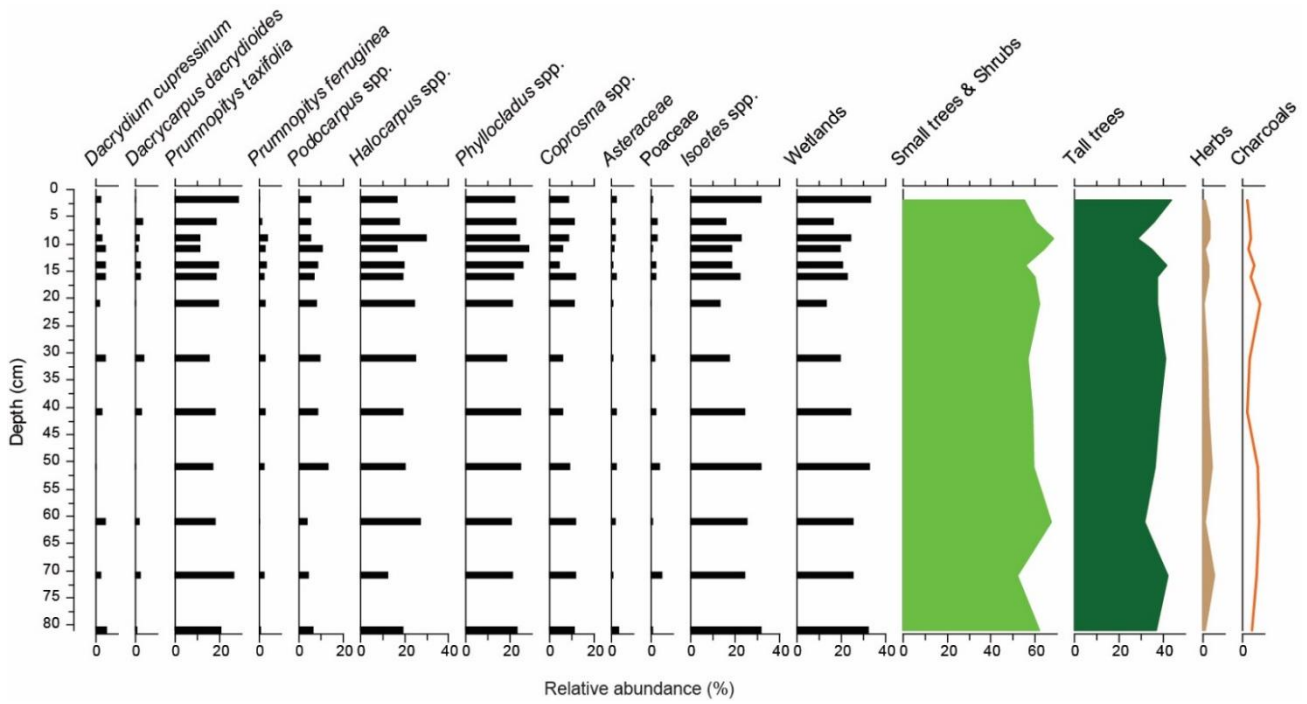


Figure S2: Dominant pollen taxa from Lake Te Puna a Taka.

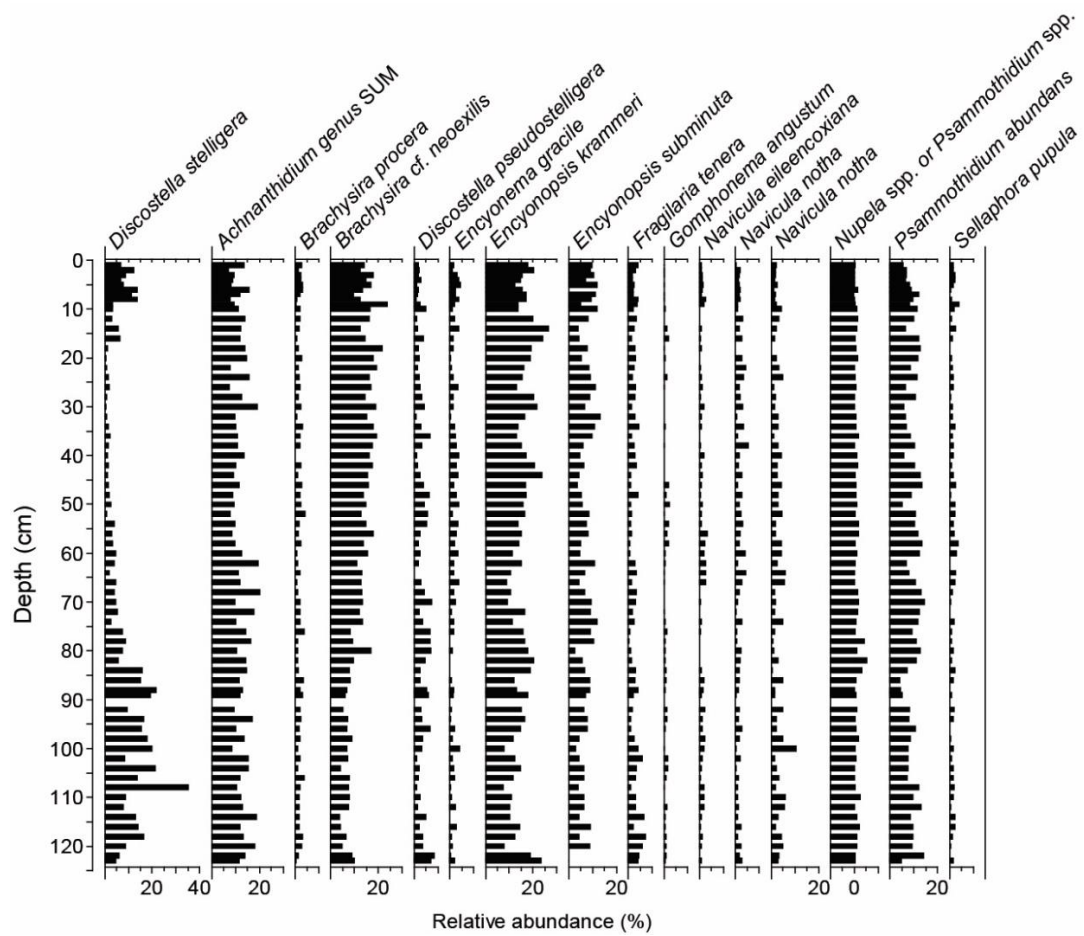


Figure S3: The dominant diatom taxa from Lake Te Puna a Taka.

## 1.2 Phytoplankton counts from Summer and Autumn 2020

**Table S1:** Diatom assemblage data (valve counts) from water samples collected from the epilimnion in Lake Ōtūroto

Taxon	February 2020	March 2020	May 2020
<i>Lindavia intermedia</i>	15	89	8
<i>Asterionella formosa</i>	75	85	83
<i>Aulacoseira ambigua</i>	21	17	34
<i>Fragilaria crotonensis</i>	74	109	168
<i>Staurosira cf. bidens</i>	11	0	1
<i>Discostella stelligera</i>	2	5	0
<i>Skabetchewskia cf. peragalloi</i>	6	0	0
<i>Staurosirella spp.</i>	4	1	0
<i>Gomphonema cf. angustatum</i>	0	1	0
<i>Encyonema spp.</i>	0	2	0
<i>Cocconeis placentula</i>	3	2	0
<i>Encyonopsis krammeri</i>	1	0	0
<i>Encyonopsis subminuta</i>	1	0	0
<b>Total</b>	<b>213</b>	<b>311</b>	<b>294</b>

**Table S2:** Diatom assemblage data (valve counts) from water samples collected from the epilimnion in Lake Ōpōrea

Taxon	February 2020	March 2020	June 2020
<i>Asterionella formosa</i>	6	142	No diatoms
<i>Tabellaria flocculosa</i>	22	3	
<i>Achnantheidium minutissimum</i>	0	23	
<i>Staurosira sp. bidens?</i>	0	4	
<i>Fragilaria crotonensis</i>	0	1	
<i>Epithemia sorex</i>	9	13	
<i>Discostella stelligera</i>	15	2	
<i>Skabetchewskia cf. peragalloi</i>	0	3	
<i>Navicula spp.</i>	2	0	

<i>Navicula radiosa</i>	5	34
<i>Stausosirella spp.</i>	0	1
<i>Stausosirella leptostauron</i>	1	1
<i>Ctenophera pulchella</i>	0	1
<i>Nitzschia linearis</i>	7	2
<i>Nitzschia palea</i>	2	5
<i>Nitzschia cf. gracilis</i>	1	3
<i>Gomphonema cf. angustum</i>	0	6
<i>Fragilaria cf. perminuta</i>	0	7
<i>Sellaphora seminulum</i>	0	2
<i>Pinnularia spp.</i>	0	1
<i>Pinnularia sp. 2</i>	0	3
<i>Aulacoseira ambigua</i>	1	0
<i>Diploneis elliptica</i>	0	2
<i>Lindavia intermedia</i>	2	3
<i>Stausosira venter</i>	4	4
<i>Encyonema silesiacum</i>	3	0
<i>Cocconeis placentula</i>	0	2
<i>Cymbella novozeelandiana</i>	0	1
<i>Pseudostaurosira cf. microstriata</i>	2	3
<i>Encyonema gracile</i>	2	0
<i>Stenopterobia spp.</i>	1	0
<i>Punctastriata lancetulla</i>	0	1
<i>Encyonopsis krammeri</i>	1	7
<i>Encyonopsis subminuta</i>	2	3
<i>Brachysira spp.</i>	0	2
<i>Rhapoladia spp.</i>	0	2
<i>Caloneis spp.</i>	0	2
<b>Total</b>	<b>88</b>	<b>289</b>

**Table S3:** Diatom assemblage data (valve counts) from water samples collected from the epilimnion in Lake Grasmere

<b>Taxon</b>	<b>February 2020</b>	<b>March 2020</b>	<b>June 2020</b>
<i>Lindavia intermedia</i>	61	217	142
<i>Tabellaria flocculosa</i>	0	2	0
<i>Fragilaria crotonensis</i>	213	51	1
<i>Epithemia sorex</i>	2	0	0
<i>Discostella stelligera</i>	1	0	0
<i>Skabetchewskia cf. peragalloi</i>	2	0	0
<i>Cocconeis placentula</i>	0	3	0
<i>Gomphonema clavatum</i>	6	0	0
<i>Gomphonema cf. angustum</i>	0	0	1
<i>Fragilaria capucina</i>	0	0	1
<i>Asterionella formosa</i>	14	31	3
<i>Cocconeis placentula</i>	6	0	11
<b>Total</b>	<b>305</b>	<b>304</b>	<b>159</b>

**Table S4:** Diatom assemblage data (valve counts) from water samples collected from the epilimnion in Lake Lyndon

<b>Taxon</b>	<b>February 2020</b>	<b>March 2020</b>	<b>June 2020</b>
<i>Achnantheidium minutissimum</i>	2	0	No diatoms
<i>Fragilaria crotonensis</i>	3	0	
<i>Epithemia sorex</i>	1	0	
<i>Discostella stelligera</i>	5	4	
<i>Navicula radiosa</i>	3	0	
<i>Encyonema spp.</i>	1	0	
<i>Gomphonema clavatum</i>	2	0	
<i>Ctenophera pulchella</i>	1	0	
<i>Psammothidiu, sacculus</i>	0	86	
<i>Staurosira construens</i>	0	2	
<i>Nitzschia linearis</i>	1	0	
<i>Sellaphora seminulum</i>	0	2	

<i>Asterionella formosa</i>	1	0.5
<i>Aulacoseira ambigua</i>	0	0
<i>Diploneis elliptica</i>	0	44
<i>Lindavia intermedia</i>	279	129
<i>Stausosira venter</i>	0	14
<i>Punctastriata lancetulla</i>	0	10
<i>Encyonopsis krammeri</i>	0	11
<i>Encyonopsis subminuta</i>	2	0
<b>Total</b>	<b>301</b>	<b>302.5</b>

### 1.3 New diatom taxa

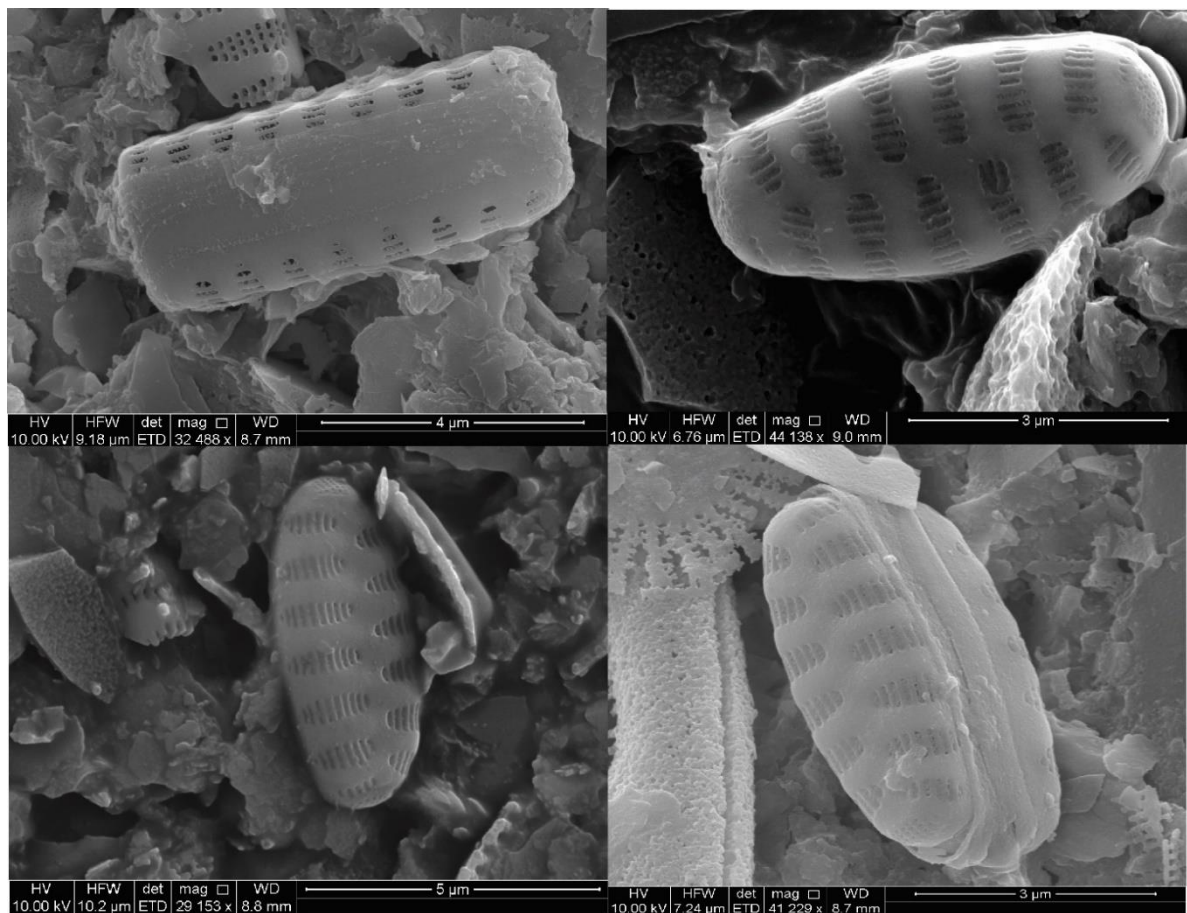


Figure S4: SEM photos of *Stausosirella cf. ovata*



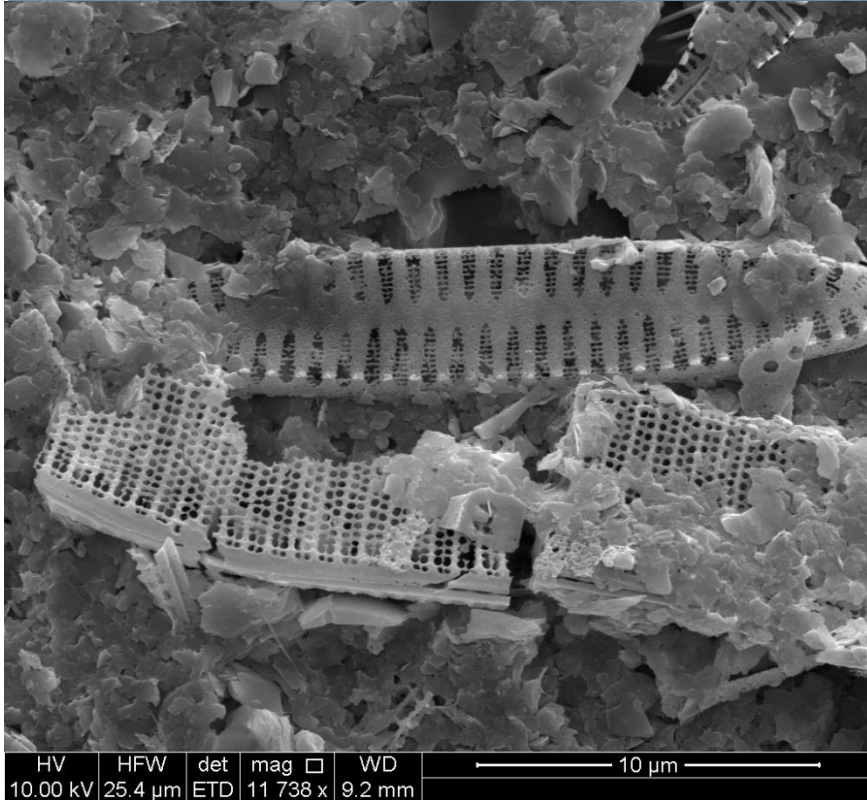
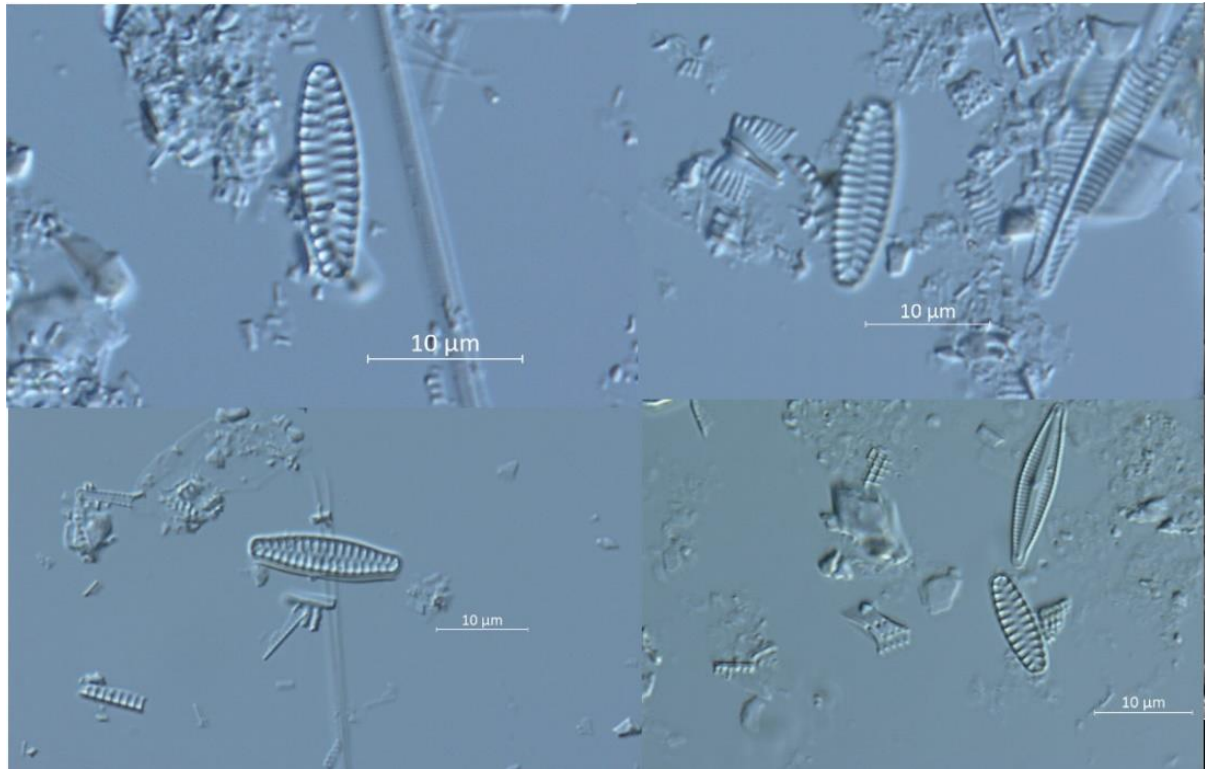


Figure S5: LM and SEM photos of *Punctastriata sp. 1*.

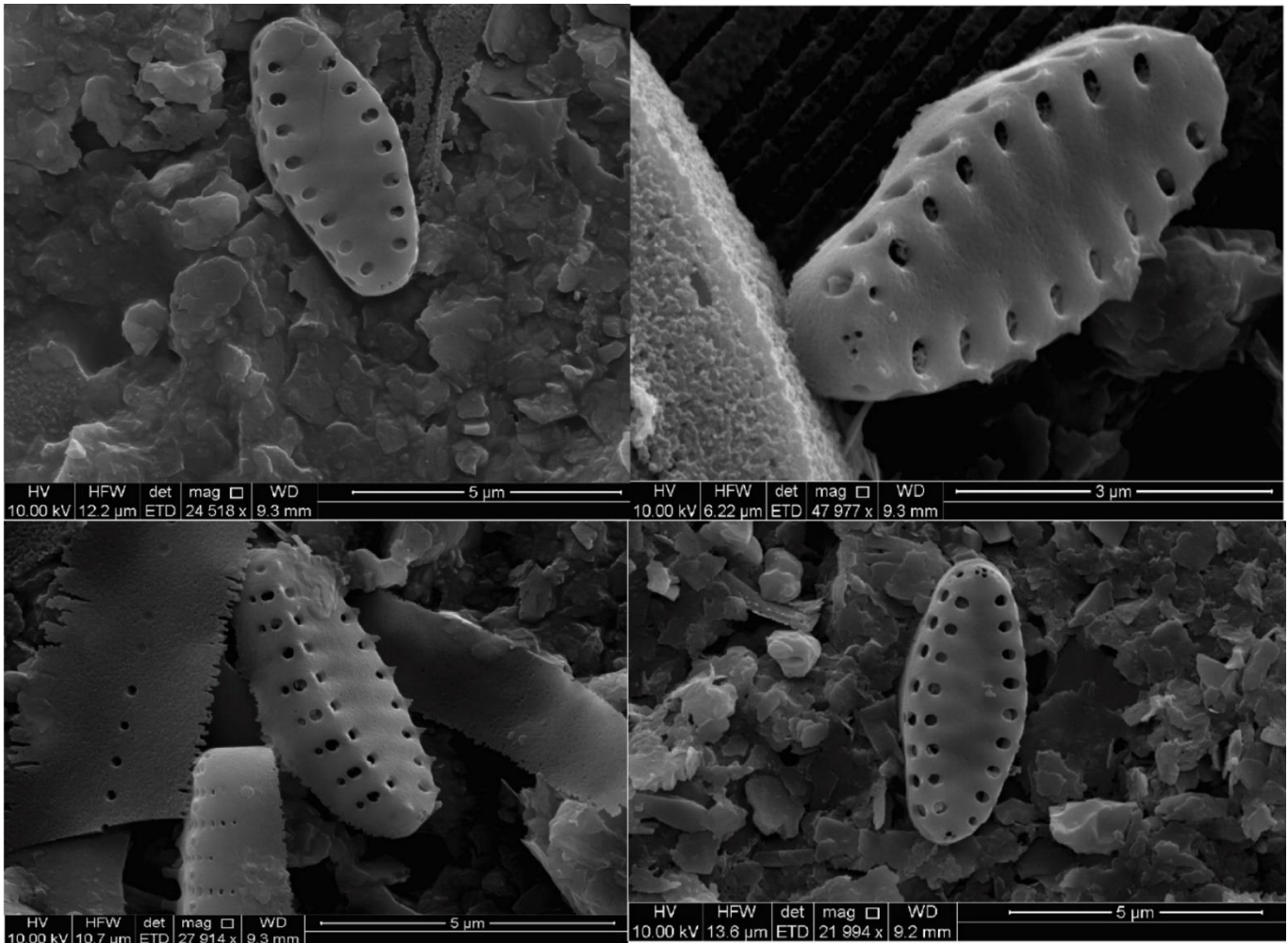
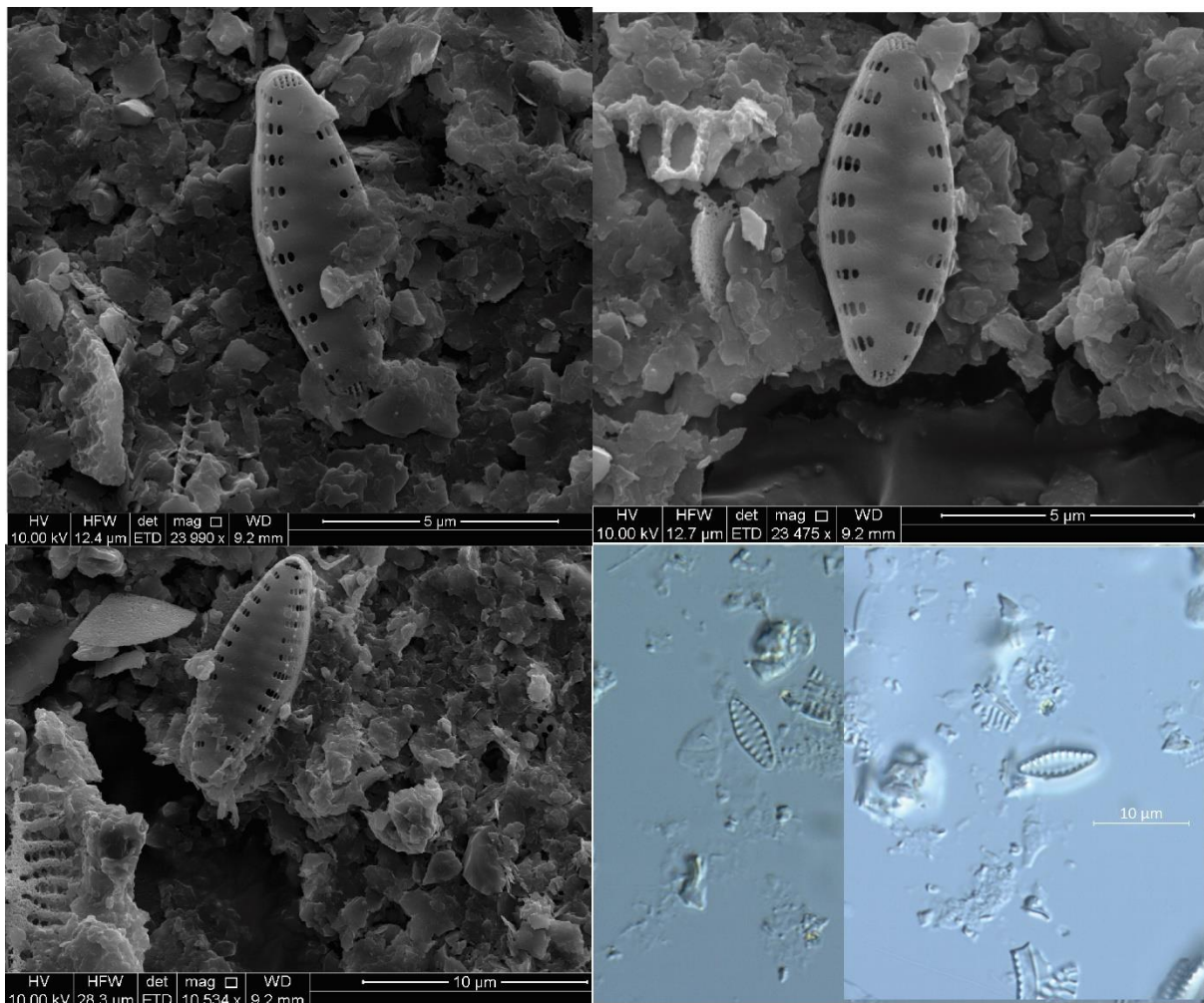


Figure S6: SEM photos of *Pseudostaurosira* sp. 1



**Figure S7:** SEM and LM photos of *Staurosirella canariensis*.

This taxon was not abundant in the surface samples or habitat scrapes, however was abundant in the longer sedimentary records.

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Woodward, C., Shulmeister, J., Zawadzki, A. & Jacobsen, G. (2014). Major disturbance to aquatic ecosystems in the South Island, New Zealand, following human settlement in the Late Holocene. *Holocene*, 24(6), 668-678. <https://doi.org/10.1177/0959683614526935>

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### Principal Author

Name of Principal Author (Candidate)	Julia Short		
Contribution to the Paper	Conceptual design, field work and sample preparation, diatom data collection and analyses, isotope data collection and analyses, data interpretation and statistical analyses (diatoms, pollen, isotopes) Producing figures, Manuscript production, writing and editing		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	19/7/22

### Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- iv. the candidate's stated contribution to the publication is accurate (as detailed above);
- v. permission is granted for the candidate to include the publication in the thesis; and
- vi. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.



Name of Co-Author	John Tibby		
Contribution to the Paper	Conceptual design, data interpretation (diatoms), manuscript editing and reviewing		
Signature		Date	19/7/22

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Contribution to the Paper	Funding, data interpretation, manuscript editing		
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Name of Co-Author	Tina Bayer		
Contribution to the Paper	Manuscript editing and data interpretation, provision of data (water quality)		
Signature		Date	4/8/22

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Contribution to the Paper	Producing and providing data (chronology), assisting with data interpretation, writing methods, manuscript editing		
Signature		Date	10/8/22

Name of Co-Author	Adelaine Moody		
Contribution to the Paper	Producing and providing data (chronology)		

Signature		Date	4/8/22
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Name of Co-Author	Christopher Moy		
Contribution to the Paper	Producing data (Lake Heron isotopes), field work and collection of samples, manuscript editing and data interpretation		
Signature		Date	11/8/22

Name of Co-Author	Xun Li		
Contribution to the Paper	Producing data (pollen)		
Signature		Date	12/08/2022

## Chapter 3

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### Using palaeolimnology to guide rehabilitation of a culturally-significant lake in New Zealand

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## Abstract

1. Lakes are degrading at an accelerating rate due to human activity and understanding their past ecology is necessary for lake management and rehabilitation. Palaeolimnology provides numerous methods that enable the historical state of lakes to be determined. New Zealand provides an ideal setting to do this as human modification of the landscape occurred later than in most of the world (~1300 CE).

2. Lake Oporoa is a shallow lake, highly significant to the local indigenous Māori community. This study used multiple proxy palaeolimnology to explore how lake ecology shifted following Māori and European settlement in the catchment and how palaeolimnological data can be used to inform lake rehabilitation and conservation measures, alongside the desires of the indigenous community. Sedimentary pollen, diatoms, bacterial communities, elemental and hyperspectral imaging scanning were used to infer ecological changes in the lake and catchment from pre-human times to present.

3. Following Māori settlement (~1620 CE) there was gradual vegetation change and a rapid shift in diatom and bacterial assemblages but not phytoplankton pigments or sediment geochemistry. An increasing abundance of diatom taxa *Discostella stelligera* and *Staurosirella* cf. *ovata* indicated early nutrient enrichment. European pastoralism from ~1840 CE resulted in further deforestation, and all proxies show evidence for enhanced primary productivity driven by a combination of nutrient enrichment and changing lake levels, particularly since the 1960s. This caused degradation in water quality and likely contributed to the decline in populations of *tuna* (eel, *Anguilla* spp.).

4. Conversations with local Māori, together with the palaeolimnological results, indicate that a culturally acceptable and realistic rehabilitation target for Lake Oporoa aligns with ecological conditions in the 1950s. The palaeoecological data provide information to guide catchment and in lake revegetation and other methods of nutrient abatement, with the eventual aim of restoring culturally important *tuna* and native fish populations.

**Key words:** diatoms, *Discostella stelligera*, eutrophication, Māori, palaeolimnology, pollen, pigments, rehabilitation, sediment DNA



## 1 Introduction

New Zealand was the last major landmass to be settled, with the arrival of Polynesians in approximately 1300 CE (Wilmshurst et al., 2008; McWethy et al., 2010). In the decades and centuries following Polynesian settlement, the landscape was transformed primarily through vegetation burning. In some regions, native forest cover was reduced from 90% to less than 50% cover (McGlone, 1983; McGlone & Wilmshurst, 1999; Perry et al., 2012; McWethy et al., 2014). Europeans settled in New Zealand from 1830 CE onwards and cleared much remnant native vegetation for conversion to agricultural land (Perry, Wilmshurst & McGlone, 2014; Baillie & Bayne, 2019). Exotic plants such as *Rumex* spp. (sorrel) and *Rubus* spp. (e.g. blackberry), and deciduous trees including *Populus* spp. (poplar) and *Salix* spp. (willow) were introduced. These changes in land cover, along with changing agricultural practices, and urbanisation have resulted in widespread degradation of many freshwater ecosystems across New Zealand (Abell et al., 2020).

New Zealand has approximately 3,200 naturally-formed, freshwater lakes greater than a hectare in area (Schallenberg et al., 2013). Many are highly valued and of national significance, provide critical ecosystem services and are of great cultural importance to Māori, the indigenous people of New Zealand (West, Leathwick & Dean-Speirs, 2019; Stewart-Harawira, 2020). However, over 40% of New Zealand's lakes, particularly those in lowland catchments, are in poor ecological health (Abell et al., 2019; Ministry for the Environment & Stats NZ, 2020). While landscape change is undoubtedly a key driver in the ecological degradation of these lakes, the timing and extent of degradation has varied, and other factors such as the introduction of non-native plant and animal species have also been detrimental (Collier, Leathwick & Rowe, 2017). Fewer than 200 of New Zealand's lakes are monitored, with the data limited by their short monitoring duration, usually less than three decades (Land, Air, Water Aotearoa, 2020). Consequently, the natural state or reference condition of the lakes is rarely known.

By studying environmental indicators preserved in lake sediments (e.g. diatoms, pollen), palaeolimnological reconstructions can assist in establishing natural, pre-human baselines, thereby contributing to practical and informed plans for restoration or rehabilitation. Palaeolimnology has a key role in informing restoration practices by identifying reference ecological conditions, helping to identify factors that have caused major shifts in lake ecosystems and providing approximate dates of ecological changes (Sayer et al., 2012; Boxem, Davis & Vermaire, 2018; Davidson et al., 2018). However, palaeolimnology has not been widely used for these purposes in New Zealand (Schallenberg, 2019).

Lake Oporoa is a small lowland lake located in the central North Island, and is of cultural significance for the *iwi* (“tribe”) Ngāti Hauiti. Oral history recounted in 2019 by *kaumatua* (highly respected elder within an *iwi*), and study author, Neville Lomax, indicates that Lake Oporoa was first discovered and settled by an early Māori explorer named Matangi. Matangi explored the landscape by foot, following the path taken by a flock of birds. As he did so, he named key features in the landscape. When the birds settled at Lake Oporoa, Matangi did likewise and built a small *whare* (house) by the lake. Ngāti Hauiti arrived later and established *mana whenua* (primary authority) status in the area.

From the nineteenth century, land was purchased by Europeans and converted to pasture for farming. As Neville Lomax explained, this resulted in many members of Ngāti Hauiti losing their cultural connection with the lake. Lake Oporoa has recently regained prominence through the efforts of Ngā Puna Rau o Rangitīkei, an *iwi* collective focused on restoring and preventing the further decline of waterways throughout the Rangitīkei River catchment, in which Lake Oporoa is situated. Historically the lake was used for harvesting traditional foods such as *tuna* (eel, *Anguilla* spp.) as it forms part of a migratory pathway for the species, via a natural outflow to the Rangitīkei River, which flows into the Tasman Sea. Due to water degradation, including the lowering of lake levels by inflow diversion, and reduced outlet flow, *tuna* harvesting has been affected. As a result, Ngāti Hauiti aim to revitalise the *mauri* (life essence) and ecological health of the lake and catchment, as part of reconnecting with this ancestral *taonga* (treasure). In particular, it would be desirable to have the return of a healthy population of native fish and *tuna* in the lake, and the reestablishment of a riparian zone comprising native vegetation (Ngā Puna Rau o Rangitīkei, 2019).

Restoration and rehabilitation of ecosystems are options for negating human impacts on the environment but will provide differing outcomes for Lake Oporoa. Restoration is generally defined as the return of an ecosystem to a reference state, and usually requires substantial recovery of original biota and ecosystem function (Gann et al., 2019). Rehabilitation, by contrast, refers to the improvement of an ecosystem to a state where key ecosystem functions or services are resumed, or improved (Gann et al., 2019). Rehabilitation can occur with a combination of both native and non-native biota. For lake restoration of Lake Oporoa, reference conditions need to be understood. By contrast, rehabilitation of Lake Oporoa could use reference conditions as the goal or aim to provide ecosystem services desired by Ngāti Hauiti. In this study these two approaches are combined, and palaeolimnology is used to understand the level of impact on Lake Oporoa with rehabilitation proposals that are framed by Ngāti Hauiti desires. This option recognises anthropogenic influences are unlikely to be completely removed from freshwater ecosystems but allows targeting of rehabilitation and conservation measures consistent with pre-impact conditions (Boulton, Ekeboom & Gíslason, 2016; Geist & Hawkins, 2016). By establishing rehabilitation measures based on the aspirations of Ngāti

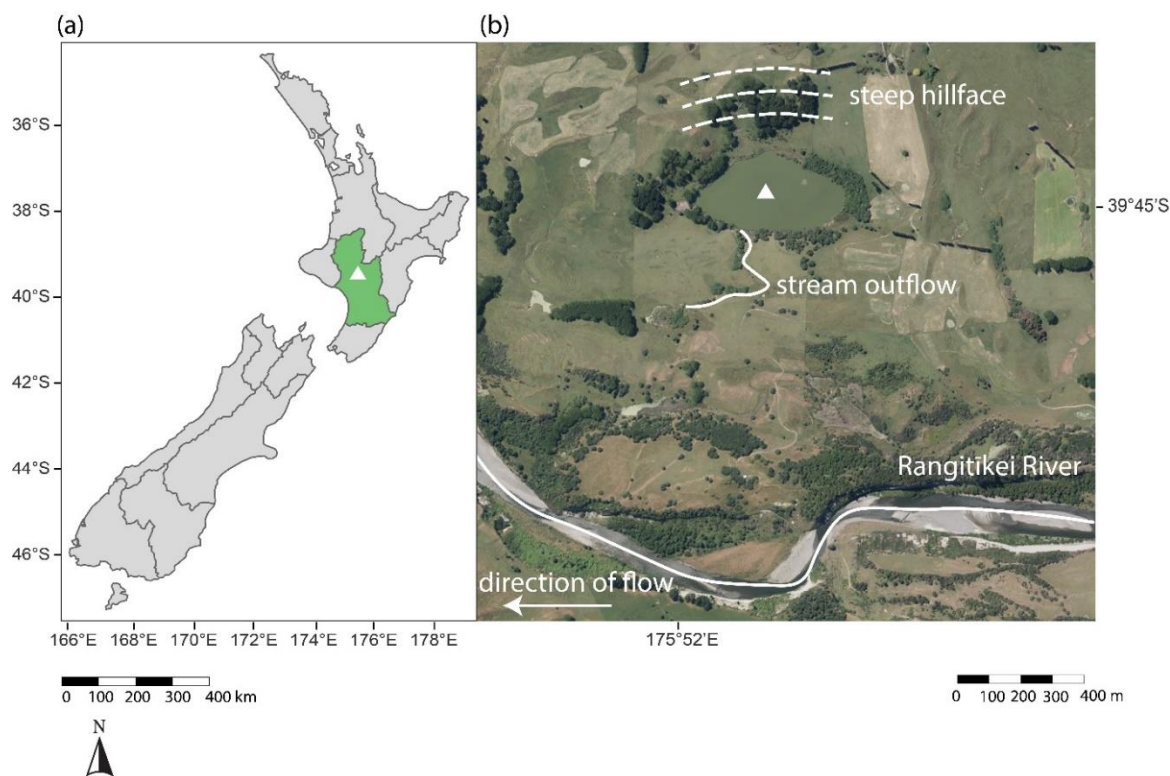
Hauti this enables Māori knowledge and values to be incorporated into future management plans. This is a practice which is increasingly encouraged in New Zealand (Lyver et al., 2015; Harmsworth, Awatere & Robb, 2016; Crow et al., 2018; Ratana, Herangi & Murray, 2019), which is in contrast to other countries such as Australia, where indigenous knowledge has rarely been as effectively incorporated into freshwater management (Moggridge & Thompson, 2021).

Establishing reference conditions using palaeolimnology requires multiple proxies to provide different insights into past ecosystem structure and function (Birks, 2006). In shallow lakes, which are especially responsive to catchment processes, a multi-proxy study can identify changes in the landscape and corresponding ecosystem response. This study used well-established palaeolimnological proxies; diatom, pollen, pigment and Itrax  $\mu$ -XRF analyses, alongside the emerging proxies of hyperspectral imaging (HSI) and sedimentary DNA (sedDNA), to infer the ecology of Lake Oporoa from before Māori settlement through to 2019 CE. The aims were: (1) to explore how lake ecology shifted following both Māori and European activities in the catchment, and (2) to demonstrate how palaeolimnological data can be used to inform lake rehabilitation. The knowledge generated in this study will help assist Ngāti Hauti in fulfilling their aspirations for rehabilitating Lake Oporoa.

## 2 Methods

### 2.1 Study site

Lake Oporoa (39°45'6.12"S, 175°52'3"E) is a land-slide formed lake, located in the upper Rangitīkei River catchment, Manawatū-Whanganui region, of the North Island (Figure 1). It is a small (7.1 ha), shallow (~2.5 m), lowland lake surrounded by productive exotic pasture and a semi-vegetated riparian zone, comprising native and non-native species (e.g. native: *Dacrydium cupressinum*, *Podocarpus toatara*, *Prymnopterys ferruginea* and *Coprosma* spp., non-native: *Populus* spp. and *Salix* spp.). An outlet is situated on the southern margin of the lake, while the northern margin has a steep hill face.



**Figure 1:** Location of Lake Oporoa in the Manawatū -Whanganui region, New Zealand (white triangle), and its catchment characteristics. Image contains data sourced from the LINZ Data Service licensed for reuse under CC BY 4.0

## 2.2 Engagement with Ngā Puna Rau o Rangitikei

Engagement with the Ngā Puna Rau o Rangitikei collective was developed in accord with Māori research protocol through a process of *whakawhanaungatanga* (relationship-building). This involved a series of *hui* (meetings), a *noho wānanga* (live-in workshop), and an invitation onto Rātā Marae. The site visit to Lake Oporoa in June 2019 was by invitation of Ngāti Hauiti *kaumatua* Neville Lomax and Ngā Puna Rau o Rangitikei project executive, Robert Martin (Ngāti Hauiti). Following a *karakia* (blessing), Neville narrated the ‘coming of Matangi’ history and described his 1950s childhood memories of Lake Oporoa. Additional interviews took place with members of Ngā Puna Rau o Rangitikei. Ethics approval was granted by Cawthron Institute’s ethics committee: CAW-ETH-190119.

## 2.3 Core sampling and sub sampling

Four cores were taken in June 2019 from the deepest part of the lake (Figure 1) using a UWITEC Gravity corer with a 2 m, 90 mm diameter polyvinyl chloride core barrel. The cores were packed with florist foam to prevent sediment movement, before being cut into one metre lengths for transportation. The cores were kept refrigerated in transit to GNS Science (Lower Hutt, New Zealand) where the longest core (master core, 123 cm) was split, described, and imaged. The master core was sampled at varying

depths (Supplementary Table S1), while remaining cores were used for correlating and preparing the hyperspectral imaging scanner, and later archived (Figure S4). The full sampling description can be found in Supplementary Information.

#### 2.4 Core chronology

The core chronology was established using numerical age constraints derived from  $^{210}\text{Pb}_{\text{ex}}$  dating, pollen biostratigraphy and  $^{14}\text{C}$  dating combined with Bayesian age-depth modelling. Fifteen  $2\text{ cm}^3$  samples of sediment were extracted for  $^{210}\text{Pb}_{\text{ex}}$  analyses from the upper 47 cm of the core at a resolution of between 1 and 5 cm. Total  $^{210}\text{Pb}$  activity was estimated by measuring its daughter product  $^{210}\text{Po}$  using chemical extraction and alpha spectrometry at the ESR National Centre for Radiation Science. The  $^{210}\text{Pb}_{\text{ex}}$  data were modelled using the Constant Rate of Supply (CRS) model in the R package Serac (Bruel & Sabatier, 2020), using sediment dry mass calculated from X-ray computed tomography (CT) densitometry and sediment water content. Bulk density was calculated from the CT data using the relationship between CT number and bulk density of Reilly, Stoner & Wiest (2017). The  $^{210}\text{Pb}_{\text{ex}}$  age model was validated using independent age estimates derived from the first occurrence and peak of non-native pollen in the core. The increase in *Salix* spp. pollen was assigned a date of between 1945 and 1955 CE as this tree was widely planted in the region at this time (Gordon, 2009). The first occurrence of *Populus* spp. pollen was assigned a date of  $1975 \pm 10$  CE ( $2\sigma$ ) because it is likely associated with local planting in the lake catchment (Karen Gibbs, Farm manager pers. comms., 2020).

Terrestrial leaf macrofossils were extracted by picking *in-situ* material from the split core surface. Macrofossils were cleaned and pre-treated using an acid–alkali–acid procedure to remove carbonates, fulvic and humic compounds (Norris et al., 2020). The pre-treated macrofossils were converted to  $\text{CO}_2$  by combustion, graphitized and measured by accelerator mass spectrometry following Baisden et al. (2013). Conventional Radiocarbon Ages were converted to calendar years using the SHCal20 calibration curve (Hogg et al., 2020), while those that return modern ages were calibrated using the Baring Head – Cape Grim (BHD-CGO) curve (Turnbull et al., 2017).

Age-depth modelling was conducted using a Bayesian framework in OXCAL 4.4 (Bronk Ramsey, 2009). Age probability density functions from the  $^{210}\text{Pb}_{\text{ex}}$  age-depth model, biostratigraphy and calibrated  $^{14}\text{C}$  dates were integrated with core depth using the P\_Sequence prior model with a variable event thickness constant  $k$  (Bronk Ramsey, 2008; Bronk Ramsey & Lee, 2013). The full method is in Supplementary Information.

#### 2.5 Pollen analysis

Pollen was extracted from  $0.25\text{ cm}^3$  sediment samples at a variable sampling interval of 1–2 and 3–4 cm in the upper 65 cm of the core and 10 cm intervals thereafter (Supplementary Table S1). Pollen

extraction was carried out following standard laboratory techniques (Faegri, Iversen & Giovannini, 1989), using 10% hot hydrochloric acid, acetolysis and 6-micron sieving. Exotic *Lycopodium* tablets (Batch# 140119320) were added to each sample to allow calculation of pollen concentrations. Pollen and spore identifications were made using standard texts (Pocknall, 1981a; Pocknall 1981b; Pocknall, 1981c; Large & Braggins, 1991; Moar, 1993) and New Zealand reference collections.

Data were presented as relative frequency of a minimum pollen sum of 150 grains. This sum includes pollen from all dryland plants: trees, shrubs and herbaceous plants, non-native plant taxa and bracken fern *Pteridium esculentum*. *Pteridium esculentum* is included in this sum as in a post disturbance landscape its functional morphology is closer to a shrub than a fern, and a stand is ecologically equivalent to shrubland (McGlone, Wilmshurst & Leach, 2005). Pollen of other groups (wetland, aquatics, ferns, tree ferns and non-palynomorphs) were excluded from the sum, but their percentages were calculated as a proportion of dryland pollen, plus the respective group.

Charcoal was counted as number of fragments and presented as concentration per cm<sup>3</sup>. Pollen data were used to delineate occupation periods of Lake Oporoa's catchment. *Pteridium esculentum* is used across New Zealand as a chronological marker for the first presence of Māori activity, as it is both an indicator of landscape disturbance and a nutritional source (McGlone & Wilmshurst, 1999; McWethy et al., 2010; Newnham et al., 2018). *Pinus* spp., and other non-native taxa were introduced by European colonialists and are used to mark European activity in a landscape. Three periods were assigned to the record and are used in this study: Pre-Human (41–122 cm), evidence of Māori settlement (31–40 cm), and post-European arrival (0–30 cm). The term “evidence of Māori settlement” indicates that specific indicators (charcoal and the increase in *Pteridium esculentum*) are markers of Māori settlement and activity in the landscape. This wording acknowledges that other evidence (in particular oral history) may place Māori settlement at an earlier time and that there may be natural causes of these ecological changes.

## 2.6 Diatoms – laboratory analysis

A total of 121 contiguous samples were taken at centimetre resolution and prepared using hydrochloric acid (15%) and hydrogen peroxide (25%) to remove carbonates and organic matter (Battarbee et al., 2002). Samples were not prepared at 0 or 87 cm (the top and bottom of the first core barrel, respectively) to alleviate the possibility of contamination from the florist foam, and when the cores were cut.

Diatom slurries were permanently mounted onto slides using Naphrax. Counting and identification was undertaken using a Zeiss AxioA1 microscope at 1,000 x magnification using differential image contrast. Additional analyses to identify taxa in the Fragilariaceae, were completed using a FEI Quanta

450 FEG scanning electron microscope (SEM), due to difficulties in identifying species under light microscope. A total of 300 ( $\pm 10$ ) valves was counted on each slide (Battarbee et al., 2002). Identifications were undertaken using: Foged, 1979; Krammer & Lange-Bertalot, 1986; Krammer & Lange-Bertalot, 1988; Krammer & Lange-Bertalot, 1991a; Krammer & Lange-Bertalot, 1991b; Sonneman et al., 1999; Morales, 2001; Krammer, 2002; Morales & Manoylov, 2006; Reavie & Kireta, 2015; John, 2018.

## 2.7 Diatoms – data analyses

Zonation of diatom results used constrained instrumental sums of squares (CONISS), calculated in Tilia Version 2.6.1 (Grimm, 2019). To assess the variability in, and floristic dissimilarity between samples, non-metric multidimensional scaling (NMDS) was calculated using a Bray-Curtis distance matrix after a Wisconsin double standardisation (Minchin, 1987) using the *vegan 2.5–6* package (Oksanen et al., 2019) in R (R Core Team, 2020). Results in two dimensions produced sufficiently low ( $< 0.1$ ) stress, indicating the NMDS results fit the distributed data.

PERMANOVA (Anderson, 2001) was used to assess whether; (1) the three different occupation periods (pre-Human, Evidence of Māori settlement and post-European activity) were significantly different in Lake Oporoa diatom assemblage data, to (2) inform the suitability of computing square chord distance (SCD; Overpeck, Webb & Prentice, 1985) calculations between ‘reference’ and ‘impact’ samples. PERMANOVA was completed in R package *vegan 2.5–6* (Oksanen et al., 2019). The Bray-Curtis distance matrix was used, with 999 permutations. To account for temporal autocorrelation of samples, a distance-based Redundancy Analysis (dbRDA; Legendre & Anderson, 1999) was also calculated with the three time periods as explanatory variables and depth partialled out as a co-variable (i.e. its statistical effect was removed before the effect of time period was calculated).

Measures of floristic change, using the square chord distance between reference and modern samples have been used to provide a simple, yet quantitative assessment of the difference between two, or more, samples (Bennion et al., 2011; Heathcote et al., 2014; Wengrat et al., 2019). SCD provides a score between 0 and 2, with 0 indicating samples are perfectly similar, and 2 meaning samples are perfectly dissimilar (Overpeck, Webb & Prentice, 1985). SCD was calculated in the R package *analogue 0.17–4* (Simpson & Oksanen, 2020) between pre- and post-human settlement diatom assemblages (Overpeck, Webb & Prentice, 1985). The suite of pre-human samples ( $n=81$ , 41–122 cm inclusive), were compared, in turn, with each sample from the post-Māori settlement period ( $n=40$ , 0–40 cm inclusive). The minimum value between each ‘impact’ sample and the corresponding reference

samples was calculated. All analyses used species with at least 2% abundance in  $\geq 3$  samples, except for CONISS, which required all data.

## 2.8 Sedimentary DNA extraction, PCR, high throughput sequencing and bioinformatics

DNA was extracted from 44 samples of approximately 0.25 g of sediment using the DNeasy PowerSoil Kit (Qiagen, Germany) following the manufacturer's instructions on a QIAcube sample preparation robot (Qiagen) (Supplementary Table S1). A negative extraction control was included every 23 samples to ensure there was no contamination in the extraction kits.

The V3-V4 region of the bacterial 16S rRNA gene was 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' (Klindworth et al., 2013) as described in Pearman et al. (2020). The primers included Illumina™ overhang adapters to allow dual indexing as described in Kozich et al. (2013). PCR reactions and library preparation was undertaken following Pearman et al. (2020). Sequencing was undertaken on an Illumina Miseq platform at the Auckland Genomics Facility. Raw sequence reads are deposited in the National Center for Biotechnology Information short read archive under the accession number: PRJNA737168.

Bioinformatics and QC of the sequencing data was undertaken using cutadapt (Martin, 2011) and DADA2 (Callahan et al., 2016) as described in Pearman et al. (2020). Amplicon sequence variants were taxonomically classified using the rdp classifier (Wang et al., 2007) against the SILVA 138 reference database (Pruesse et al., 2007)

## 2.9 Sedimentary DNA – data analysis

The phyloseq package (McMurdie & Holmes, 2013) was used to analyse the data. Sequences assigned as eukaryotes, chloroplasts and mitochondria were removed. Samples were subsampled, for comparison, to an even depth of 32,400 sequences (minimum read depth of the samples).

Composition at the class level (agglomeration of ASVs belonging to the same class) was analysed for each depth and NMDS, at the class level, was calculated to assess dissimilarity between samples. The NMDS was completed in *vegan 2.5–6* package (Oksanen et al., 2019) in R (R Core Team 2020), after a log+1 transformation, as was PERMANOVA and dbRDA (with depth partialled out as a co-variable), to examine the differences in bacterial communities between each occupation period. All analyses used classes with at least 2% abundance in  $\geq 3$  samples.



### 2.10 Itrax Scanning

Relative downcore major and trace elemental abundance data were obtained at 1 mm resolution using a Cox Analytics Itrax  $\mu$ -XRF Core Scanner at the University of Otago Repository for Core Analysis. The surficial 1–2 mm of the sediment surface was scraped to remove potential contaminants and then scanned using a molybdenum and a chromium X-ray tube configured at 30 kv, 55 ma and 10 s integration time. While a suite of elements was analysed, only calcium (Ca) relative concentrations normalised to titanium (Ti) are presented as a proxy for authigenic carbonate production (Ca/Ti) (Davies, Lamb & Roberts, 2015; Hinojosa et al., 2019).

### 2.11 Hyperspectral Imaging Scanning

The core was scanned using a Specim sCMOS-CL-50-V10E-SCB camera following Butz et al. (2015). Measurements were captured with a spectral resolution of 1.3 nm and a spatial resolution of 41  $\mu$ m. Several relative absorption band depth (RABD) indices have been developed that quantify absorption features associated with pigments in surface sediments (Rein & Sirocko, 2002; Butz et al., 2015; Butz et al., 2017; Schneider et al., 2018). This study analyses spectral data using RABD<sub>660-670</sub>, which is correlated to sedimentary pigments chlorophyll *a* and its degradation products. Results are converted to a spectral index (Butz et al., 2015) with a range of values between 1–2.5. Higher values are associated with more of these compounds. This index is interpreted as autochthonous chlorophyll *a* and an indicator of algal abundance (Butz et al., 2017; Schneider et al., 2018; Zander et al., 2021). Results were averaged at 1 cm resolution.

### 2.12 Sedimentary Pigment analysis

Samples (n=40, Supplementary Table S1) were thawed at 4°C, weighed into tubes and extracted three-times using acetone and ultrasonication for 30 minutes in a bath sonicator with ice. The pooled extract was dried under a stream of nitrogen gas at 40°C and stored at –20°C until analysis. On the day of analysis, the dried extract was resuspended in acetone and transferred to a septum-capped amber vial. Extracts were analysed by high-performance liquid chromatography (HPLC) with diode array detection (DAD) using an Agilent 1260 HPLC-DAD system (Santa Clara, USA). Full HPLC-DAD methods are available in Supplementary Information.

### 2.13 Spectrophotometry methods:

Pigment extracts analysed by HPLC-DAD were also assessed by spectrophotometry. The extract was diluted in acetone (1/10 for all samples or higher dilutions were used detector saturation occurred; e.g., 1/20, 1/40 or 1/200) prior to spectrophotometry analysis, and measured for UV/visible light absorption between 220–1,000 nm using a ThermoFisher Evolution 201 benchtop spectrophotometer (Waltham, USA). Absorbance values at 662 and 665 nm were used to calculate the 'Spectro

Chlorophyll-*a'* concentration according to the formula described by Lichtenthaler & Buschmann (2001).

#### 2.14 Pigments – data analyses

Statistical analyses of the pigment data (HPLC-DAD) only used the most specific indicator pigment for each phytoplankton group. This was undertaken to avoid introducing bias as multiple pigments can occur in the same phytoplankton group; e.g., diatoxanthin and fucoxanthin are both produced by diatoms. Spectro chlorophyll *a* (overall primary productivity), alloxanthin (cryptophytes), peridinin (dinoflagellates), echinenone (cyanobacteria), fucoxanthin (diatoms), lutein (green algae) and bacteriochlorophyll *a* (purple sulphur bacteria) were included for these analyses. NMDS, PERMANOVA and dbRDA were calculated using the same methods as were used for the sedDNA data.

### 3 Results

#### 3.1 Chronology

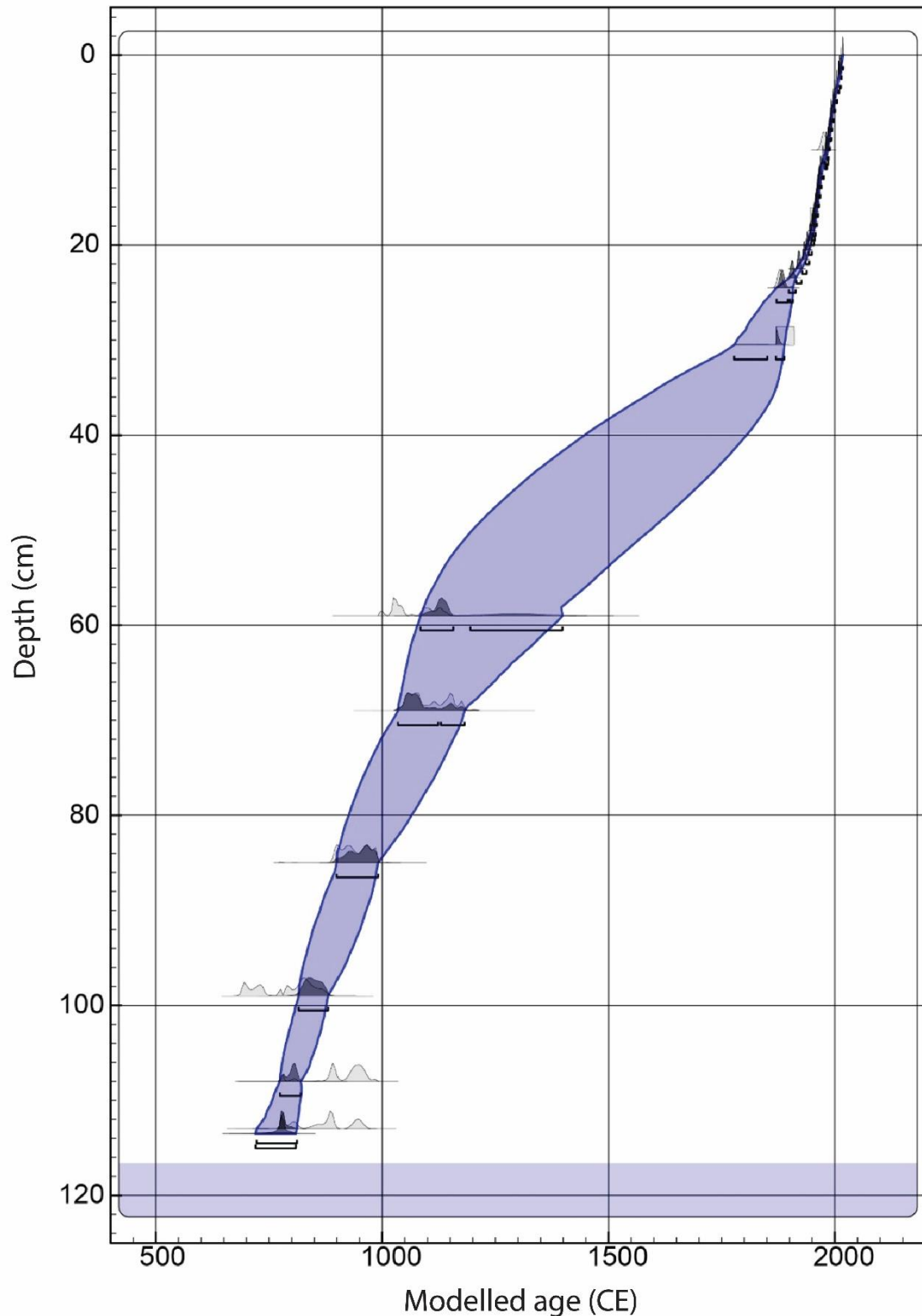
A combination of  $^{210}\text{Pb}_{\text{ex}}$ , pollen biostratigraphy and  $^{14}\text{C}$  derived chronology provides a continuous age-depth model for the core (Figure 2). The  $^{210}\text{Pb}_{\text{ex}}$  CRS derived age model provides chronology for the upper 25 cm producing a date for this depth of  $1887 \pm 8$  ( $2\sigma$ ) (Supplementary Figure S1; Table S4). The temporal precision of the model for this section ranged from 1 year (the 95% highest probability density function (HPDF) range) near the core top to 16 years at 25 cm. Modelled ages agreed with independent sediment ages derived from the non-native pollen markers and a “bomb spike” radiocarbon date thus confirming the accuracy of the  $^{210}\text{Pb}$  CRS model (Supplementary Figure S1). The chronology below 25 cm was constrained by six radiocarbon dates on terrestrial macrofossils (Supplementary Table S4). The integrated age model has an average precision of 149 years (width of the 95% HPDF range) reaching maximum values of <5 years for the upper 15 cm of the core and a minimum value of 400 years at a depth of 100 cm (Figure 2). The 95% HPDF-based age ranges for the three occupation phases are; pre-Human: 722–811 CE to 1447–1804 CE, evidence of Māori settlement: 1447–1804 CE to 1784–1890 CE, and post-European: 1784–1890 CE to 2018 CE. The median age between the range of dates at 95% HDPDF range, was used for data analyses: pre-Human: ~ 800–~1620 CE, evidence of Māori settlement: ~1620–~1840 CE, and post-European arrival: ~1840 CE–2018.

#### 3.2 Pollen and charcoal

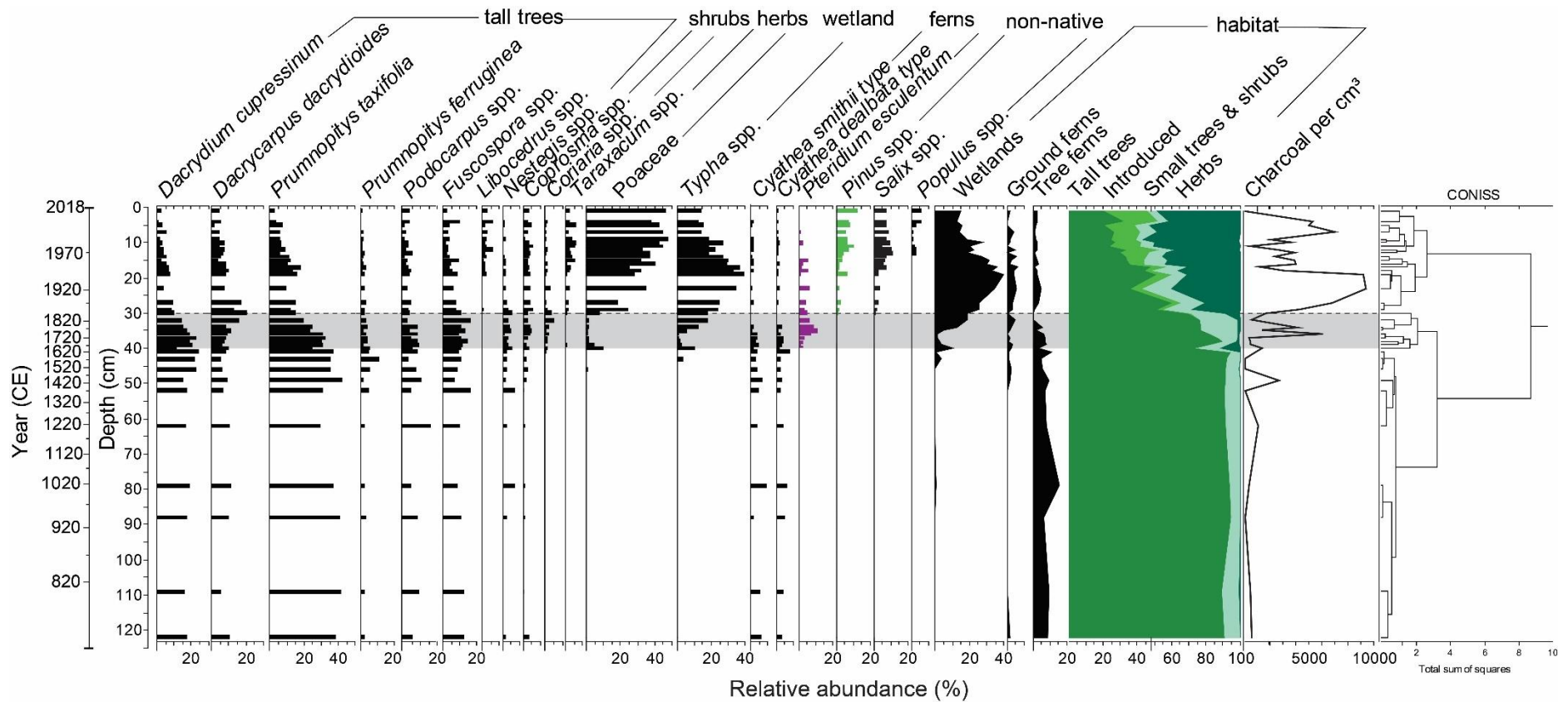
A total of 70 taxa were identified from the pollen samples (Supplementary Table S5). Before human activity, assemblages were stable with canopy trees; *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Prumnopitys ferruginea*, *Fuscospora* spp. and *Podocarpus* spp.,

comprising ~85% of the assemblage, while small trees: *Nestegis* spp. and *Coprosma* spp. comprised the rest of vegetation (Figure 3).

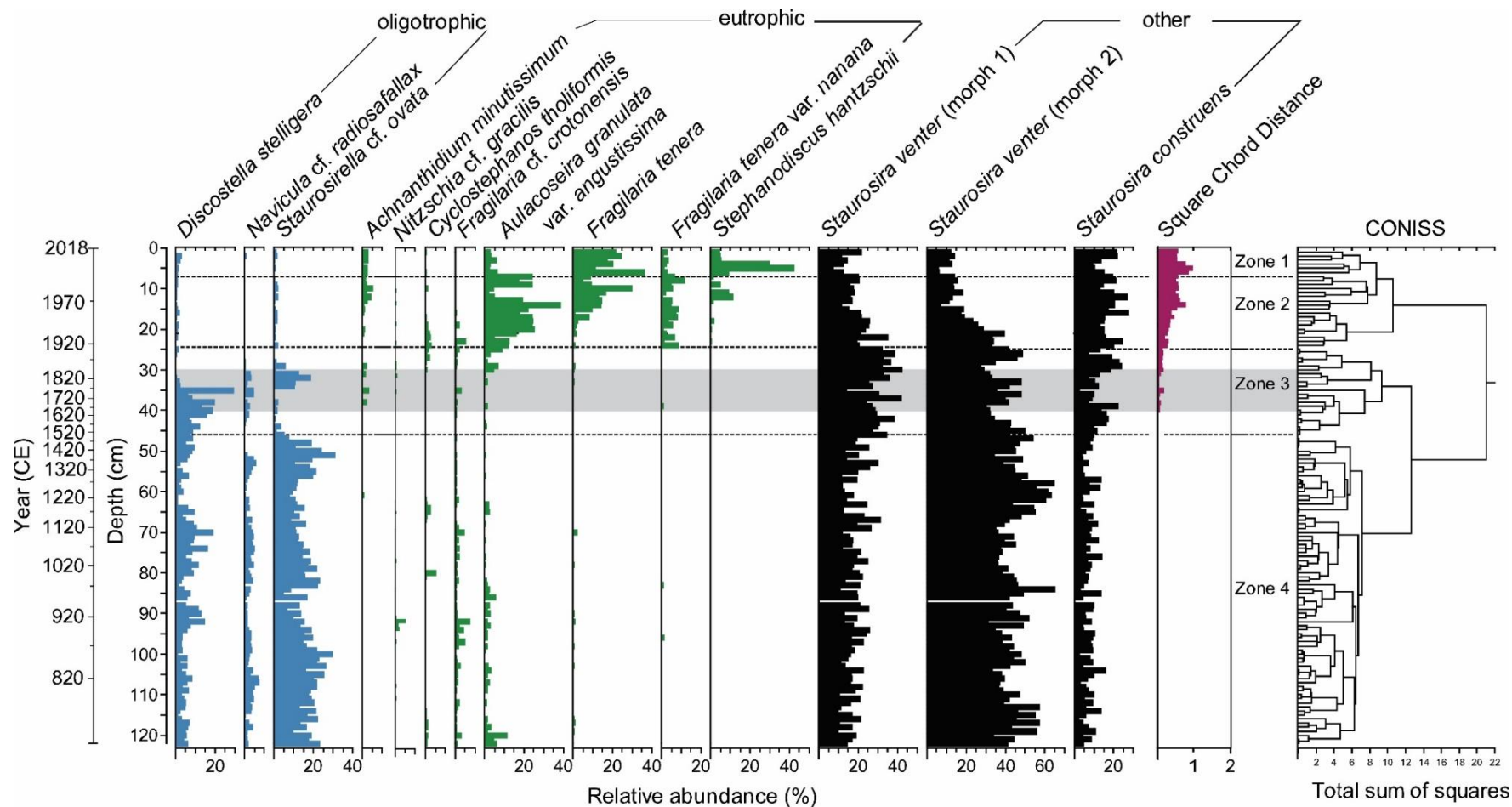
The abundances of *D. cupressinum*, *P. taxifolia* and *Podocarpus* spp. started gradually declining from ~1620 CE (Figure 3), co-occurring with the first recorded appearance of *Pteridium esculentum*, grasses (Poaceae) and an increase in the concentration of charcoal. Prior, there were only intermittent records of low counts of charcoal. In addition, the abundance of *Cyathea* spp. declines, while there is a steady increase in the wetland plant *Typha* spp. The decline in native tree species continues from ~1840 CE and accelerates when non-native *Pinus* spp. and *Salix* spp. and grasses become more abundant in the catchment, marking the start of European activity. Charcoal abundance is more pronounced following European arrival, and the non-native grasses and herbaceous taxa became dominant, as did *Typha* spp. In ~1960 CE, *Populus* spp. is first recorded and *Typha* spp. declined.



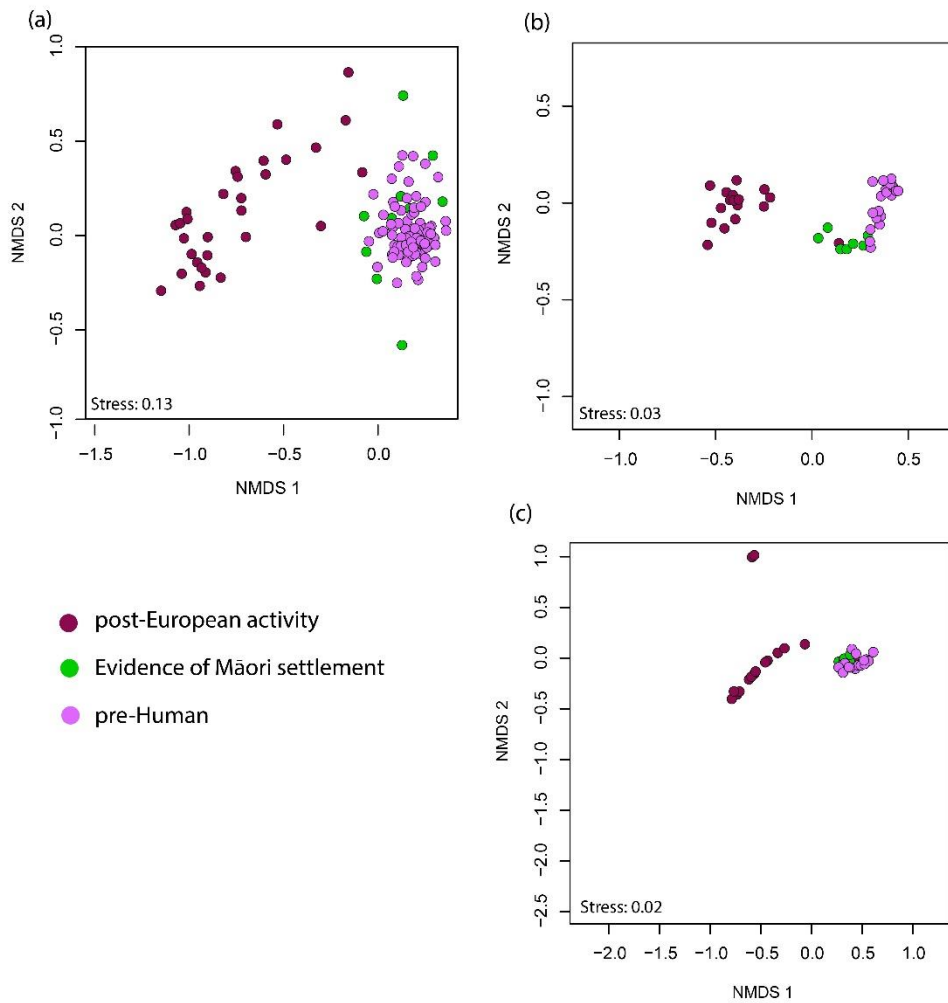
**Figure 2:** The age–depth model for the Lake Oporoa core, based on  $^{210}\text{Pb}_{\text{ex}}$  dating, pollen biostratigraphy, and radiocarbon dates. Radiocarbon dates were calibrated with the SHCal20 calibration curve (Hogg et al.,2020) and integrated with the other chronology using the P\_SEQUENCE algorithm in OXCAL4.4 (Bronk Ramsey & Lee,2013). The graphic shows the calendar age likelihood (light grey) and posterior probability density functions (dark grey) for all sources of chronology, as well as the model age uncertainty (blue curves) at the 95% level of confidence.



**Figure 3:** Lake Oporoa pollen stratigraphy. Only species recorded at  $\geq 5\%$  abundance are shown. The shaded area denotes evidence of Māori settlement using *Pteridium esculentum* (shaded purple) and charcoal as chronological markers, and the timing of European activity in the catchment using *Pinus* spp. (shaded green).



**Figure 4:** Lake Oporoa diatom stratigraphy. Only species with  $\geq 5\%$  abundance are shown, along with the minimum squared chord distance between each pre-Māori sample and the pre-Māori reference samples. The shaded area denotes evidence of Māori settlement. This period is defined by pollen chronological markers (*Pteridium esculentum* and *Pinus* spp.)



**Figure 5:** Non-metric multidimensional scaling results from (a) diatom community, (b) bacterial sedDNA, and (c) pigment data (HPLC). The points are colour coded according to the occupation phase of the catchment that they represent

### 3.3 Diatoms

A total of 77 diatom species from 31 genera were recorded (Supplementary Table S6). Of these 14 were  $\geq 5\%$  relative abundance. There was difficulty in assigning identifications to some taxa, due to lack of published material and the likelihood they were new to science. Taxa were therefore given an affinitive name. This is relevant for *Staurosirella cf. ovata*, a spineless taxon where SEM analysis was inconclusive (Supplementary Figure S2).

CONISS analyses divided the record into four zones: (1)  $\sim 1991$  CE – 2018 CE (0–7 cm), (2)  $\sim 1990$ –1897 CE (8–24 cm), (3)  $\sim 1485$ –1885 CE (25–46 cm), and (4)  $\sim 1460$ –800 CE (47–122 cm; Figure 4). The zones were different to the human occupation periods outlined by the pollen, but are used to describe shifts in the diatom assemblages. There was significant dissimilarity in the assemblages recorded between each occupation period: Pre-human, Evidence of Māori settlement and Post European arrival

(PERMANOVA:  $F= 58.72$ ;  $p < 0.001$ ) (Figure 5). This difference remained even when the effect of depth as an explanatory variable was removed (dbRDA:  $F= 19.39$ ;  $p < 0.001$ ).

The fragilarioid, benthic taxa *Staurosira construens*, *Staurosira venter* and *Staurosirella* cf. *ovata* dominate the record (> 75% of diatom community) between 800–~1940 CE, after which they decline (Figure 4). Also contributing to Zones 3 and 4 are *Discostella stelligera* and *Navicula* cf. *radiosafallax*. These are most abundant in the pre-human record and start declining from ~1740–1800 CE, after evidence of Māori settlement, although *Discostella stelligera* peaks during this time period at 30% (~1740 CE). *Navicula* cf. *radiosafallax* and *Staurosirella* cf. *ovata*, follow a similar trend. Before any human activity in Zone 2 there were small, intermittent pulses of *Aulacoseira granulata* var. *angustissima*, *Nitzschia* cf. *gracilis* and *Cyclostephanos tholiformis*. Following the decline in the fragilarioid taxa from the boundary of Zone 2 onwards (~1940 CE), there is a corresponding, sequential increase in planktonic taxa: *Aulacoseira granulata* var. *angustissima*, *Fragilaria tenera*, *Fragilaria tenera* var. *nanana* and *Stephanodiscus hantzschii*.

The minimum SCD values between each ‘impact’ sample and the group of reference samples show an increasing trend towards present, indicating that the species composition of diatom assemblages is diverging from that recorded prior to human activity. The minimum value recorded was 0.01, just before the start of European activity, while the maximum was 0.91 recorded in 1998 CE.

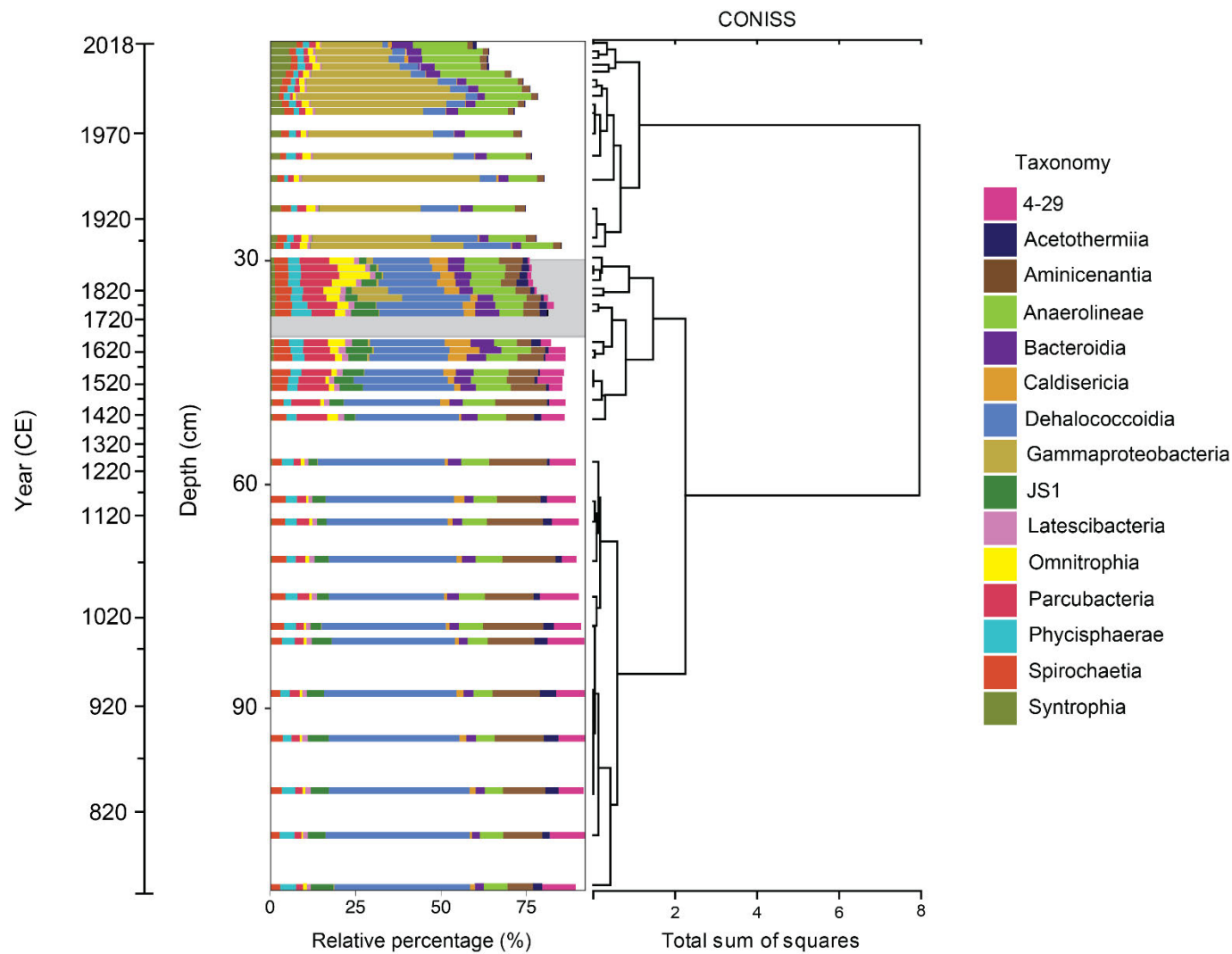
### 3.4 Sedimentary DNA

There were 38,005 ASVs ranging from 3,697 in ~1855 CE, to 1011 ASVs in 1460 CE. The pre-human period had the lowest diversity ( $1,325 \pm 292$  ASVs; Figure 6), with the evidence of Māori settlement ( $3,093 \pm 533$  ASVs) and post European activity ( $2,988 \pm 345$  ASVs) having similar diversities.

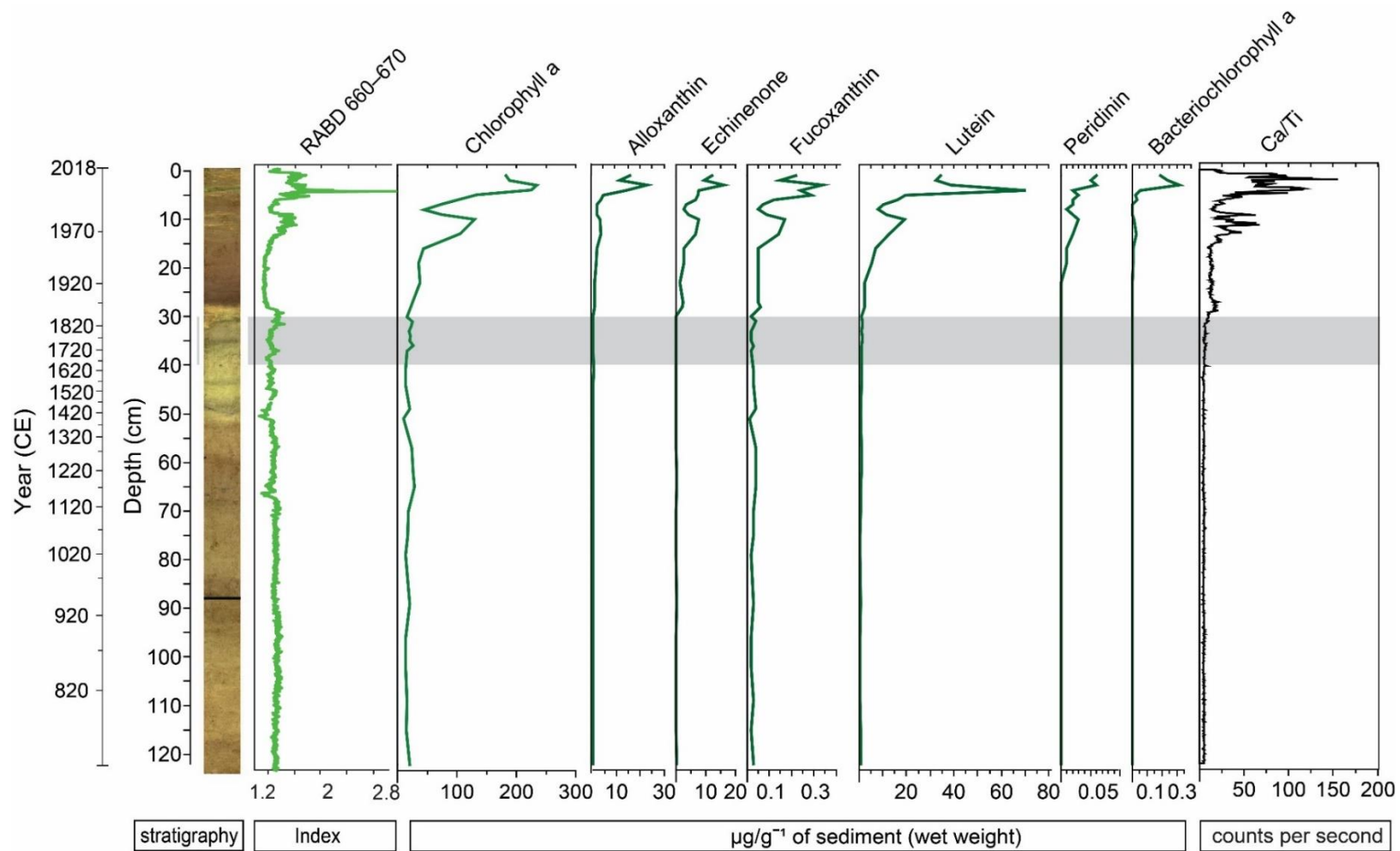
Before human activity Dehalococcoidia was the dominant bacterial class although there was also substantial contribution from Aminicenantia. Dehalococcoidia were still dominant after Māori settlement, but there were increases in Parcubacteria and Omnitrophia, and a decline of Aminicenantia. Following European arrival, Dehalococcoidia declined in relative abundance, while Gammaproteobacteria became the dominant class (Figure 6).

NMDS analysis showed that there was a temporal trend in the data (Figure 5; stress=0.03), and that microbial communities were significantly different between the occupation phases (PERMANOVA:  $F= 83.08$ ;  $p < 0.001$ , dbRDA:  $F= 29.17$ ;  $p < 0.001$ ). The distance between samples before human activity shows the microbial community to have a narrow range in dissimilarity. Distinct ecological shifts occur after evidence of Māori settlement, although a narrow range of variability remains. After European activity, the ecological distance and variability between samples in this occupation period is greater.





**Figure 6:** Bacterial sedDNA amplicon species variant richness, presented as relative abundance at the class level. The shaded area denotes evidence for Māori settlement, similarly, delineated from the pollen chronology



**Figure 7:** Core stratigraphy, relative pigment abundances, RABD660–670ratio from the hyperspectral analysis, and Ca/Ti data. The shaded area denotes evidence of Māori settlement

### 3.5 Itrax-derived sedimentary Ca/Ti

Ca/Ti values were low and relatively constant from ~800 CE to 1875 CE. At ~1960 CE and 1998 CE there are two abrupt high-amplitude increases that mirror the positive excursions observed in RABD<sub>660–670</sub> and many pigment profiles (Figure 7). These recent increases in Ca/Ti are an order of magnitude higher than at any other intervals in the core.

### 3.6 Hyperspectral Imaging Scanner

The RABD<sub>660–670</sub> index values remain relatively constant, with only subtle fluctuations, from ~800 CE – ~1840 CE, and an average of 1.3 although these values increase slightly during the Māori settlement period (Figure 7). Following European activity in the catchment, the index becomes variable, initiated by a relative decline from ~1840 CE–~1960 CE. The index in this period averaged 1.2 before increasing post 1960 CE (average 1.5) with a peak of 2.9 at 2000 CE.

### 3.7 Sedimentary pigments

Before Māori settlement, all pigment concentrations were relatively consistent with only minor fluctuations. Fucoxanthin (diatoms) was present at higher levels compared to other phytoplankton pigments during this period (Figure 7). Shifts in pigments began after European activity in ~1840 CE, with increased concentrations observed across all pigment groups, although this trend was recorded earlier with echinenone (cyanobacteria) and fucoxanthin (diatoms). Maximum concentrations were recorded for all pigments from 2001–2006 CE. Ordination of the data showed dissimilarity between samples from different depths (Figure 5, stress: 0.02) while the composition of pigments was found to be statistically significantly different between the different periods of human inhabitation (PERMANOVA:  $F = 33.12$ ;  $p < 0.001$ ; dbRDA:  $F = 10.97$ ,  $p < 0.001$ ).

## 4 Discussion

### 4.1 The ecological history of Lake Oporoa and its catchment

#### Pre-human: 800–~1620 CE

In the centuries before Māori settlement, the dominant vegetation in the catchment was stable podocarp forest (*Prumnopitys taxifolia*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Podocarpus* spp.) with a subcanopy of beech (*Fuscospora* spp.) and tree ferns (*Cyathea* spp.). *Prumnopitys taxifolia* is a dryland species and was abundant in pre-deforestation vegetation of the North Island (McGlone et al., 2017). Other pollen records in New Zealand similarly indicate landscape and vegetation stability before Māori settlement (Byrami et al., 2002; McWethy et al., 2014; Newnham et al., 2018).

The pre-human diatom record is characterised by the dominance of benthic taxa in genera *Staurosira* and *Staurosirella*. *Staurosira construens*, *S. venter*, *Staurosirella* cf. *ovata*, and other species in these genera, dominate (up to ~90%) shallow lake ecosystems (Bennion, Fluin & Simpson, 2004; Bennion et al., 2010) and are abundant in New Zealand lakes (Reid, 2005). The dominance of *Staurosira* and *Staurosirella* in the pre-human period is indicative of persistent shallow lake conditions, and indicate that light could reach the bottom of the lake. These factors combined explain the dominance of these taxa (Sayer, 2001; Bennion, Fluin & Simpson, 2004; Reid, 2005). This interpretation is supported by the low relative abundance of planktonic *Discostella stelligera* and an absence of other planktonic diatoms (cf. Sayer, 2001; Bennion, Fluin & Simpson, 2004; Reid, 2005). *Discostella stelligera* is often found in low nutrient lakes with little to no human disturbance, including those in New Zealand (Tibby, 2004; Reid, 2005; Rühland, Paterson & Smol, 2008; Saros & Anderson, 2015). Its presence in Lake Oporoa, indicates similar oligotrophic conditions.

The low nutrient conditions, and thus low aquatic productivity inferred from the diatom taxa are supported by productivity measures; RABD<sub>660-670</sub>, and chlorophyll *a*. There is long-term consistency, and low concentrations of these indicators before human arrival. The relative proportions of the phytoplankton groups remained constant, indicated by the lack of any trends in the data. Similarly, Ca/Ti values are low and invariant indicating that authigenic carbonate is not a key constituent in the sediment. Lastly, the bacterial community showed remarkable stability during the pre-human period, dominated by class Dehalococcoidia.

#### Evidence of Māori Settlement: ~1620–~1840 CE

Coniferous tree pollen, and tree fern spores exhibit a gradual decline but remain abundant following evidence of Māori settlement in ~1620 CE, despite disturbance indicated by the elevated levels of markers for Māori activity (*Pteridium esculentum* and charcoal). The dominance of podocarp forest in the pollen record from Lake Oporoa contrasts with many other New Zealand palynological studies (Wilmshurst, McGlone & Partridge, 1997; McGlone & Wilmshurst, 1999; Horrocks et al., 2000, Byrami et al., 2002; Wilmshurst et al., 2004) suggesting that widespread forest clearance did not occur in the catchment immediately following human arrival. Rather, it was gradual and probably began locally around the lake increasing approximately 100 years later (c. 1740 CE), transforming the catchment into more open forest. However, a major floristic change in the pollen record is the occurrence of *Typha* spp., indicating the presence of *Typha* spp. stands along the lake margin. *Typha* spp. (Raupō) had a broad range of uses by Māori (McCallum & Carr, 2012) and it is possible it was introduced into the catchment as a product of crop cultivation (Lyver et al., 2015).

Despite the gradual initial change in local and regional tall forest vegetation, both the diatom and microbial (sedDNA) communities responded within 50 years of the first evidence of Māori settlement. PERMANOVA of the diatom and microbial assemblages shows a statistical difference between the pre-human and Māori settlement period. Incremental increases in *Discostella stelligera*, and its subsequent decline with *Staurosirella cf. ovata*, are detected simultaneously with the increases of *Typha* spp. and *P. esculentum*. While *D. stelligera* is competitive in low nutrient environments, experimental studies demonstrate it responds opportunistically to an increase in nutrients, in particular nitrogen (Saros & Anderson, 2015). *Discostella stelligera* has responded to extensive catchment burning in some lakes in New Zealand, and subsequent sediment erosion (McWethy et al., 2010, Stephens et al., 2018). The combination of Lake Oporoa's small depth and size makes it susceptible to subtle changes in the landscape.

In the microbial community, Dehalococcoidia was still the dominant class, despite the presence of Parcubacteria and Omnitrophia, although Dehalococcoidia later started to decline relative to the pre-human phase. These shifts in the microbial communities, concomitantly with the diatoms indicate changing biogeochemical processes and ecosystem function across two trophic levels, in response to relatively minor changes in the catchment's forest. Despite these shifts across the trophic levels, the proxies of algal abundance (RABD<sub>660-670</sub> or chlorophyll *a*) do not reveal any major shifts in lake productivity, nor is there any change observed in Ca/Ti values. The species data from the diatoms and microbial communities thus provide insights into early ecological shifts in Lake Oporoa that would have gone undetected by only examining overall proxies for algal abundance.

#### Evidence for earlier Māori settlement prior to ~1620 CE

While *P. esculentum* was used to delineate evidence of Māori settlement, cluster analysis of the diatom record, and the presence of *Typha* spp. prior to *P. esculentum* allude to settlement of the catchment before any extensive modification of the surrounding forest occurred. The CONISS boundary between Zone 4 and 3 at ~1480 CE is characterised by loss of *Staurosirella cf. ovata*, and increase of *Staurosira venter* morph 1 and *Discostella stelligera*, likely indicating some low-level nutrient increases (Figure 4). Secondly, *Typha* spp. appears around the same time as the diatom flora shifts in ~1550 CE. In other sites across New Zealand, pollen records show *Typha* spp. increasing following landscape burning (Figure 3; Byrami et al., 2002; Lyver et al., 2015). It is possible that both *Typha* spp. and the Zone 3 diatom boundary are indicators of Māori activity in the catchment, which would place evidence of settlement stratigraphically earlier in the record than the appearance of *P. esculentum*, occurring between ~1480 CE or ~1550 CE, rather than later around ~1620 CE as indicated by *P. esculentum*

The broad timing of these changes, while recognising the age uncertainties within the age model, accords with the timeline of Māori arrival at Lake Oporoa. The oral history record by Neville Lomax's great-great grandfather—who recounted the story of Matangi to the historian Thomas William Downes (Downes, 1910)—places the settling of Matangi at Lake Oporoa in the 1600s.

#### Post-European arrival: ~1840 CE–2019 CE

Between ~1840–1896 CE, the Rangitikei catchment was progressively dominated by European styles of agriculture (Gordon, 2009) and subsequent changes in vegetation. This vegetation shift is signalled by a further opening and reduction of native forest and decline in dryland podocarps, with greater presence of grassland and herbs (Figure 3). This transition is signalled by a decline in native species, and an increase in non-native trees; *Pinus* spp. and *Salix* spp., and later, *Populus* spp. The latter were planted after World War II as a means of sediment stabilisation on the banks of rivers and lakes (Gordon, 2009), the likely explanation for their presence in the record.

Foremost, the NMDS and PERMANOVA show clear differences in the diatom community, bacteria and pigments post-European settlement when compared to both the pre-Human and Māori settlement sections of the record. In the diatom assemblage, planktonic taxa *Aulacoseira granulata* var. *angustissima*, and later, *Stephanodiscus hantzschii* become abundant during this period. These species are indicators of nutrient enrichment in many locations around the globe and can be abundant in shallow eutrophic lakes (Kilham, Kilham & Hecky, 1986; Reynolds et al., 2002; Bicudo et al., 2016; Brugam & Munoz, 2018). *Fragilaria tenera*, is also dominant and is inferred to prefer shallow and turbid waters (Reynolds et al., 2002; Padisák, Crossetti, & Naselli-Flores, 2009). The shifts between *A. granulata* var. *angustissima*, *Fragilaria tenera*, and *Stephanodiscus hantzschii* reveal complex interactions between resource availability (silica, P and N) and catchment processes (Tilman, Kilham & Kilham, 1982; Anderson, 1989), especially since the 1960s.

As Lake Oporoa became more eutrophic, and planktonic taxa increased, there was a noticeable decline in benthic *Fragilareaceae*. Benthic algal contribution to primary productivity can decrease with nutrient enrichment as an abundance in planktonic species increases light attenuation to littoral and benthic habitats (Vadeboncoeur et al., 2003; Vadeboncoeur et al., 2008). In theory, benthic algal growth should not be limited by nutrients due to their ability to utilise both nitrogen (N) and phosphorus (P) from sediment (McCormick, Phillips & Ives, 2019), which further implies light was the limiting factor in Lake Oporoa in the late European phase.

The profound changes in diatom community, are matched with shifts in the microbial community, with classes Gammaproteobacteria, and Anaerolineae becoming dominant. Environmental lineages

(containing no cultured representatives) within the Gammaproteobacteria predominated, with taxa such as JS1 contributing (Figure 6). This taxon has been observed in subsurface environments (Webster et al., 2007; Kadnikov et al., 2012; Han et al., 2017) and is associated with organic rich environments linked with methane (Han et al., 2017). Hence, the increase in Gammaproteobacteria could be due to landscape deforestation, and subsequent sediment erosion into the lake, combined with their integral role in methane oxidation in freshwater systems (Knief, 2015; Guggenheim et al., 2020). Gammaproteobacteria and Anaerolineae are also associated with the denitrification cycle, or sediment nitrate (Pan et al., 2020; Zhang, Ji & Pei, 2021). While there is little ecological information available for the other bacterial groups (e.g., Syntrophia), the fact there is an observed shift in lake microbial communities, following European agricultural practices in the catchment, provides additional evidence of profound ecosystem change.

Before European settlement, fucoxanthin (predominantly derived from diatoms) was the dominant taxon-specific pigment in the record, implying that diatoms were always a major component of the phytoplankton community. Since ~1840 CE, however, trends in fucoxanthin and echinenone, suggest co-dominance of cyanobacteria and diatom communities, while other phytoplankton communities; dinoflagellate (peridinin), green algae (lutein) and cryptophyte (alloxanthin) increased since ~1940 CE. A combination of increasing agricultural intensification following the advent of aerial top dressing in the 1950s, the use of superphosphates (Gordon, 2009) and sustained application of fertilisers (N, in particular) across New Zealand in recent decades (Snelder, Larned & McDowell, 2018; StatsNZ, 2021) has likely driven the increase in productivity. Similarly, this enhanced productivity has driven periods of anoxia in Lake Oporoa as indicated by bacteriochlorophyll *a*, a proxy for anoxia as it is produced by anoxygenic phototrophic bacteria (Makri et al., 2021). Eutrophication can drive anoxia, through enhanced biomass production and subsequent decomposition (Friedrich et al., 2014; Jenny et al., 2016; Le Moal et al., 2019; Makri et al., 2021).

The synchronous increase in Ca/Ti along with pigment, HSI index, bacteriochlorophyll *a* and eutrophic diatom taxa supports the interpretation of enhanced productivity and indicates a marked change in Lake Oporoa after ~1960 CE. Biologically-mediated calcite precipitation has been observed in lakes undergoing eutrophication due to enhanced nutrient influx (Hodell et al., 1998; Romero et al., 2006). In these settings, enhanced productivity by phytoplankton and, or, cyanobacteria (Thompson et al., 1997) removes carbon dioxide from the water column, elevates pH and promotes conditions for calcite precipitation. Synchronous shifts in diatoms, pigments, HSI index, and Ca/Ti indicate that biologically-mediated calcite precipitation driven by enhanced nutrient delivery and subsequent eutrophication is an important process operating in Lake Oporoa since 1960.

## 4.2 Rehabilitation and future management

Lake Oporoa is a culturally important site for Ngāti Hauiti, and the focus of cultural reconnection and ecological rehabilitation (Šunde & Foster, 2021). The diatom and pigment datasets highlight eutrophication of Lake Oporoa, particularly in the last 60 years. Recounting the history of Lake Oporoa, Ngāti Hauiti *kaumatua* (elder) Neville Lomax recalls the lake being ‘*that colour*’ for the last thirty to forty years (i.e. since the early 1980s). This observation of changes since the 1980s is supported by the peaks in *Stephanodiscus hantzchii*, RABD<sub>660-670</sub>, and cyanobacterial pigments and indicates that it was not until later in the 1980s that ecological shifts were visible as deterioration in water clarity.

In the context of lake rehabilitation, the personal memories and intergenerational knowledge held by *kaumatua* Neville Lomax indicate the lake’s ecological conditions in the 1950s is a culturally acceptable target. Neville recalls the lake as having good water clarity, being able to see up to two metres below the lake surface, and hosting a substantial population of *tuna* which is a valuable food source (see Šunde & Foster, 2021). However, at this time (1950s) the diatom *A. granulata* var. *angustissima* peaks, which in other studies indicates increasing productivity and turbidity (e.g. Gell et al., 2005). This indicates some nutrient enrichment of Lake Oporoa had already occurred, but not to the point where visibility, as a result of excessive phytoplankton growth (i.e. cyanobacteria, green algae), had reduced. The SCD scores of the diatom assemblages verify this trajectory of eutrophication, and identifies the 1950s, as the start of increasing differentiation from the pre-impact conditions.

Despite the palaeolimnological record indicating some nutrient enrichment in the 1950s, Lake Oporoa was still in “good health”, without excessive cyanobacterial and other phytoplankton growth. Importantly, Lake Oporoa supported the cultural and spiritual associations of Ngāti Hauiti, especially with *tuna* harvesting and recreational activities. Using the 1950s as a rehabilitation target for Lake Oporoa utilises the traditional knowledge of lake conditions, but also provides a tangible goal, as cultural practices were still maintained. Were the palaeolimnological data used to delineate a rehabilitation target they would suggest earlier than the 1950s, such as 1900–1920 (i.e. before increases in *Fragilaria tenera* and *A. granulata* var. *angustissima*). This would reduce the risk of the 1950s target not being sufficiently stringent while ensuring further decline is prevented. However, achieving such a goal is likely to be difficult, given that catchment vegetation and nutrient inputs need to be similar to the early 1900s and land management practices would likely need to change considerably. Additionally, reference conditions guided by palaeolimnology have, at times, provided unrealistic goals given the long-term nature of human interaction with the environment (Bradshaw, Nielsen & Anderson 2006). As an alternative, palaeolimnology can provide a range of rehabilitation (or restoration) targets (Bennion et al., 2011), and in this case verifies that a 1950s target is suitable for both cultural and improved ecological health.



Therefore, the conversations with a Ngāti Hauiti elder and tribal environmental leaders, together with the palaeolimnological data, indicate that both an acceptable and realistic rehabilitation target for Lake Oporoa is aligned with ecological conditions from the 1950s. More specifically, the palaeolimnological data provide hope for lake conservation and rehabilitation in that there has not been a complete floristic turnover of diatom community. Species from *Staurosira* and *Staurosirella*, which were abundant during pre-human periods, are still present, while small populations of *Discostella stelligera* and *Staurosirella cf. ovata* also remain.

#### 4.3 Conservation and rehabilitation approaches for Lake Oporoa

While there were ecological shifts in Lake Oporoa following Māori settlement, the greatest rates of change occurred following European arrival and settler land use activities. The shifts largely coincide with both the conversion of the landscape from remnant open podocarp forests to pasture and associated nutrient increase, and enhanced fertiliser use in the post-war period. It has been suggested that remnant species of *tuna* are likely to be present in Lake Oporoa (Kelly & Waters, 2018; Ngā Puna Rau o Rangitīkei, 2019), although population numbers are likely to be low. Lake Oporoa is in the distribution range of native fish; *Gobiomorphus cotidianus*, *Galaxias brevipinnis* (Kelly & Waters, 2018). Although no fisheries data are available, because of the continuing decline in the health of the lake (as indicated by increasing departure of the SCD values) it is important to conserve remnant biota and as a precursor to rehabilitation.

One of the primary methods for reducing the nutrient load into water bodies is to substantially revegetate both riparian zones and catchments (Franklin, Robinson & Dickinson, 2019; Vidon, Welsh & Hassanzadeh, 2019). A recent study indicates nutrient inflow into Lake Oporoa is in the mesotrophic range (TN = 250 mg/m<sup>3</sup> and TP = 9.3 mg/m<sup>3</sup>, Kelly & Waters, 2018). Revegetation would ideally comprise native trees and lower canopy vegetation reminiscent of the pre-human landscape, which in Lake Oporoa, can be inferred from the pollen record (e.g. *Prumnopitys taxifolia*, *Dacrycarpus dacrydioides*, *Cyathea* spp.). Planting of riparian zone vegetation around Lake Oporoa began in early-2019, while established non-native trees (*Salix* spp. and *Populus* spp.) have been poisoned, except around the steep northern margin of the lake, to provide root stability to the slopes. The planting of the riparian species needs to be complemented by other techniques and modifications to farming practices, as the extent of the vegetation will not be the same as it was before European activity commenced, and therefore not mature nor dense enough for significant nutrient abatement.

The replanting of native vegetation in the riparian zone and catchment should support both nutrient abatement, and the cultural heritage of the lake. Given the cultural significance of Lake Oporoa to Ngāti Hauiti, their desire is to re-plant the area with native vegetation. The reintroduction, and

establishment of native emergent macrophytes, or marginal riparian species could assist with nutrient sequestration. This includes *Typha* spp. (raupō) and *Sophora* spp. (kōwhai) and similar native plants that provide habitat attractive to native birds like the tūī (*Prosthemadera novaseelandiae*). The palaeoecological reconstruction indicates that *Typha* spp. was an important feature of the lake's margin, but also records low levels of the macrophyte *Potamogeton* and Fabaceae (which may include *Sophora* spp. (Table S5)). Other species native to New Zealand, such as *Carex virgata*, *Austroderia richardii*, *Cordyline australis* are highly effective at reducing the transfer of N to waterways (Franklin, Robinson & Dickinson, 2019). While there is no specific indication of their presence in the pollen record, this may be an artefact of poor pollen dispersal (e.g. *Cordyline australis*, Deng et al., 2006), or pollen being indistinguishable below family level identification (e.g. *Carex virgata* classified under Cyperaceae and *Austroderia* spp. under Poaceae).

Re-introducing native submerged macrophytes (*Potamogeton* spp. or *Myriophyllum* spp.) is likely to assist with nutrient sequestration and sediment retention, as well as restoring ecosystem functions, such as habitat for fish and zooplankton (Barko & James, 1998; Jeppesen et al., 1998; Madgwick et al., 2011). It is possible there are some remnant populations of native macrophytes, as the shallowness of Lake Oporoa would support submerged macrophytes, yet as the lake became more eutrophic, it is likely they declined in abundance (*sensu* Sayer et al., 2010). In this case any rehabilitation efforts should focus on assisting with conservation of remnant populations. Pollen data revealed some evidence of submerged aquatic taxa (Table S5), aligning with evidence in the diatom data of some epiphytic species (i.e. *Epithemia sorex*). To determine historical submerged macrophyte communities, additional sediment cores could be taken from a number of sites across the lake and analysed for plant macrofossils, and, or sedDNA of past macrophyte communities. The 1950s macrophyte community could then be used as a restoration target in line with the desires of Ngāti Hauiti. Additionally, a survey of current macrophyte populations should be undertaken.

A challenge for lake rehabilitation is the legacy of sedimentary phosphorus, and internal TP loading, which means that catchment nutrient reduction measures are not always immediate or effective (Søndergaard, Jensen & Jeppesen, 2003). Dredging is an option to remove phosphorus enriched sediments, and can effectively remove legacy phosphorus (Bormans, Maršálek & Jančula, 2016). Dredging of the upper 35 cm of sediment would be sufficient to remove post-European settlement sediment. While dredging is a viable technical option, Ngāti Hauiti are highly unlikely to support this option due to the potential impacts on their cultural and spiritual relationship with the lake.

Restoring the stream outflow on the southern margin of Lake Oporoa would reinstate the migratory pathway for *tuna* to the Rangitīkei River, while possibly improving water quality in the lake. Currently

surface runoff into the lake is diverted by farm tracks into the surrounding pastoral land. This is likely to have contributed to lake level decline, and subsequent reduction in stream outflow. Restoring lake levels and stream outflow is crucial for both cultural and ecological values and should be explored as a management option. To measure success of these rehabilitation techniques, regular monitoring of diatoms in modern sediments (via grab samples or sediment traps), and comparing SCD scores, a measure of dissimilarity, between the changes during the monitoring time and the reference samples, would allow a rapid assessment of the success of lake management strategies.

## 5 Conclusion

This study revealed that Lake Oporoa, a shallow nutrient-enriched lake on New Zealand's North Island, has undergone a series of progressive ecological changes in response to Māori and European activity. While early Māori deforestation was minimal and gradual, marked ecological change in the lake was recorded in both the diatom and bacterial communities. The low nutrient indicator diatom species *Discostella stelligera* and *Staurosirella cf. ovata*, all but disappeared following Māori settlement. Both taxa highlighted sensitivity to catchment and lake processes and were responsive to changing conditions when the pigment and XRF data indicated otherwise. Nevertheless, the most pronounced ecological shift in Lake Oporoa coincided with rapid catchment deforestation and conversion to pasture following European settlement. At this time, rapid eutrophication and change in lake ecology was recorded across Lake Oporoa's diatom and bacterial communities, and pigments.

These palaeolimnological insights can be used to guide rehabilitation for Lake Oporoa, while acknowledging the complex process of rehabilitating freshwater systems. These suggestions could ultimately underpin the aspirations of Ngāti Hauiti and the multi-tribal collective Ngā Puna Rau o Rangitīkei whose catchment strategy and action plan (Ngā Puna Rau o Rangitīkei, 2019) outlines a commitment to ecological restoration throughout the region over the next 100 years. The collaborative approach of the *iwi* and the collective has ensured that landowners, the community, scientists and government gain an appreciation for the cultural and ecological significance of Lake Oporoa. Memories of elders such as Neville Lomax, who recall stories of the early explorers, capture the treasured status of Lake Oporoa (Šunde & Foster, 2021). Indigenous peoples have a pivotal role in the rehabilitation of freshwater ecosystems, and palaeolimnological records can assist with this process. This study has provided a template for other researchers wishing to engage with indigenous peoples, particularly for the management and conservation of freshwater.

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## 8 Supplementary Information

### Using palaeolimnology to guide rehabilitation of a culturally-significant lake in New Zealand

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## 2 Methods

### 2.3 Core sampling and sub sampling

Four cores were collected in June 2019. The master core (123 cm) was split into two. One half of the split core was subsampled for diatom, pollen, sedDNA, and chronological analyses (<sup>14</sup>C and <sup>210</sup>Pb). In the sub-sampling process, sediment touching the core barrel was not included. This was to reduce the chance of contamination. The other half of the master core was used for non-destructive analyses; measurements with a hyperspectral imaging (HSI) scanner and an Itrax X-ray fluorescence (XRF) core scanner. Before subsampling for sedDNA, the top 2–3 mm of sediment was removed with a sterile spatula. Sub-samples were taken at the centre of the half-core using a sterile spatula and kept frozen (-20°C) in the dark until DNA extraction.

### 2.4 Chronology

Chronology was established using numerical age constraints derived from <sup>210</sup>Pb<sub>ex</sub> dating, pollen informed biostratigraphy and <sup>14</sup>C dating combined with Bayesian age-depth modelling. Fifteen 2 cm<sup>3</sup> samples were extracted from the upper 47 cm of the core providing a down core resolution of

between 1 and 5 cm. These were weighed, freeze dried and then re-weighed to provide estimates of water content. Total  $^{210}\text{Pb}$  activity was estimated by measuring its daughter product  $^{210}\text{Po}$  using chemical extraction and alpha spectrometry. Alpha spectrometry was performed by the Environmental Radioactivity Laboratory group of ESR's National Centre for Radiation Science using Mirion/Canberra PIPS detectors model A450-18AM. Activities are reported in  $\text{Bq.kg}^{-1}$  as mean values with 95% confidence limits. Excess  $^{210}\text{Pb}$  was calculated by subtracting supported  $^{210}\text{Pb}$ , which was estimated by averaging the lowermost samples ( $n=3$ ) in the core where the decay profile of total  $^{210}\text{Pb}$  asymptotes to stable values (Table S2). The  $^{210}\text{Pb}_{\text{ex}}$  data were modelled using the Constant Rate of Supply (CRS) model in the R package Serac (Bruel & Sabatier, 2020), using sediment dry mass (g) calculated from X-ray computed tomography (CT) densitometry and sediment water content (%). The core was CT scanned using a GE BrightSpeed medical CT scanner set to 120 kV, 250 mA, pitch of 0.625 mm and a 100  $\text{cm}^2$  window. Bulk density was calculated from the CT data using the relationship between CT number and bulk density of Reilly, Stoner & Weist (2017).

The  $^{210}\text{Pb}_{\text{ex}}$  age model was validated using independent age estimates derived from the first occurrence and peak of non-native pollen in the core (Figure 2). The increase in *Salix* spp. pollen at 18 cm depth was assigned a date of between 1945 and 1955 CE as this taxon was widely planted to stabilise riverbanks in the region at this time (Gordon, 2009). The second increase and sustained percentage of *Populus* spp. pollen at 10 cm depth was assigned a date of  $1975 \pm 10$  CE ( $2\sigma$ ) because it is likely associated with local planting of this taxa in the lake catchment (Karen Gibbs, Farm manager pers. comms., 2020). The first occurrence of *Pinus* spp. pollen at 30 cm depth was also used to constrain the integrated age-depth model and was assigned an age of 1870–1910 CE because it was used regionally to form shelter belts at this time (Gordon, 2009).

Terrestrial leaf macrofossils were extracted from the core by picking *in-situ* material from the split core surface. Macrofossils were cleaned and pre-treated using a standard acid–alkali–acid procedure to remove carbonates, fulvic compounds and humic compounds (Norris et al., 2020). The pre-treated macrofossils were converted to  $\text{CO}_2$  by combustion, graphitized and measured by accelerator mass spectrometry according to the methods of Baisden et al. (2013). Conventional Radiocarbon Ages (CRA) were converted to calendar years using the SHCal20 calibration curve (Hogg et al., 2020), while those that return modern ages were calibrated using the BHDCGO curve (Turnbull et al., 2017).

Age-depth modelling was conducted using a Bayesian framework in the software OXCAL 4.4 (Bronk Ramsey, 2009a). Age probability density functions from the  $^{210}\text{Pb}_{\text{ex}}$  age-depth model, biostratigraphy and calibrated  $^{14}\text{C}$  dates was integrated with core depth using the P\_Sequence prior model with a variable event thickness constant  $k$  (Bronk Ramsey, 2008; Bronk Ramsey & Lee, 2013). Allowing  $k$  to

vary between two orders of magnitude above and below  $1 \text{ cm}^{-1}$  ensured the model found best fit value of  $k$ , avoiding an over parameterised model (Bronk Ramsey & Lee, 2013). Temporal outliers in the chronology were identified and treated using an outlier analysis that sequentially down weighted outliers in subsequent runs of the Monte Carlo simulation used to produce the age-depth relationship. This reduced the influence of outliers on the final age model (Bronk Ramsey, 2009b). Outliers were assumed to be distributed according to the student's  $t$  distribution with five degrees of freedom and each date was assigned a 0.05 prior probability of being an outlier.

## 2.8 Sedimentary DNA, DNA extraction, PCR, high throughput sequencing and bioinformatics

DNA was extracted from approximately 0.25 g of sediment using the DNeasy PowerSoil Kit (Qiagen, Germany) following the manufacturer's instructions on a QIAcube sample preparation robot (Qiagen). A negative extraction control was included every 23 samples to ensure there was no contamination in the extraction kits.

The V3-V4 region of the bacterial 16S rRNA gene was 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' (Klindworth et al., 2013). The primers included Illumina™ overhang adapters to allow dual indexing as described in (Kozich, Westcott, Baxter, Highlander, & Schloss, 2013). PCR reactions and library preparation was undertaken as described in Pearman et al (2020). Raw sequence reads are deposited in the National Center for Biotechnology Information (NCBI) short read archive under the accession number: PRJNA737168.

Primers were removed from the raw reads with cutadapt (Martin, 2011) allowing one mismatch. Sequences without primer sequences were discarded. The remaining sequences were processed with the DADA2 package (Callahan et al., 2016) within the R framework (R Team, 2018). Forward reads were truncated to 230 base pairs (bp) while reverse reads were truncated to 228 bp. The number of allowed maximum "expected errors" (maxEE) was two and four for the forward and reverse respectively. The first  $10^8$  bp were used to construct a parametric error matrix. Sequences are dereplicated and amplicon sequence variants (ASVs) were inferred based on this error matrix. After inference singletons were discarded and remaining reads were merged with a maximum of 1 bp mismatch and a required minimum overlap of 10 bp. Chimeric sequences were removed from the analysis using the removeBimeraDenovo function within DADA2.

The resulting ASVs were taxonomically classified in DADA2 using the rdp classifier (Wang, Garrity, Tiedje, & Cole, 2007) against the SILVA 132 database (Pruesse et al., 2007) with a bootstrap of 70. The results were combined into a phyloseq object (McMurdie & Holmes, 2013) and any ASVs classified as eukaryotes, chloroplasts or mitochondria were removed. Negative controls were assessed and read numbers for ASVs found in the negative blanks were removed via subtraction.

## 2.12 Sedimentary pigment analysis

Sedimentary pigment analysis is often used to identify historic dynamics of phytoplankton communities (McGowan et al., 2012; Moorhouse, 2018). Samples ( $n = 40$ , Supplementary Table S1) were thawed at 4°C, weighed into Falcon tubes (0.9–1.1 g) and extracted three-times using acetone and ultrasonication for 30 min in a bath sonicator with ice. The pooled extract was dried under a stream of nitrogen gas at 40°C and stored at –20°C until analysis. On the day of analysis, the dried extract was resuspended in acetone (0.5 mL) and transferred to a septum-capped amber vial.

Extracts were analysed by high-performance liquid chromatography (HPLC) with diode array detection (DAD) using an Agilent 1260 HPLC-DAD system (Santa Clara, CA, USA). Sample components were separated using a C<sub>30</sub> column (Develosil RP-Aqueous C<sub>30</sub>, 5- $\mu$ m, 250  $\times$  4.6 mm; Phenomenex, Torrance, CA, USA) maintained at 30°C and a gradient of methanol + 0.1% triethylamine (Solvent A) to 40:60 methanol/isopropyl alcohol + 0.1% triethylamine (Solvent B). Sample was injected (20  $\mu$ L injection) in 100% Solvent A, which was maintained for 5 minutes before proceeding in a linear gradient to 65% Solvent B over 35 min. The column was washed with 90% Solvent B for 5 min and re-equilibrated in 100% Solvent A for 5 min between each injection. The flow rate was 1 mL/min throughout the chromatographic gradient. Light absorption data were collected over a 320–800 nm wavelength range, but only specific wavelength ranges were used for compound quantitation during post-processing (see Supplementary Table S7 for specifics).

A five-point mixed standard curve (0.5–20  $\mu$ g/mL) of chlorophyll-a (Sigma-Aldrich, St. Louis, MO, USA), chlorophyll-b (Sigma-Aldrich) and lutein (Carotenature, Münsingen, Switzerland) was analysed with each HPLC run with qualitative standards for each pigment being analysed. Standards were calibrated by spectrophotometry at 664 nm (chlorophyll-a), 647 nm (chlorophyll-b) and 445 nm (lutein) using the extinction coefficients described in Roy et al. (2011). Equivalence factors for alloxanthin, canthaxanthin, diadinoxanthin, diatoxanthin, echinenone, fucoxanthin, myxoxanthophyll, peridinin, violaxanthin and zeaxanthin were determined in relation to lutein by analysing standards at known concentrations alongside a lutein standard. An equivalence factor for bacteriochlorophyll-a was determined in the same manner, but in relation to the chlorophyll-a standard. These equivalence factors were used for the routine quantification of the other pigments, rather than preparing a standard curve for each HPLC run. Information on the HPLC-DAD analysis for each pigment measured can be found in Supplementary Table S4.



**Table S1:** List of proxies sampled, sample depth, and total number of samples from Lake Oporoa

Proxy	Sample depth (cm)	Number of samples
Diatoms	Every centimetre, except 0 and 87 cm.	121
Pollen and charcoal	1, 4, 5, 7, 9–19, 23, 27, 29, 30, 32, 34–41, 43, 46, 49, 52, 62, 79, 88, 109, 122	37
sedDNA	1–10, 13, 16, 19, 23, 27, 28, 30–37, 41–43, 45–47, 49, 51, 57, 62, 65, 70, 75, 79, 81, 88, 94, 101, 107, 114	44
Pigments (HPLC)	1–10, 13, 16, 19, 23, 27, 28, 30–37, 41, 44, 49, 51, 57, 62, 65, 70, 75, 79, 89, 96, 102, 109, 115, 122	40
Hyperspectral Scanning	41 $\mu$ m	whole core
Itrax $\mu$ -XRF	1 mm	whole core

**Table S2:** Total  $^{210}\text{Pb}$ ,  $^{210}\text{Pb}_{\text{ex}}$  and  $^{210}\text{Pb}_{\text{sup}}$  activities for the Lake Oporoa core.

Top Depth (cm)	Sample ID	ESR Sample Number	Total $^{210}\text{Po}$ (Bq.kg $^{-1}$ )	Total $^{210}\text{Po}$ (Bq/kg) error	Excess $^{210}\text{Pb}$ (Bq/kg)	Excess $^{210}\text{Pb}$ (Bq/kg) error
0	L380_POROA_LC4U_1B_Pb_12.5-13.5cm	2020-1452	83.3	8.2	72.98	8.3
1	L380_POROA_LC4U_1B_Pb_13.5-15cm	2020-1453	100.4	9.3	90.08	9.39
2.5	L380_POROA_LC4U_1B_Pb_15-16cm	2020-1454	97.3	9.4	86.98	9.49
4.5	L380_POROA_LC4U_1B_Pb_17-18cm	2020-1455	76	7.6	65.68	7.71
6.5	L380_POROA_LC4U_1B_Pb_19-20cm	2020-1456	49.4	6.1	39.08	6.23
8.5	L380_POROA_LC4U_1B_Pb_21-22cm	2020-1457	69.2	7.8	58.88	7.9
10.5	L380_POROA_LC4U_1B_Pb_23-24cm	2020-1458	59.3	6.9	48.98	7.02
13.5	L380_POROA_LC4U_1B_Pb_26-27cm	2020-1459	25.8	4.2	15.48	4.39
16.5	L380_POROA_LC4U_1B_Pb_29-30cm	2020-1460	23.5	3.7	13.18	3.91
19.5	L380_POROA_LC4U_1B_Pb_32-33cm	2020-1461	29.8	4.5	19.48	4.68
24.5	L380_POROA_LC4U_1B_Pb_37-38cm	2020-1462	24.9	4.2	14.58	4.39

30.5	L380_POROA_LC4U_1B_Pb_ 43-44cm	2020- 1463	9.3	2.3
37.5	L380_POROA_LC4U_1B_Pb_ 50-51cm	2020- 1464	8.1	2.2
42.5	L380_POROA_LC4U_1B_Pb_ 55-56cm	2020- 1465	12.6	3
47.5	L380_POROA_LC4U_1B_Pb_ 60-61cm	2020- 1466	11.3	2.6
Background <sup>210</sup> Pb = 10.325 (Bq/kg)				
Background <sup>210</sup> Pb error = 2.525 (Bq/kg)				

**Table S3:** Total <sup>210</sup>Pb activities, <sup>210</sup>Pb<sub>ex</sub> activities and CRS model age-depth model for the Lake Oporoa core. Age uncertainties are 2σ

Depth (cm)	Sample ID	CRS Age (CE)	CRS Max Age (CE)	CRS Min Age (CE)
24.5	Pb210_24.5cm	1887	1878.96	1895.77
23.5	Pb210_23.5cm	1910	1903.37	1915.66
22.5	Pb210_22.5cm	1924	1919.27	1929.26
21.5	Pb210_21.5cm	1934	1930.23	1938.77
20.5	Pb210_20.5cm	1941	1937.24	1944.76
19.5	Pb210_19.5cm	1947	1943.45	1950.22
18.5	Pb210_18.5cm	1951	1948.27	1954.51
17.5	Pb210_17.5cm	1955	1951.94	1957.8
16.5	Pb210_16.5cm	1958	1955.07	1960.63
15.5	Pb210_15.5cm	1960	1957.67	1962.97
14.5	Pb210_14.5cm	1963	1960.87	1965.91
13.5	Pb210_13.5cm	1967	1964.86	1969.58
12.5	Pb210_12.5cm	1972	1969.55	1973.86
11.5	Pb210_11.5cm	1977	1975.19	1979.06
10.5	Pb210_10.5cm	1983	1980.88	1984.33
9.5	Pb210_9.5cm	1987	1985.9	1989.01
8.5	Pb210_8.5cm	1991	1989.89	1992.73
7.5	Pb210_7.5cm	1994	1992.7	1995.36
6.5	Pb210_6.5cm	1997	1995.44	1997.93
5.5	Pb210_5.5cm	2000	1998.96	2001.24
4.5	Pb210_4.5cm	2004	2003.14	2005.15
3.5	Pb210_3.5cm	2008	2007.4	2009.13
2.5	Pb210_2.5cm	2012	2011.66	2012.95
1.5	Pb210_1.5cm	2016	2016.06	2016.76

Depth (cm)	Sample ID	Label Code (NZA)	F(Mod)	F(Mod) sigma	CRA	CRA sigma	$\delta^{13}C$	$\delta^{13}C$ sigma
113	L380_POROA_LC4U_2B_RC 25-26cm	68767	0.8597	0.0022	1214	20	- 29.4 9	0.2
108	L380_POROA_LC4U_2B_RC 20-21cm	68768	0.8616	0.0022	1196	20	-29.8	0.2
99	L380_POROA_LC4U_2B_RC 11-12cm	68815	0.8521	0.0023	1285	21	- 31.4 4	0.2
85	L380_POROA_LC4U_1A_RC 97-98cm	68816	0.8651	0.0023	1163	20	Not meas ured	
69	L380_POROA_LC4U_1A_RC 81-82cm	68766	0.8870	0.0022	963	20	- 31.8 4	0.2
59	L380_POROA_LC4U_1A_RC 71-72cm	68813	0.8792	0.0023	1034	20	Not meas ured	
2	L380_POROA_LC4U_1A_RC 14-15cm	68814	1.0491	0.0026	Modern			

**Table S4:** Conventional radiocarbon ages (CRAs) for macrofossils picked from Lake Oporoa cores.

**Table S5:** Pollen taxonomic groupings recorded in Lake Oporoa. Listings with \*\* were found at least once with a 2% abundance.

<b>Species</b>	<i>Metrosideros</i> spp.
<i>Acaena</i> spp.	Monolete fern spores undiff.
<i>Alectryon</i> spp.	<i>Muehlenbeckia</i> spp.
Apiaceae (family)	<i>Myrsine</i> spp.**
<i>Astelia</i> spp.	<i>Nestegis</i> spp.**
Asteraceae total **	Poaceae**
<i>Blechnum</i> spp.**	<i>Paesia</i> spp.
Brassicaceae (family)	<i>Passiflora</i> spp.
<i>Bulbinella</i> spp.	<i>Phormium</i> spp.
Chionochloa type	<i>Phyllocladus</i> spp.
<i>Coprosma</i> spp.**	<i>Phymatosorus diversifolius</i>
<i>Coriaria</i> spp.**	<i>Pinus</i> spp.**
<i>Cyathea dealbata</i> type**	<i>Plagianthus</i> spp.**
<i>Cyathea smithii</i> type**	<i>Plantago novae-zelandiae</i> type **
Cyperaceae total	<i>Podocarpus</i> spp. **
<i>Dacrycarpus dacrydioides</i> **	<i>Populus</i> spp. **
<i>Dacrydium cupressinum</i> **	<i>Potamogeton</i> spp.?
<i>Dicksonia squarrosa</i> **	<i>Prumnopitys ferruginea</i> **
<i>Dodonaea viscosa</i>	<i>Prumnopitys taxifolia</i> **
<i>Elaeocarpus</i> spp.	<i>Pseudopanax</i> spp.
Ericaceae (family)	<i>Pteridium esculentum</i> **

Fabaceae	<i>Pyrrosia</i> spp.
<i>Fuchsia</i> spp.	<i>Quintinia</i> spp.
<i>Fuscospora</i> spp.**	Ranunculaceae (family)
<i>Halocarpus</i> spp.	Rosaceae (family) **
<i>Haloragis</i> spp.	<i>Rumex acetocella</i>
<i>Hebe</i> spp.	<i>Rumex flexuosus</i>
<i>Hedycarya</i> spp.	<i>Salix</i> spp.**
<i>Histiopteris incisa</i>	<i>Taraxacum</i> spp. **
<i>Hypolepis</i> spp.	<i>Toronia</i> spp.
Lamiaceae	<i>Triletes</i>
<i>Leptospermum</i> type	<i>Typha</i> spp. **
<i>Leucopogon</i> spp.	<i>Weinmannia</i> spp.
<i>Libocedrus</i> spp.	
Liliaceae Family	
<i>Lophozonia</i> spp.**	
<i>Lycopodium varium</i>	
<i>Melicytus</i> spp.	

**Table S6:** Diatom species found in Lake Oporoa, and respective authorities. Species with \*\* were found at least once with a 2% abundance.

<b>Taxon</b>	<b>Authority</b>
<i>Achnantheidium exiguum</i>	(Grunow) Czarn 1994
<i>Achnantheidium minutissimum</i> **	Kutzing, Czarnecki
<i>Amphora pediculus</i> **	(Kutzing), Grunow 1875
<i>Amphora</i> spp. ( <i>ovalis</i> ?)	
<i>Asterionella formosa</i>	Hassall 1850
<i>Aulacoseira ambigua</i> **	(Grunow), Simonsen 1979
<i>Aulacoseira granulata</i> var. <i>angustissima</i> **	(Ehrenberg), Simonsen 1979
<i>Caloneis bacillum</i>	(Grunow), Cleve 1894
<i>Cocconeis placentula</i>	Ehrenberg 1838
<i>Craticula halophila</i>	(Grunow), Mann 1990
<i>Craticula cuspidata</i>	(Kutzing), Mann 1990
<i>Cyclostephanos tholiformis</i> **	Stoermer, Håkansson & Theriot 1988
<i>Cyclotella meneghiniana</i> **	Kutzing 1844
<i>Cyclotella</i> ?	
<i>Cymbella novazeelandiana</i> **	Krammer 2002
<i>Diploneis elliptica</i> .	(Kütz.) Cleve 1894
<i>Discostella pseduostelligera</i>	(Hustedt) Houk & Klee 2004
<i>Discostella stelligera</i> **	(Cleve & Grunow) Houk & Klee 2004
<i>Enyconopsis</i> cf. <i>neerlandica</i>	
<i>Encyonema silesiacum</i>	(Bleisch) D.G.Mann 1990
<i>Epithemia adnata</i>	(Kützing) Brébisson 1838
<i>Epithemia sorex</i>	Kützing 1844
<i>Fragilaria tenera</i> **	(W.Smith) Lange-Bertalot 1980
<i>Fragilaria</i> sp. 2**	
<i>Fragilaria</i> sp. 3	
<i>Fragilaria tenera</i> var. <i>nanana</i> **	(Lange-Bertalot) Lange-Bertalot & S.Ulrich 2014
<i>Fragilaria</i> cf. <i>crotonensis</i> **	Kitton 1869
<i>Fragilaria capucina</i> **	Desmazières 1830

<i>Fragilaria</i> sp. 7	
<i>Geissleria</i> cf. <i>schoenfeldii</i>	(Hustedt) Lange-Bertalot & Metzeltin 1996
<i>Gomphonema</i> cf. <i>angustatum</i>	(Kützing) Rabenhorst 1864
<i>Gomphonema</i> sp. 2	
<i>Gomphonema parvulum</i>	Kützing 1849
<i>Gomphonema truncatum</i>	Ehrenberg 1832
<i>Gomphonema</i> ? sp.**	
<i>Karayevia clevei</i>	(Grunow) Bukhtiyarova 1999
<i>Navicula</i> sp. 1	
<i>Navicula</i> sp. 2	
<i>Navicula</i> sp. 3	
<i>Navicula</i> sp. 4	
<i>Navicula capitatoradiata</i>	H.Germain ex Gasse 1986
<i>Navicula minimna</i>	Grunow 1880
<i>Navicula radiosafallax**</i>	Lange-Bertalot 1993
<i>Navicula submuralis</i>	Hustedt 1945
<i>Navicula viridula</i>	(Kützing) Ehrenberg 1836
<i>Navicula veneta</i>	Kützing 1844
<i>Navicula erifuga</i>	Lange-Bertalot 1985
<i>Navicula pseudoventralis</i>	Hustedt 1953
<i>Navicula?</i> sp. **	
<i>Nitzschia amphibia</i>	Grunow 1862
<i>Nitzschia</i> cf. <i>gracilis**</i>	Hantzsch 1860
<i>Nitzschia</i> sp. 1	
<i>Nitzschia</i> sp. 2	
<i>Nitzschia</i> sp. 3	
<i>Nitzschia</i> sp. 4	
<i>Nitzschia palea</i>	(Kützing) W.Smith 1856
<i>Pinnularia</i> sp. 1	
<i>Pinnularia</i> sp. 2	
<i>Placoneis placentula</i>	(Ehrenberg) Mereschkowsky 1903
<i>Planothidium lanceolatum**</i>	(Brébisson ex Kützing) Lange-Bertalot 1999
<i>Planothidium</i> cf. <i>lanceolatum</i>	(Brébisson ex Kützing) Lange-Bertalot 1999
<i>Pseudostaurosira brevistriata</i>	(Grunow) D.M.Williams & Round 1988
<i>Pseudostaurosira</i> sp. 1	
<i>Punctastriata lancetulla**</i>	(Schumann) P.B.Hamilton & Siver 2008
<i>Sellaphora bacillum</i>	(Ehrenberg) D.G.Mann 2018
<i>Sellaphora pupula</i>	(Kützing) Mereschkovsky 1902
<i>Sellaphora</i> sp. 1	
<i>Sellaphora?</i> sp.	
<i>Stauroneis</i> sp. 1	
<i>Stauroneis</i> sp. 2	
<i>Stauroneis phoenicenteron**</i>	(Nitzsch) Ehrenberg 1843
<i>Staurosira venter (morph 1)**</i>	(Ehrenberg) Cleve & J.D.Möller 1879
<i>Staurosira construens**</i>	
<i>Staurosira venter (morph 2)**</i>	(Ehrenberg) Cleve & J.D.Möller 1879
<i>Staurosirella</i> cf. <i>ovata**</i>	Ehrenberg 1843
<i>Staurosirella</i> sp. 1	
<i>Stephanodiscus hantzschii**</i>	Grunow 1880
Unknown girdle	

**Table S7:** Specifics for the high-performance liquid chromatography analysis of pigments in sediment samples.

Pigment	RT <sup>a</sup> (min)	Wavelength <sup>b</sup> (nm)	Equivalence Factor	Calibration Standard
Alloxanthin	11.8	435-455	1.20	Lutein
Bacteriochlorophyll-a	10.9	760-780	0.65	Chlorophyll-a
Canthaxanthin	16.1	460-480	1.06	Lutein
Chlorophyll-a	23.1	655-675	-	Chlorophyll-a
Chlorophyll-b	15.2	460-480	-	Chlorophyll-b
Diadinoxanthin	8.0	435-455	1.21	Lutein
Diatoxanthin	10.9	435-455	1.26	Lutein
Echinenone	32.9	435-455	0.63	Lutein
Fucoxanthin	4.8	435-455	0.55	Lutein
Lutein	9.6	435-455	-	Lutein
Myxoxanthophyll	12.7	460-480	1.26	Lutein
Peridinin	4.1	460-480	0.72	Lutein
Violaxanthin	5.9	435-455	0.88	Lutein
Zeaxanthin	10.3	435-455	1.56	Lutein

<sup>a</sup> Retention time. <sup>b</sup> The wavelength range used for pigment quantitation.

**Figure S1:** <sup>210</sup>Pb<sub>ex</sub> age-depth model for the upper 25 cm of the Lake Oporoa master core. Depth uncertainties are ±1 cm while the age uncertainties are ±2σ ranges. Red bars represent uniform age probability density functions for independent chronology derived from exotic pollen biostratigraphy and bomb spike radiocarbon dating.

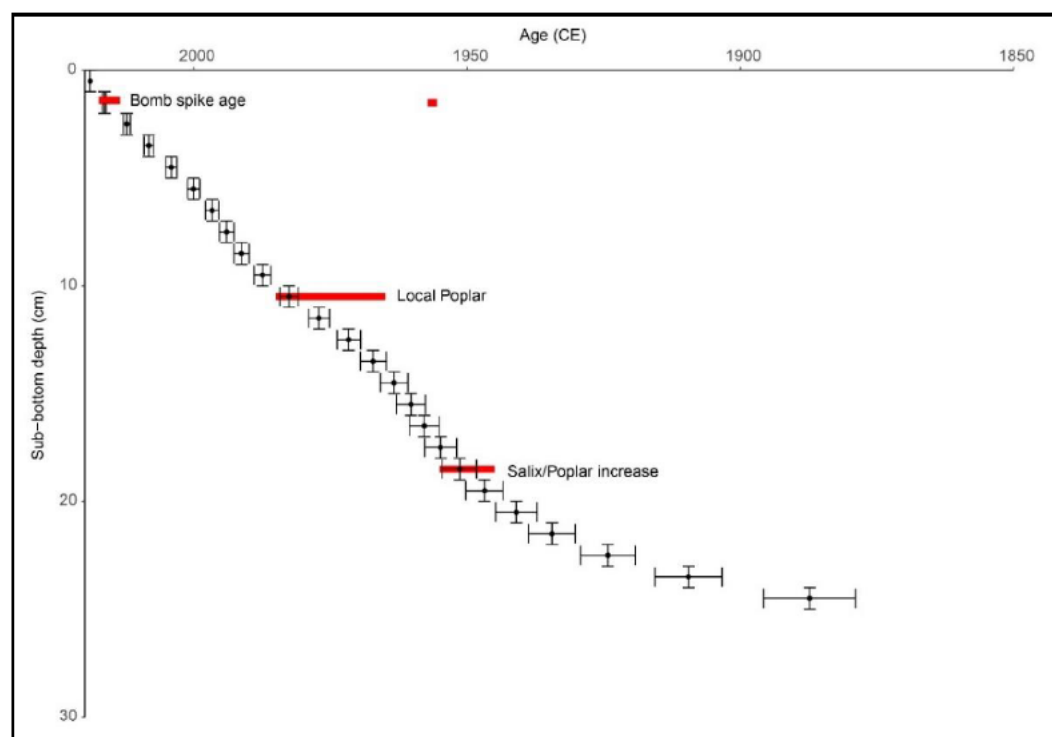


Figure S2: SEM photos of *Stausosirella* cf. *ovata*, a spineless species belonging to the genus.

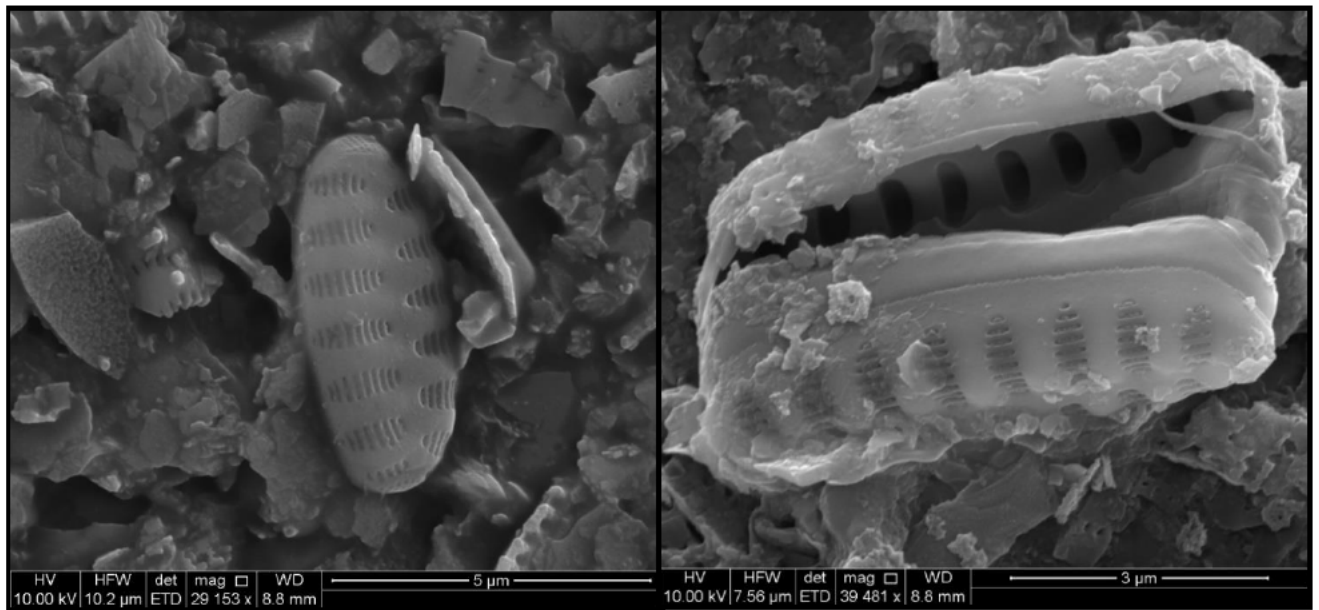
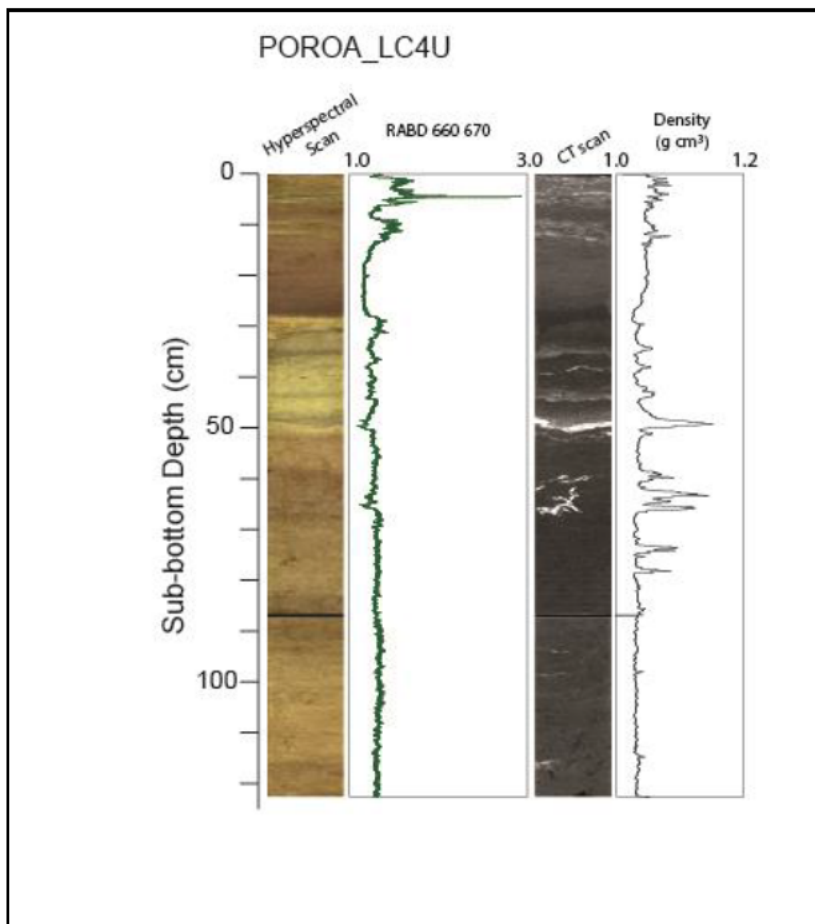
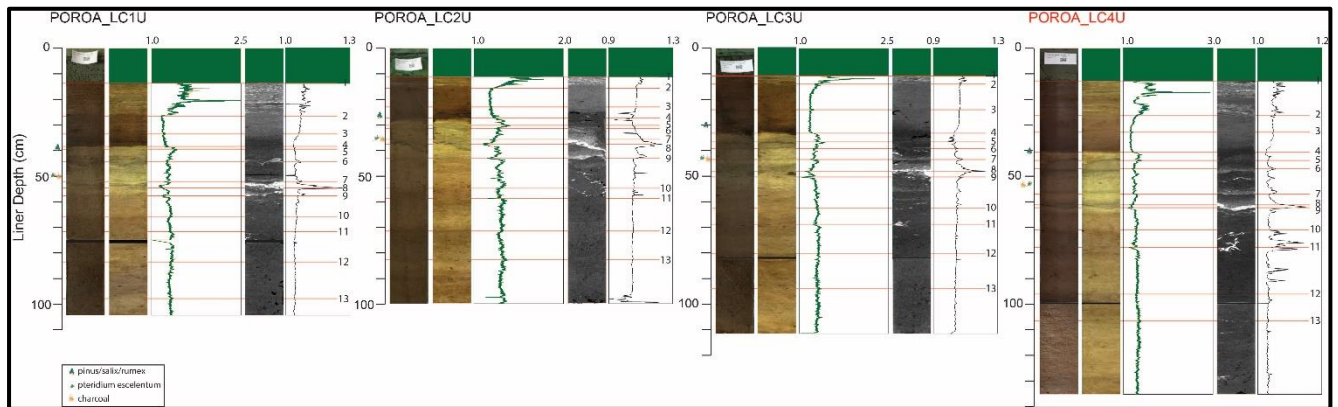


Figure S3: Hyperspectral linescan image, RABD 660-670, CT sagittal slice and bulk density for the master core (Poroa\_LC4U) from Lake Oporoa.



**Figure S4:** The hyperspectral imaging correlations between each core and the master core (Poroa\_LC4U) from Lake Oporoa. The master core was the longest core retrieved (123 cm).



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### Principal Author

Name of Principal Author (Candidate)	Julia Short		
Contribution to the Paper	Conceptual design, field work and sample preparation, diatom data collection and analyses, isotope data collection and analyses, data interpretation and statistical analyses (diatoms, pollen, isotopes) Producing figures, Manuscript production, writing and editing		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	19/7/22

### Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the thesis; and
- iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Funding, data interpretation (pollen), manuscript editing.		
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Signature		Date	10/8/22

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Signature		Date	11/8/22

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Contribution to the Paper	Producing and providing data (chronology)		
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Contribution to the Paper	Producing data (pollen)
Signature	Date 12/08/2022

## Chapter 4

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Initial human impacts on landscape vegetation drove nutrient change and aquatic transitions in lake ecosystems

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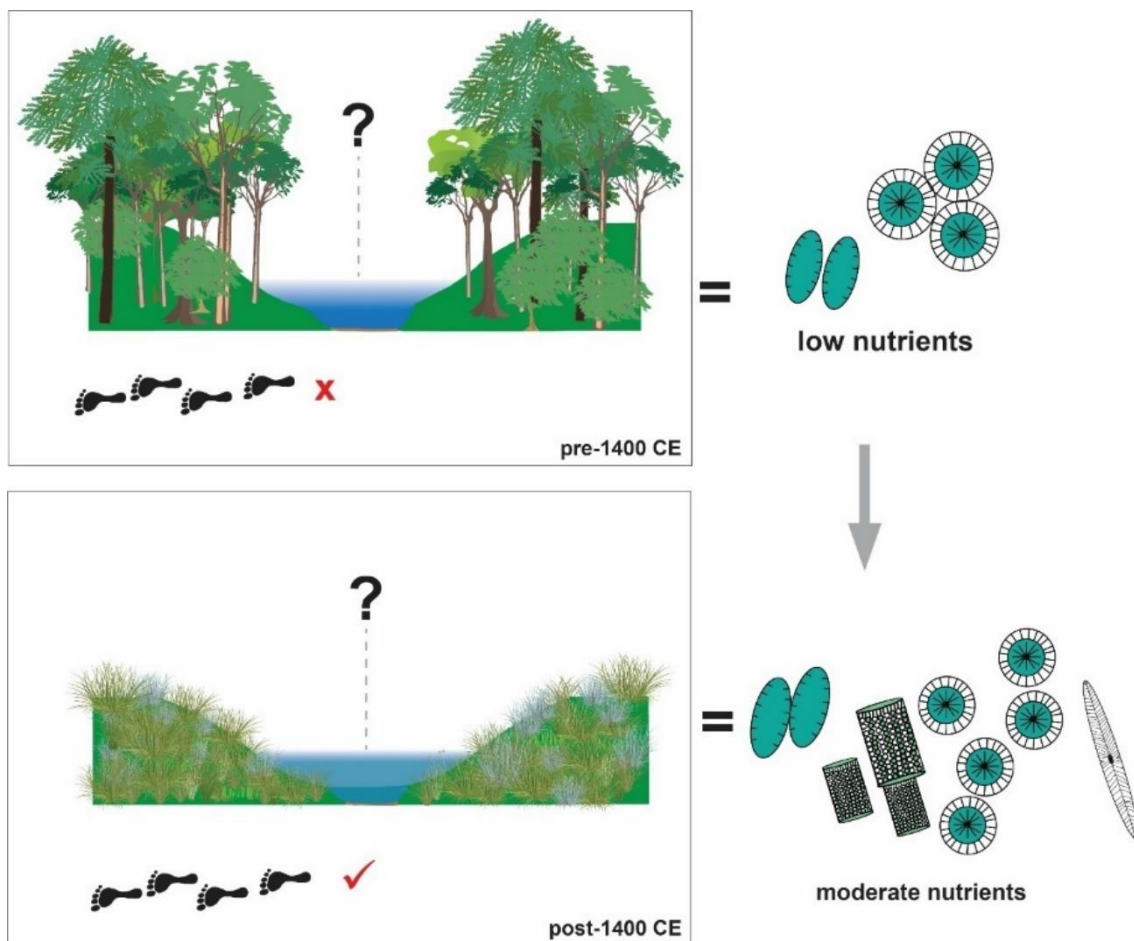
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## Abstract

Understanding how aquatic ecosystems responded to the first human-induced changes in landscape vegetation is often impossible due to long human habitation in many regions of the world, (i.e. in Africa, Australia and southern Asia), or because human migrations co-occurred with marked climate change. Due to its short period of human occupation, New Zealand provides an opportunity to gain insights into how lake ecosystems responded to initial human-driven changes in the landscape. Polynesians arrived in New Zealand 750–800 years ago and settled rapidly across the two main islands. Vegetation in many parts of the country was subsequently transformed, and in the Canterbury high country (South Island), the region of this study, native forests became dominated by tussock grassland. To infer lake ecosystem response to this initial catchment perturbation, we examined the diatom, geochemical, and pollen records from two shallow lakes; Lakes Kirihonuhonu and Emily, and two deep lakes; Lakes Ōtūroto and Ōpōrea. Major shifts in water quality occurred following initial catchment vegetation change, resulting in significant biogeochemical changes, termed aquatic transitions, at all sites. However, the responses were not uniform across the four study lakes. In Lake Ōpōrea, diatom assemblages rapidly and markedly shifted from a mix of planktonic and benthic taxa to a planktonic-dominated assemblage indicative of a decline in water clarity. In Lake Ōtūroto, there were major shifts between planktonic diatoms *Discostella stelligera* and *Aulacoseira ambigua*, likely in response to increased water column nutrients. Lakes Kirihonuhonu and Emily also experienced significant changes in diatom assemblages which indicate nutrient enrichment and changes in catchment hydrology. This study demonstrates that lake ecosystems are highly vulnerable to landscape alterations and demonstrates the complexity of lake system responses.

**Key words:** aquatic transition, human impact, diatoms, pollen, *Discostella stelligera*, low nutrients

## Graphical abstract



Lakes in New Zealand are of considerable socio-ecological importance. New Zealand was one of the last major landmasses to be settled by humans and due to the shorter duration of human settlement, provides a unique opportunity to explore how aquatic systems responded to first human activity. Sediment records from a suite of lakes in the Canterbury high country were analysed for their pollen and diatom assemblages. The data revealed that prior to evidence of first Māori settlement in the region in c. 1400 CE, the landscape was heavily forested, and lakes had low nutrients. After c. 1400 CE, there was a reduction in vegetation cover and the lakes subsequently became enriched with nutrients, and never recovered. This study is one of the few examples globally where the water quality and ecology of lakes prior to, and immediately following first human arrival, is well understood.

## 1 Introduction

Anthropogenic activities have resulted in the transformation of ecosystems for millennia, with their influences on the environment intensifying during the late Pleistocene (~12–50 kya; Steffen et al., 2007; Boivin et al., 2016; Malhi et al., 2016; Ellis et al., 2021). Anatomically modern humans (*Homo sapiens*) dispersed across the globe and colonised landmasses at different times, e.g. Europe (by ~45 kyr, Higham et al., 2011; Hublin et al., 2020), Australia (~ 65 kya, Clarkson et al., 2017) and North America (> 16 kya, Potter et al., 2018; Bennett et al., 2021). As people migrated, ecosystems and landscapes were shaped by their activities, through habitat alteration, hunting and foraging, the Neolithic Revolution, and pre-industrial urban eras, which changed biodiversity patterns (Braje & Erlandson, 2013; Ellis et al., 2013; Penny & Beach, 2021). Due to the differences in timing of human settlement and in the susceptibility of ecosystems to human pressures, the effect of anthropogenic activities are disparate in nature. Knowledge on the extent of ecosystem transformation and data on the long-term ecological history of landscapes is critical to biodiversity conservation (Willis & Birks, 2006; Dietl & Flessa, 2011; Barnosky et al., 2017; Nogué et al., 2017). These perspectives are also fundamental to the broader conceptualisation of the Anthropocene (Ellis et al., 2013; Roberts et al., 2021), which is the informal recognition of the geological epoch succeeding the Holocene, where humans are recognised as the dominant driver of ecosystem and environmental processes (Crutzen, 2002; Steffen et al., 2011). Integral to biodiversity conservation and understanding the Anthropocene, is understanding how ecosystems and biodiversity responded to the first human settlement and activity.

Examinations of ecosystem responses to the first occurrence of human activity have predominantly focused on terrestrial environments, through pollen records preserved in sediments, e.g. Hannon et al. (2005) or Rull (2021), animal and plant fossils, e.g. Burney et al. (2001), or archaeological remains e.g. Siegel et al. (2015). By contrast, freshwater ecosystems have been understudied despite being some of the most vulnerable and threatened ecosystems (Dudgeon et al., 2006; Reid et al., 2019) requiring complex management strategies (Heino et al., 2021). Understanding how freshwater systems responded to human settlement (Dubois et al., 2018; Vázquez-Loureiro et al., 2019) is often confounded by the longevity of human activity, e.g. Bradshaw et al. (2006). In many cases, settlement co-occurred with major climatic changes, including the evolution of post glacial landscapes (Timmermann & Friedrich, 2016; Tierney, Demenocal & Zander, 2017; Lesnek et al., 2018; De Deckker et al., 2019; Becerra-Valdivia & Higham, 2020). Dubois et al. (2018) reviewed studies that aimed to understand how freshwater systems responded to first human settlement. Despite the breadth of studies globally, it is thought that first human activities were only detected in lake systems thousands



of years after initial human activity, and even then, most were not substantial enough to be classed as aquatic transitions (Dubois et al., 2018). The term “aquatic transition” was used to characterise a change in the biological, and, or, chemical structure in lakes, or a change in the functions of lakes, such as a shifting from one trophic state to another, that occurred as a result of first human activity (Dubois et al., 2018).

Landmasses with recent human occupation are of particular interest (Hannon et al., 2005; Nogué et al., 2021) as there is an opportunity to understand how aquatic systems responded to human arrival. There are few places where this can be achieved, and these are largely confined to islands, e.g. Iceland (Lawson et al., 2007; Eddudóttir, Erlendsson & Gísladóttir, 2020) and Macaronesia (Vázquez-Loureiro et al., 2019; Castilla-Beltrán et al., 2021). Investigation of island localities is often complicated by the scarcity or lack of suitable freshwater bodies for continual sediment accumulation, or disturbance by volcanic activity, e.g. Canary Islands (Nogué et al., 2013; de Nascimento et al., 2016), Cape Verde (Castilla-Beltrán et al., 2019), Easter Island (Herrera & Custodio, 2008; Rull, 2021), and French Polynesia (Prebble, Anderson & Kennett, 2013). New Zealand is, by contrast, a recently colonised landmass, where Western Science suggests that humans first settled about 750–800 years ago (McWethy et al., 2010; Wilmshurst et al., 2011), with Māori oral history sometimes suggesting earlier settlement (Moon, 2013). New Zealand also has an abundance of freshwater lakes which are of great biodiversity (Weeks et al., 2016) and cultural significance (Harmsworth, Awatere & Robb, 2016).

The late human settlement of New Zealand provides a globally unique opportunity to understand how aquatic systems responded to human activities in the landscape, and to document the pre-human conditions of lakes. The progressive nature of human settlement of the Southern Pacific islands (starting ~3 kyr) is well understood, with New Zealand being one of the final landmasses to be settled (Goodwin et al., 2014; Montenegro, Callaghan & Fitzpatrick, 2016; Sear et al., 2020). The ecological response of lakes in New Zealand, and any subsequent recovery, can be used as a case study for understanding the scale and magnitude of first human pressure globally. Landscape changes following both Māori (the indigenous people of New Zealand) and European settlement are well studied and provide a critical background for understanding lake response to first human activity. Anthropogenic fires were widespread during the first two centuries of Māori settlement (McWethy et al., 2010; Newnham et al., 2018). The timing of native forests burning across New Zealand was not synchronous (Perry, Wilmshurst & McGlone, 2014) and the scale varied regionally. In some parts of the North Island vegetation reduction was greatest centuries after Māori arrival (Wilmshurst et al., 2004; Newnham et al., 2018; Short et al., 2022), while in areas of the eastern South Island, burning soon after Māori settlement resulted in vegetation dominated by tussock grasslands, replacing native forests

(McWethy et al., 2010). Lakes in this region responded to this transformation of the landscape and recorded significant changes in water quality (McWethy et al., 2010; Woodward et al., 2014 a, b). It was suggested that water depth increased in shallow lakes, due to increases in water availability as forest cover declined, while there was evidence for some recovery several centuries after initial nutrient enrichment (Woodward et al., 2014 a, b). This region provides an ideal location to test whether aquatic transitions accompanied landscape modification.

Palaeolimnological methods, examining material preserved in lake sediments, can reveal the past ecology of lakes, and their catchments. These data can be used to infer how lake ecosystems respond temporally to varying stressors, including those associated with first human activity, relative to historic ecological conditions (Willis et al., 2010; Randsalu-Wendrup et al., 2016; Seddon, 2021). Diatoms are one of the most sensitive indicators of environmental change (Battarbee et al., 2002) and are frequently used to infer past aquatic conditions (e.g. Renberg, 1990; Streib et al., 2021). Using palaeolimnological methods we studied four lakes, which varied in depth and size, in a region of New Zealand where the vegetation was transformed following Māori settlement to examine the ecological response of lakes to first human activity, and to determine whether any aquatic transitions had occurred. This study focuses on the time frame associated with evidence of first Māori activity but not the period following European arrival (c. the last 200 years).

## 2 Methods

### 2.1 Study area

The Canterbury high country (600–800 m.a.s.l) is on the eastern side of the Southern Alps of New Zealand's South Island. Four glacial lakes were selected for this study, three located in the Ōtūwharekai (Ashburton) district in a single inter-montane basin, with the other lake in the Selwyn-Waihora district in the adjacent inter-montane basin, approximately 60 km east (Figure 1). Descriptions of each site can be found in Table 1.

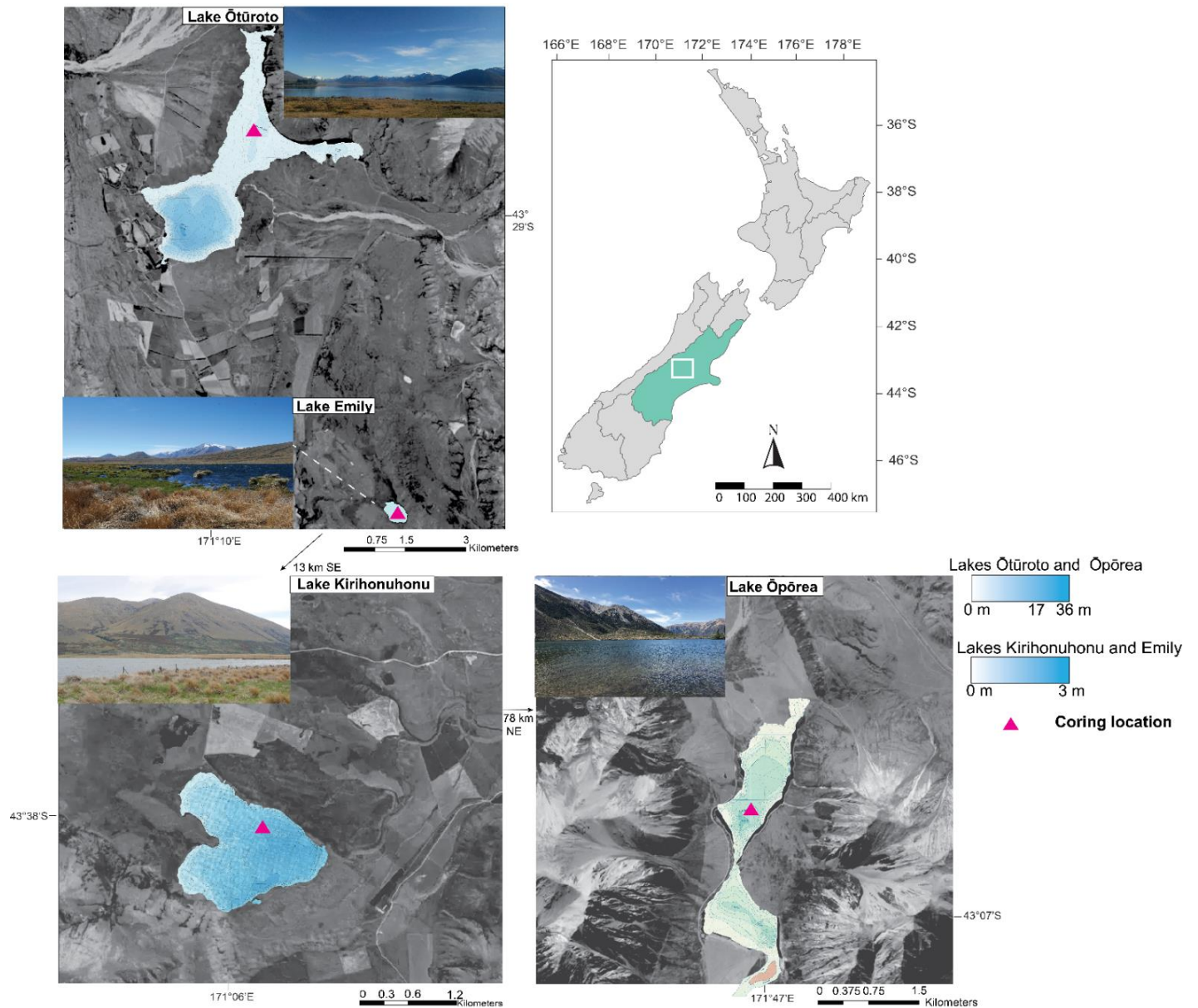
There are recorded archaeological sites confirming Māori activity and settlements in Ōtūwharekai (Te Rūnanga o Arowhenua, Pauling & Norton, 2010; Te Rūnanga o Ngāi Tahu, 2022). Additionally, Ōtūwharekai was used for traditional food gathering (*mahinga kai*) and is situated on a key route which was used to travel from the west to east coast (Te Rūnanga o Ngāi Tahu, 2022).

**Table 1:** Physical and chemical characteristics of the four study lakes. TN = Total Nitrogen; TP = Total Phosphorus.

	Ōtūroto (Heron)	Kirihonuhonu (Emma)	Emily	Ōpōrea (Pearson)
Region	Ōtūwharekai			Selwyn-Waihora
Location	43°29'16"S, 171° 9' 58"E	43°38'19"S, 171° 6' 23"E	43°33'10"S, 171° 13' 35"E	43°6'10"S, 171°46'41"E
River catchment	Upper Rakaia	Rangitata and Ashburton	Upper Ashburton, Lake Heron Basin	Upper Waimakariri
Max. depth (m)	36	3	2.5	17
Size (ha)	695	167	19	202
Trophic Level (based on data from 2005)*	Oligotrophic TN: 93 µg/L TP: 3 µg/L	Mesotrophic TN: 320 µg/L TP: 12 µg/L	Mesotrophic TN: 450 µg/L TP: 15 µg/L	Microtrophic TN: 90 µg/L TP: 2 µg/L
Catchment vegetation and characteristics	Native vegetation, gravel and rock slopes, low productivity grassland**	Low productivity grassland and wetland margin.	Low productivity grassland, wetland and swamp margin	Low and high productivity grassland.

\*Data compiled from Bayer & Meredith (2020) using the earliest available monitoring data (c. 2005) to differentiate from the effect of recent acceleration of nutrient inputs.

\*\*Low productivity grassland comprises native and non-native grasses with no fertilizer or intense agricultural use (Hewitt et al., 2012).



**Figure 1:** Location and images of the four study Lakes: Ōtūroto, Emily, Kirihonuhonu and Ōpōrea with coring sites marked. The approximate distances between each site are provided. Note the differences in depth profiles for each site, so refer to Table 1 for the maximum depths. Data sourced from the LINZ Data Service and licensed for reuse under the CC BY 4.0 licence. Bathymetry maps: Irwin (1970), Irwin (1984), Irwin (1985).

## 2.2 Sediment core sampling and subsampling

Four sediment cores were taken from each of the lakes in November 2019 (Figure 1) using a UWITEC Gravity corer, with a 95 mm diameter core barrel, before being packed with florist foam to prevent sediment movement during transport. Each core was split with one half being used for destructive analyses (pollen, diatoms, geochemistry) and the other half used for computed tomography (CT) and other non-destructive analyses (not reported in this study). Cores were sampled at varying depths

(Supplementary Table S1–S4). A full description of the sampling resolution and methodology for all proxies is given in Supplementary Information.

### 2.3 Sediment chronology

The chronology for all sediment cores was established using numerical age constraints derived from  $^{210}\text{Pb}_{\text{ex}}$  dating, pollen biostratigraphy and  $^{14}\text{C}$  dating combined with Bayesian age-depth modelling. The sampling resolution varied between lakes and was informed by availability of macrofossils, and the diatom and sediment stratigraphy. The analyses for  $^{210}\text{Pb}$  dating were completed at two different locations using different methods. From 2 cm<sup>3</sup> samples, total  $^{210}\text{Pb}$  activity was estimated by measuring its daughter product  $^{210}\text{Po}$  using chemical extraction and alpha spectrometry at the ESR National Centre for Radiation Science (New Zealand, Lake Ōtūroto) and the Australian Nuclear Science and Technology Organisation (Australia, Lakes Kirihonuhonu, Emily and Ōpōrea). The  $^{210}\text{Pb}_{\text{ex}}$  data were modelled using the Constant Rate of Supply (CRS) model in the R package *serac* (Bruel & Sabatier, 2020, Lake Ōtūroto), and following the method by Appleby (2001) (Lakes Kirihonuhonu, Emily and Ōpōrea) using sediment dry mass calculated from X-ray computed tomography (CT) densitometry and sediment water content. Bulk density for all lakes was calculated from the CT data using the relationship between CT number and bulk density of Reilly, Stoner & Wiest (2017). The  $^{210}\text{Pb}_{\text{ex}}$  age model was validated using independent age estimates from the first occurrence of *Rumex* spp. which was introduced through European pastoral activities which commenced in the region in 1857 (Acland, 1946), and using the invasive diatom *Lindavia intermedia* in Lakes Ōtūroto and Ōpōrea, as it has been in New Zealand since 2002 CE (Kilroy et al., 2021).

Radiocarbon dating was measured by accelerator mass spectrometry using the methods of Baisden et al., (2013). In Lakes Ōtūroto and Ōpōrea terrestrial macrofossils were collected by sieving samples from consecutive 1 cm core slices, while in Lakes Kirihonuhonu and Emily aquatic macrofossils (likely Cyperaceae) were collected as there was an absence of terrestrial macrofossils. The macrofossils were cleaned and pre-treated using an acid–alkali–acid procedure (Norris et al., 2020), and converted to CO<sub>2</sub> by combustion, graphitised and measured by accelerator mass spectrometry following Baisden et al., (2013). Conventional radiocarbon ages were converted to calendar years using the SHCal20 calibration curve (Hogg et al., 2020), while modern ages were calibrated using the Baring Head–Cape Grim (BHDCGO) curve (Turnbull et al., 2017). Age-depth modelling was conducted using the P\_sequence prior in OxCal4.4 with a variable event thickness constant (k) (Bronk Ramsey & Lee, 2013), and independent age constraints informed by the  $^{210}\text{Pb}$  age-depth models, pollen biostratigraphy and the radiocarbon dates (Supplementary Table S5–8). As Lakes Ōtūroto, Kirihonuhonu and Emily are

geographically separated by less than 20 km, two pollen-derived isochrons were used to cross-reference the age models from these three lakes. These were 1) the regionally extensive peak in *Fuscospora* spp. (Wood, Wilmshurst & McGlone, 2018), that was recorded in Lake Kirihonuhonu at 29 cm, and in Lake Emily at 82 cm; and 2) the onset of *Pteridium esculentum* in Lakes Ōtūroto, Kirihonuhonu and Emily at 88 cm, 20 cm and 73 cm, respectively.

The ages provided in the figures show the full range of dates of the evidence of Māori settlement period at 95% High Probability Density Function (HPDF) range, while the median of this range was used for discussion of data (Table 2). Dates are presented in years CE and rounded to the nearest decade.

## 2.4 Pollen and Charcoal analysis

Samples were processed following methods outlined in Faegri, Iversen & Giovannini (1989), from 0.25 cm<sup>3</sup> sediment taken at a variable sampling interval (Supplementary Table S1–S4), using 10% hot HCl, acetolysis and 6-µm sieving. *Lycopodium* tablets (Lund University, Batch numbers: 1031, 140119321, 050220211 and 1031) were added to each sample to determine pollen concentration. Pollen and spore identifications were made using: Large & Braggins (1991), Pocknall (1981a), Pocknall (1981b), Pocknall (1981c), Moar (1993), and New Zealand pollen reference collections. Pollen data are presented as the relative frequency of a sum of 150 pollen grains, minimum, and includes the pollen of all dryland plants: trees, shrubs, herbs and *Pteridium esculentum*. *Pteridium esculentum*, is included in this group, as the functional morphology of a stand of *P. esculentum* especially in a disturbed landscape, is similar to shrubland (McGlone, Wilmshurst & Leach, 2005). Wetland plants and fern spores were not included in this pollen sum but are expressed as a proportion of that sum. Charcoal fragments were counted alongside pollen and presented as concentration per cm<sup>3</sup>.

Specific periods of ecological history were assigned to each record (pre-human, evidence of Māori settlement and post-European activity), informed by pollen stratigraphy. In New Zealand, *Pteridium esculentum* is a chronological marker for evidence of Māori activity (e.g. McGlone & Wilmshurst 1999; McWethy et al., 2010; Newnham et al., 2018) and represents local stands of the species, rather than a regional pollen signal. In all lakes it was used together with changes in Poaceae pollen and charcoal, to constrain first evidence of Māori activity, which is subsequently termed “Evidence of Māori settlement”. This term acknowledges that other evidence (oral history in particular) may place settlement earlier. The time before first *P. esculentum*, is referred to as the pre-human phase, while the start and subsequent consecutive occurrence of *Rumex acetosella* or *Pinus* spp. marks the start of European activity in the landscape as they are non-native taxa, introduced by European colonists.

## 2.5 Sedimentary Diatom analyses

For all sites, the top 10 cm of core was sampled contiguously at 1 cm resolution, with every second centimetre sampled thereafter. Diatom samples were treated using both hydrochloric acid (15%) and hydrogen peroxide (25%) to remove carbonates and organic matter, respectively (Battarbee et al., 2002). Slurries were permanently mounted on slides using Naphrax and counted ( $300 \pm 10$  valves) using Differential Image Contrast on a Zeiss AxioA1 microscope at 1000x magnification under oil immersion. Identifications were made using: Krammer & Lange-Bertalot (1986), Krammer & Lange-Bertalot (1988), Krammer & Lange-Bertalot (1991a), Krammer & Lange-Bertalot (1991b), Vyverman, et al. (1995), Sonneman et al. (1999), Morales (2001), Knapp, Furey & Lowe (2006), Van de Vijver et al. (2008), Delgado et al. (2015), Reavie & Kireta (2015), John (2018), Rusanov et al. (2018), Wetzels & Ector (2021). We also used a Scanning Electron Microscope FEI Quanta 450 FEG, to assist with identifying taxa belonging to Fragilariaceae. Unless appearing in low abundances, species with distinct morphological differences between valves were treated as individual taxa, e.g. *Punctastriata lancetulla* morph 1, morph 2 and morph 3.

## 2.6 Data analyses: Pollen and Diatoms

Diatom results were converted to relative abundance data. To determine floristic dissimilarity between samples in the pre-human and Māori phases in each lake, non-metric multidimensional scaling (NMDS) was calculated on diatom assemblage data after a square root transformation, using the Bray-Curtis distance, in the *vegan 2.6–2* (Oksanen et al., 2020) package in R (R Core Team, 2021). Three samples (60, 62 and 64 cm) in Lake Ōtūroto and one sample (159 cm) in Lake Ōpōrea were removed before analysis due to low diatom counts. Diatom analyses were completed with species that occurred at  $\geq 2\%$  in three or more samples.

To provide a measure of species turnover through time (Hill & Gauch, 1980), a Detrended Correspondence Analysis (DCA) was completed for the dryland pollen data using taxa with an abundance of at least 1%, and for the diatom data with taxa that occurred at  $\geq 2\%$  in three or more samples, using *vegan 2.6–2* (Oksanen et al., 2022) in R (R Core Team, 2021). A changepoint analysis on the mean, was then completed on DCA Axis 1 Scores in the *changepoint 2.2.2* package (Killick, Haynes & Heckley, 2016) in R (R Core Team, 2021) using the Binary Segments method, with a manual penalty of value  $2 \cdot \log(n)$ , except for Lake Ōpōrea which had a penalty value of 1 as there was no changepoint found using a penalty of  $2 \cdot \log(n)$ . Parameters were set to allow for several changepoints to be detected, but only one was detected for each proxy.

## 2.7 Sediment Geochemistry

Bulk total organic carbon (TOC) and nitrogen (N) stable isotope compositions and concentrations were measured on sediment samples from all lakes to track downcore changes in aquatic productivity and sedimentary organic matter (SOM) provenance (Meyers & Teranes, 2002; Leng & Marshall, 2004) (Supplementary Table S1–4). A total of 47 samples from Lake Ōtūroto were measured at the Stanford University Stable Isotope Lab using a Thermo Delta V Advantage isotope ratio mass spectrometer coupled to a Thermo FlashSmart Elemental Analyzer via a ConFlo IV. Approximately 8 mg of freeze-dried, homogenised sediment was weighed into silver capsules and acidified *in situ* with 6% sulfurous acid to remove carbonate phases (Verardo, Froelich & McIntyre, 1990). An identical set of samples were weighed into tin capsules to measure the  $\delta^{15}\text{N}$  and obtain total carbon concentrations. One standard deviation of replicate pairs ( $n = 5$ ) for C (acidified) and N (unacidified) stable isotopes provide an indication of instrument reproducibility and is 0.04‰ and 0.05‰, respectively. Carbon isotope data are expressed using conventional  $\delta^{13}\text{C}$  notation relative to the PDB standard using USGS-40 as a reference.

Lakes Ōpōrea, Kirihonuhonu and Emily were analysed at the Mawson Analytical Spectrometry Services laboratories at the University of Adelaide. Before analysis, samples were treated with 10% HCl for 1 hour to ensure removal of carbonates, triple rinsed with deionised water, freeze dried and homogenised. Samples were combusted in tin capsules using a Perkin Elmer 2400 Series II Elemental Analyser to establish elemental (TOC, N) concentration. Following this, samples were weighed using target masses (range 1–18 mg) reflecting the amount of TOC in each sample to optimise C mass for isotope analyses.  $\delta^{13}\text{C}_{\text{org}}$  values were measured on the carbonate-free sample aliquots utilising a Nu Horizon IRMS coupled with an EuroVector EuroEA elemental analyser at. Data are expressed in the conventional  $\delta^{13}\text{C}$  notations relative to the PDB standard. Standardisation was based on in-house glycine ( $\delta^{13}\text{C}$ : -31.2‰), glutamic acid ( $\delta^{13}\text{C}$ : -16.7‰), and triphenylamine ( $\delta^{13}\text{C}$ : -29.2‰) standards which have been calibrated against international standards (USGS40 & USGS41). Long-term precision is < 0.2‰ and replicates of individual samples generally lie within 0.3‰. C/N ratios in all lakes are presented as atomic weight following Meyers & Teranes (2002).

## 3 Results

### 3.1 Chronology

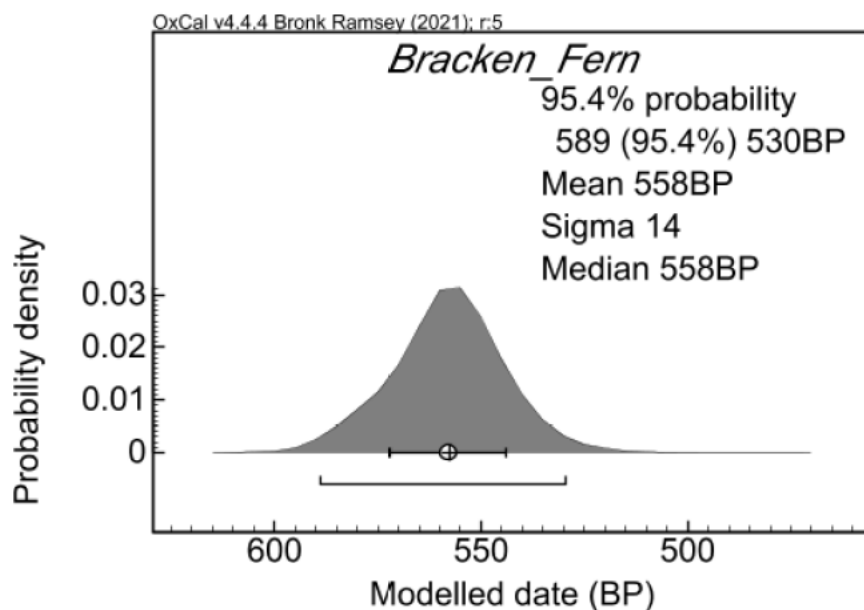
The focus of this chapter is the period associated with the first Māori activity in the region, and therefore, the results for the chronology are presented with this focus. The results of the age models for all four lakes, and methods associated with  $^{210}\text{Pb}$  and recent (c. 150 years) biostratigraphy, are



presented in Chapter 5. The returned ages and model inputs are found in Supplementary Information Tables S5–8.

**Integrated chronology:** The Bayesian age-depth models integrating numerical age data from the unsupported  $^{210}\text{Pb}$ , pollen and diatom derived biostratigraphy, and radiocarbon dates provide chronology for the diatom, pollen and geochemistry data series. The cross-referenced P\_Sequence age-depth models for Lakes Kirihonuhonu, Emily and Ōtūroto produced an agreement index (a measure of model fit to the input numerical age data) of 70%, which is sufficiently above the 60% threshold for acceptable model fit (Bronk Ramsey, 2008). These age-depth models indicate that the median basal ages for the sediment cores from Lakes Kirihonuhonu, Emily and Ōtūroto are 6138 CalBP (9239–4315 CalBP; 95% Highest Probability Density Function (HPDF) Range), 5615 CalBP (6572–5021 CalBP; 95% HPDF Range), 920 CalBP (959–885 CalBP 95% HPDF Range), respectively (Figure 3). Cross-referencing the onset of *Pteridium esculentum* pollen in Lakes Ōtūroto, Kirihonuhonu and Emily produced a median age of 558 CalBP (589–530 CalBP; 95% HPDF Range) for the first anthropogenic land use (Figure 2) in catchments of these lakes. The P\_Sequence age-depth model for Lake Ōpōrea has a high agreement index of 99% demonstrating good fit between the modelled ages and the independent age data. The interpolated date for the base of the core was 9392 CalBP (12611–6821 CalBP; 95% HPDF Range).

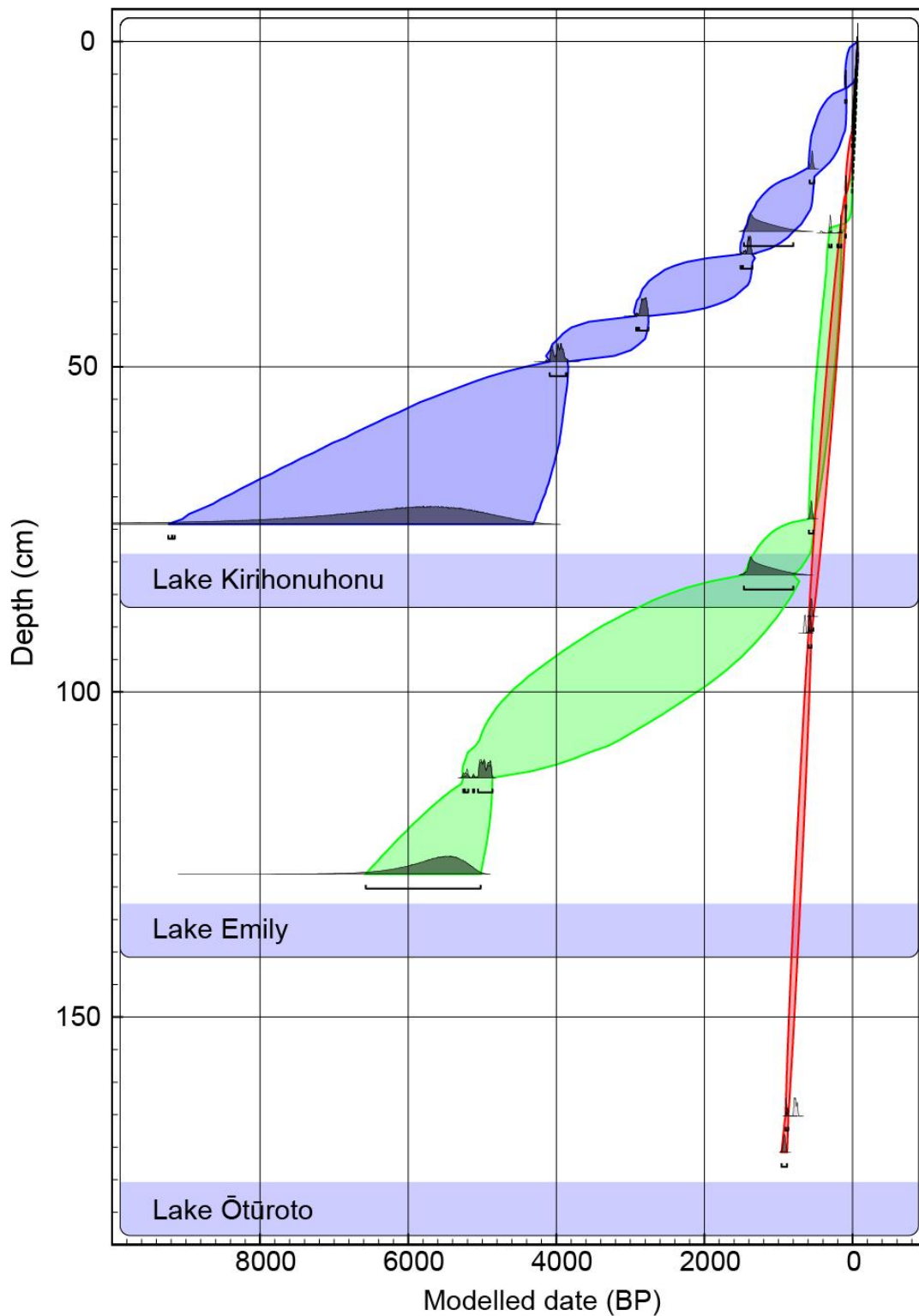
Model uncertainty is highly variable both within and between the four age-depth models ranging from just a few years to millennia (Figures 3 and 4). The variability in uncertainty is largely due to the sparse distribution of radiocarbon dates in some records given the multimillennial timescales that most of the records span. Nonetheless, the age-depth models provide constraint on the timing of initial human land use in the Ōtūwharekai and Selwyn-Waihora regions of the Canterbury high country.



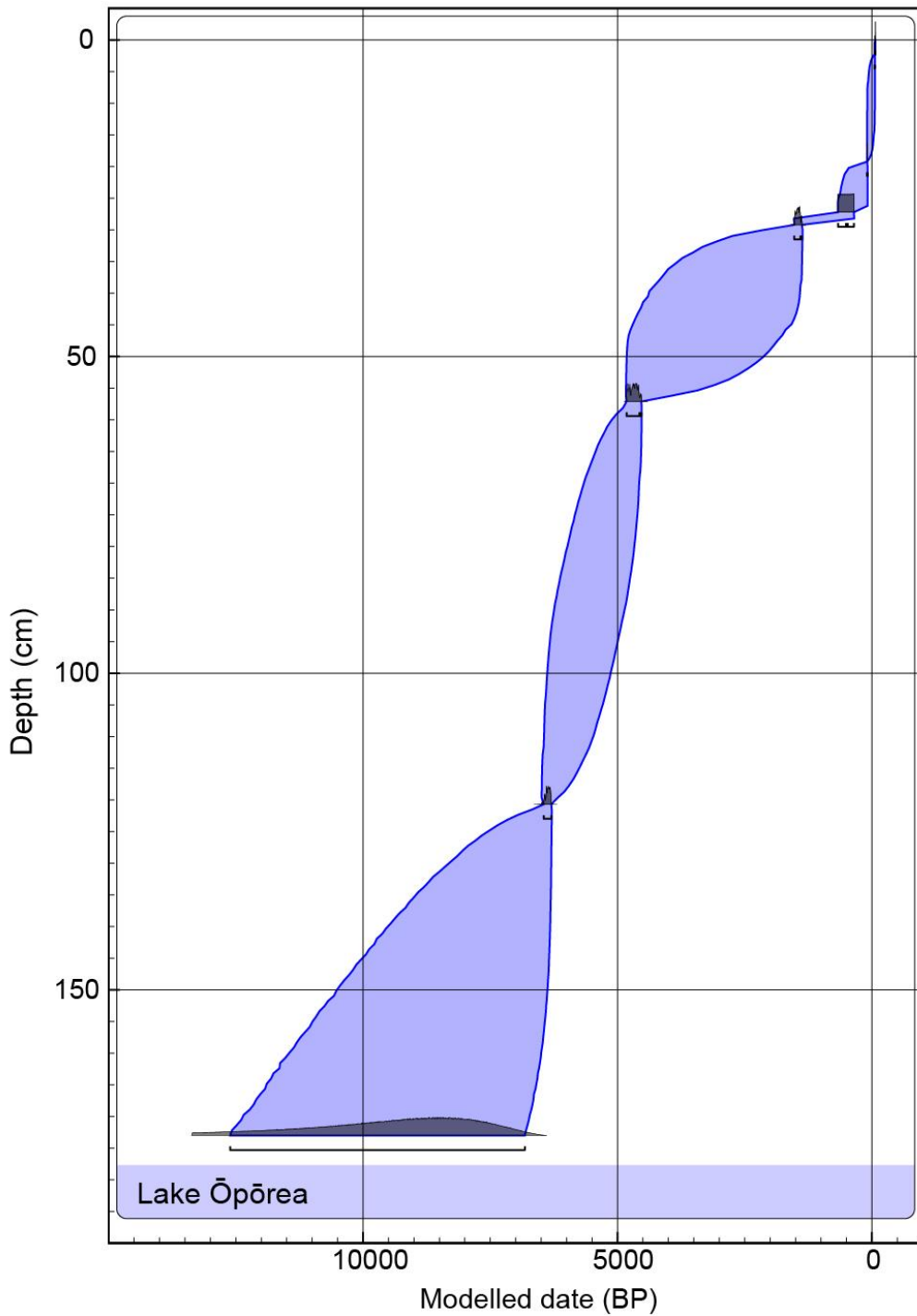
**Figure 2:** Age probability density function for the onset of *Pteridium esculentum* pollen in Lakes Kirihonuhonu, Emily and Ōtūroto produced by cross-referenced age-depth models for these lakes.

**Table 2:** The range of possible dates for evidence of Māori settlement (informed by *Pteridium esculentum*) at 95% HPDF, the calibrated <sup>14</sup>C ages from each lake, and their corresponding depth.

Lake	Depth (cm)	Evidence of Māori settlement range at 95% HPDF (Years CE)	Median (Year CE)
Ōtūroto	88	1361–1420	1393
Kirihonuhonu	20	1361–1420	1392
Emily	73	1361–1420	1392
Ōpōrea	27	1279–1598	1441



**Figure 3:** Cross-referenced chronological models for Lakes Kirihonuhonu (blue), Emily (green) and Ōtūroto (red). The radiocarbon dates were calibrated with the SHCal20 calibration curve (Hogg et al., 2020). They show the calendar age likelihood (light grey) and posterior age probability density functions (dark grey), and age-depth models at the 95% level of confidence.



**Figure 4:** Age-depth model for Lake Ōpōrea. The radiocarbon dates calibrated with the SHCal20 calibration curve (Hogg et al., 2020). They show the calendar age likelihood (light grey) and posterior age probability density functions (dark grey), as well as the age-depth models at the 95% level of confidence.

### 3.2 Pollen analysis

The pollen in the pre-human phase was similar in Lakes Ōtūroto, Kirihonuhonu and Emily records (Figures 5 and 6). The vegetation remained stable during this phase with the dominant tall tree species, *Prumnopitys taxifolia* as well as smaller amounts of *Dacrydium cupressinum* and *Podocarpus* spp. The dominant understorey taxa were shrub conifers: *Halocarpus* spp., *Phyllocladus* spp. and *Coprosma* spp. (Supplementary Figures S5, S7 and S8). In all catchments, particularly Lake Emily, microcharcoal was detected before evidence of Māori settlement. In Lake Ōtūroto *Pteridium esculentum* first appears in approximately 1390 CE at which point charcoal and Poaceae pollen increase while native tall tree and shrub conifer pollen decline. The same pattern occurs in the sediment records from Lakes Kirihonuhonu and Emily, and likely at a similar time due to their proximity to Lake Ōtūroto.

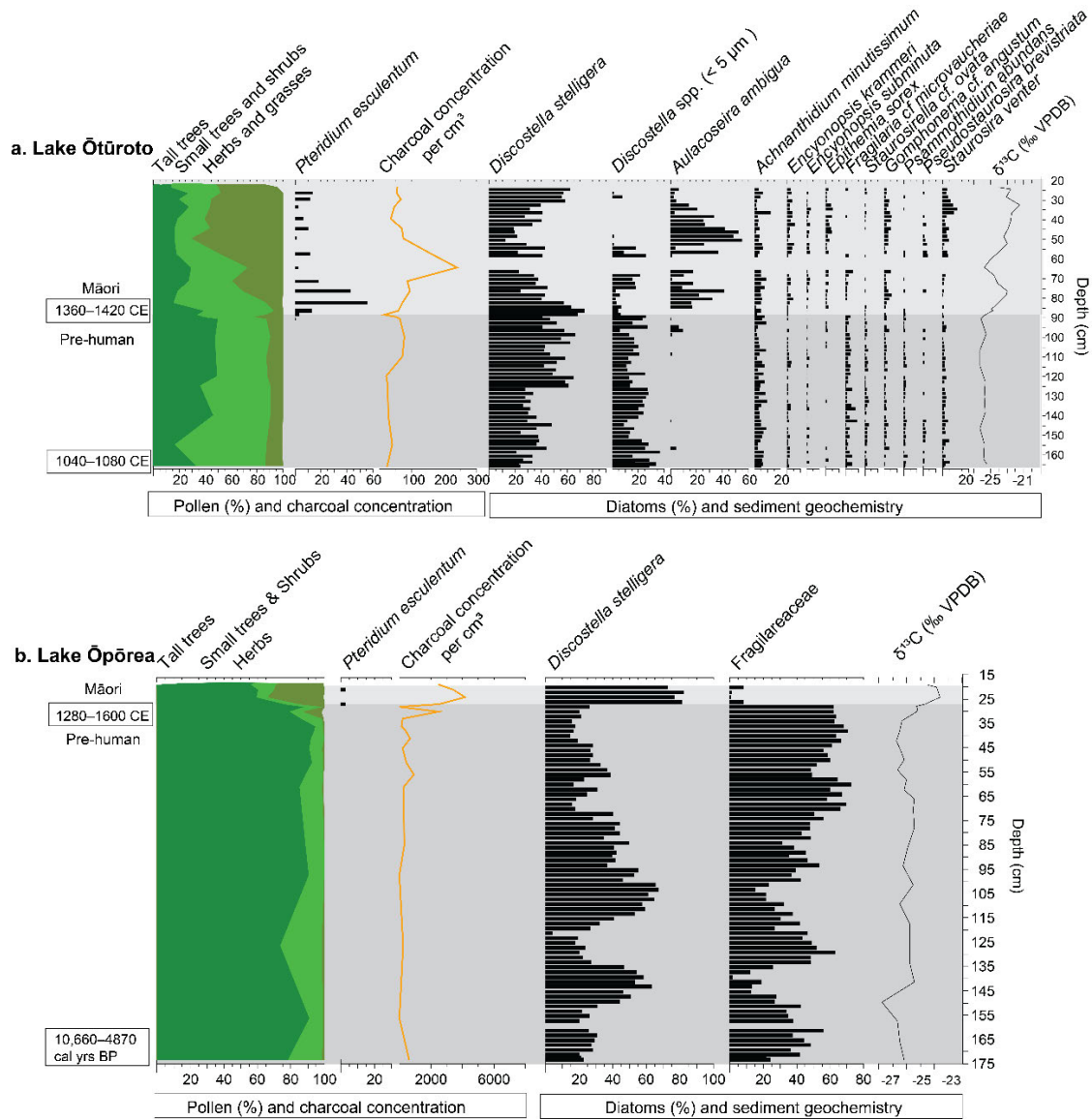
In Lake Ōpōrea prior to human arrival, *Fucospora* spp. was the dominant tall tree taxon, while tree species, *P. taxifolia* and *D. cupressinum*, were also found in abundance. Understorey taxa were represented by smaller populations of *Phyllocladus* spp. and *Coprosma* spp. (Supplementary Figure S6). Despite some minor fluctuations in these taxa, and low amounts of charcoal, the overall vegetation was stable. *Fucospora* spp. and other native taxa decline as *Pteridium esculentum* and Poaceae increase.

### 3.3 Sedimentary diatom analysis

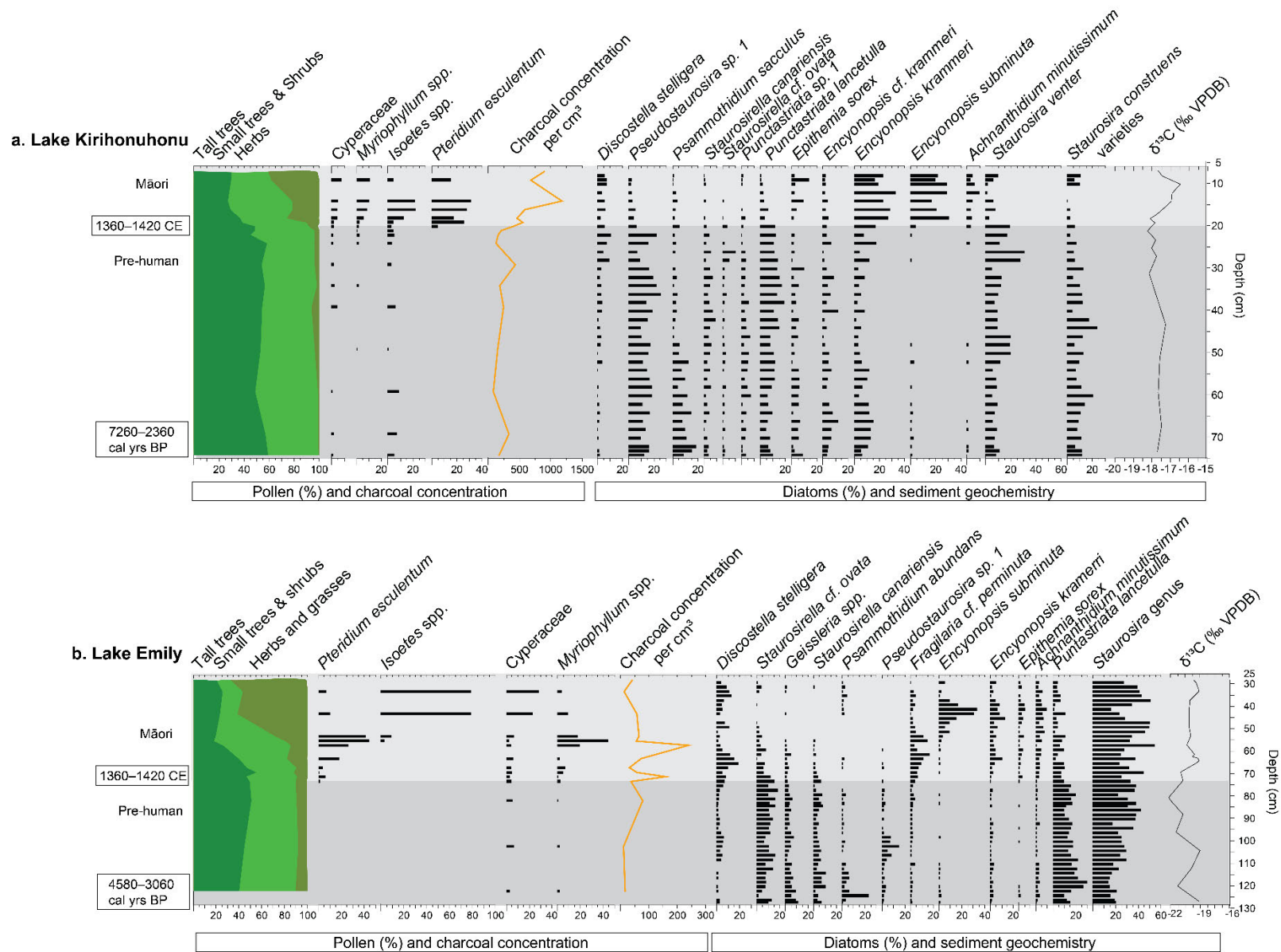
The NMDS analysis showed a clear separation of diatom communities between the pre-human and Māori phases in all study lakes (Figure 7), with the dominant taxa in each lake listed in Table 3. An Results in two dimensions produced sufficiently low (< 0.15) stress indicating the results fit the distributed data (Clarke, 1993; Dexter, Rollwagen-Bollens & Bollens, 2018). The changepoint analysis (Figure 8) shows the changepoint for the diatom assemblages, in all lakes occurred prior to the changepoint in the pollen. Some of the key shifts following first evidence of Māori activity were, 1) in Lake Ōtūroto, *Aulacoseira ambigua* became the dominant taxon as *Discostella stelligera* declined while in Lake Ōpōrea all Fragilariaceae declines as *Discostella stelligera* became dominant, 2) in Lake Kirihonuhonu benthic Fragilariaceae (*Staurosirella* spp.) decline as *Encyonopsis subminuta* and *Fragilaria* cf. *perminuta* become dominant; and 3) A similar pattern occurs in Lake Emily where *Encyonopsis subminuta* and *E. krammeri* become abundant as benthic Fragilariaceae decline.

**Table 3:** Key diatom taxa and sediment geochemistry trends for each lake from the pre-human and evidence of Māori activity phases.

	Ōtūroto (Heron)	Kirihonuhonu (Emma)	Emily	Ōpōrea (Pearson)
<b>Pre-human</b>				
<b>Diatoms</b>	<i>Discostella stelligera</i> and <i>Discostella</i> spp. < 5 µm Small benthic Fragilareaceae.	<i>Pseudostaurosira</i> sp. 1, <i>Psammothidium</i> cf. <i>sacculus</i> , <i>Staurosirella canariensis</i> , <i>Punctastriata lancetulla</i>	<i>Staurosirella</i> cf. <i>ovata</i> , <i>S. canariensis</i> , <i>Punctastriata lancetulla</i> , <i>Staurosira venter</i>	<i>Discostella stelligera</i> , Fragilareaceae ( <i>Staurosirella</i> cf. <i>ovata</i> , <i>Staurosira venter</i> morph 2, <i>Pseudostaurosira</i> sp. 1)
<b>δ<sup>13</sup>C</b>	Stable, average: -25.8 ‰, σ 0.28	Stable, average: -17.7 ‰, σ 0.28	Fluctuating, average: -20.5 ‰, σ 1.15	Mostly stable, average: -26.0 ‰, σ 0.58
<b>Evidence of Māori settlement</b>				
<b>Diatoms</b>	<i>Discostella stelligera</i> , <i>Aulacoseira ambigua</i>	<i>Encyonopsis krammeri</i> , <i>Encyonopsis subminuta</i>	<i>Fragilaria</i> cf. <i>perminuta</i> , <i>Encyonopsis subminuta</i> , <i>Staurosira construens</i> and <i>S. venter</i> , <i>Discostella stelligera</i> .	<i>Discostella stelligera</i>
<b>δ<sup>13</sup>C</b>	Fluctuating increase, average: -23.7 ‰, σ 1.15	Increasing, average: -17.4 ‰, σ 0.51	Increase, then stable with some fluctuation, average: -19.8 ‰, σ 0.51	Rapid increase, average: -24.2 ‰, σ 0.39
<b>δ<sup>13</sup>C range (pre-human and Māori)</b>	-26.2– -21.5	-18.2– -16.5	-22.2– -19.0	-27.8– -23.6
<b>C:N range (pre-human and Māori)</b>	7.9–10.2	10.1–14.6	10.5–16.0	8.4–13.3

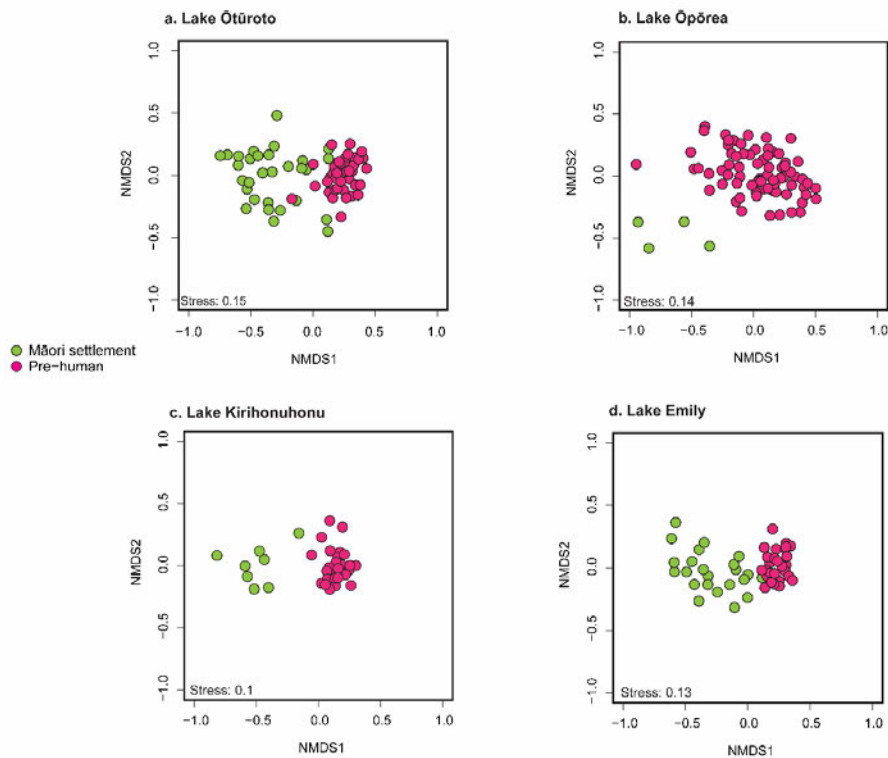


**Figure 5:** Pollen (habitat groupings of dryland pollen sum), charcoal, diatom and sediment geochemistry from (a) Lake Ōtūroto and (b) Lake Ōpōrea. Only key pollen and diatom taxa are shown. Shading marks the occupation phases of each record. The age range for Māori settlement, and the basal age of the core, at 95% HPDF is provided. For the full age model, see Figures 3 and 4.  $\delta^{13}\text{C}$  is expressed as parts per million Vienna Pee Dee Belemnite (VPDB). Fragilariaceae in Lake Ōpōrea is the sum of all taxa belonging to the genera *Pseudostauroneis*, *Punctastriata*, *Stauroneis* and *Stauroneisella*.

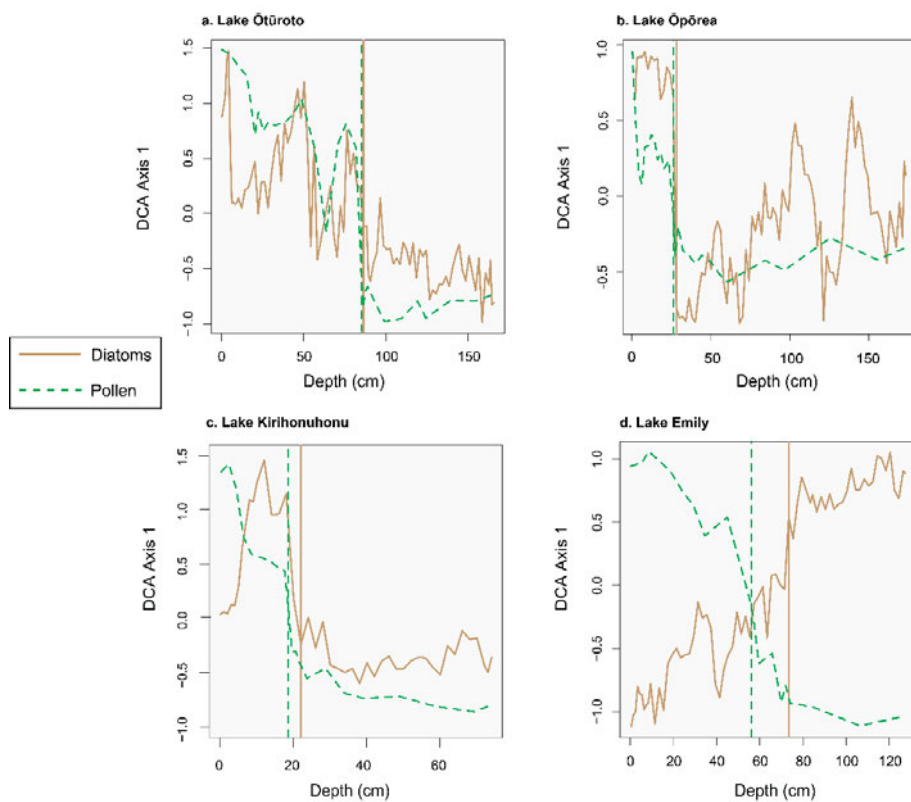


**Figure 6:** Pollen (habitat groupings of dryland pollen sum), charcoal, diatom and sediment geochemistry from (a) Lake Kirihonuhonu and (b) Lake Emily. Only key pollen and diatom taxa are shown. Shading marks the pre-human and Māori phases of each record. The age range for Māori settlement, and the basal age of the core, at 95% HPDF is provided. For the full age model, see Figure 3.  $\delta^{13}\text{C}$  is expressed as parts per million Vienna Pee Dee Belemnite (VPDB). Māori refers to Evidence of Māori settlement.





**Figure 7:** Non-metric Multidimensional Scaling of diatom assemblages from each lake. The samples are colour coded according to their occupation phase.



**Figure 8:** Change point analyses on Detrended Correspondence Analysis Axis 1 data from diatom (brown) and pollen (green) assemblages. The vertical lines indicate the location of the changepoint.

### 3.4 Sediment geochemistry

Sedimentary organic matter (SOM) was likely algal in origin for Lakes Ōtūroto and Ōpōrea as C:N values were generally less than 10 (Meyers & Teranes, 2002; Supplementary Figures S1, S2 and S9), although occasionally higher (11–13.5) for Lake Ōpōrea (Table 3). Therefore, the  $\delta^{13}\text{C}$  signal can be used as an indicator of algal productivity, which is associated with the nutrient concentration of the water column (Meyers & Teranes, 2002), although occasionally in Lake Ōpōrea,  $\delta^{13}\text{C}$  may be a signal of macrophyte productivity (Heyng et al., 2012). For Lakes Kirihonuhonu and Emily, C:N ratios of the sediment possibly reflect a combination of both algal and aquatic macrophytes following Heyng et al., (2012), where modern samples of aquatic macrophytes had C:N values less than 20 (Supplementary Figures S3, S4 and S9). Therefore, in Lakes Kirihonuhonu and Emily,  $\delta^{13}\text{C}$  will reflect both macrophyte and algal productivity, although through time, C:N values decrease towards a more algal dominant signature (Supplementary Figure S4 and S5).

## 4 Discussion

### 4.1 Aquatic transitions in response to changes in landscape vegetation

Each lake experienced significant changes in diatom assemblages following landscape change as indicated by the changepoint analysis and NMDS of diatom assemblage data. None of the lakes in this study recovered to their pre-human condition. Collectively these data demonstrate there has been a biogeochemical change in the ecology of the lakes, showing that aquatic transitions have occurred in these lakes (Dubois et al., 2018). It is likely the ecological change occurred before the complete stabilisation of the landscape to tussock grassland, as indicated through the changepoint analysis (Figure 8) and the sensitivity of diatoms to changes in their surrounding environment (*sensu* Lotter, Pienitz & Schmidt, 2010; Smol & Stoermer, 2010). In the following sections we consider these ecological shifts, in context of the long-term ecological history of these lakes.

### 4.2 Catchment vegetation and lake ecology prior to human activity

Before human arrival, the vegetation in the catchments of the four study lakes was stable, with native forests dominated by tall podocarp trees and shrub conifers (*Prumnopitys taxifolia*, *Phyllocladus* spp. and *Halocarpus* spp.) and southern beech (*Fuscospora* spp.) (Figures 5, 6 and Supplementary Figures S5–S8). Podocarp and shrub conifers are typical of dryland and lowland to montane regions in New Zealand and are found in the driest regions of the South Island (McGlone et al., 2017). The charcoal records from Lakes Ōtūroto, Kirihonuhonu, and Emily indicate that occasional natural fires occurred in the catchment as noted elsewhere in the region (Pugh & Schulmeister, 2010; Woodward et al., 2014). The high abundance of southern beech in Lake Ōpōrea's catchment is indicative of cooler mean

temperatures at this site in comparison to the Ōtūwharekai region (McGlone, 2002; McGlone et al., 2017).

Diatom assemblages and the algal productivity signal ( $\delta^{13}\text{C}$ ) indicate that the lakes had very low nutrient concentrations in the water column. *Discostella stelligera*, an oligotrophic and open water indicator was the dominant taxon in Lakes Ōtūroto and Ōpōrea (Rühland et al., 2008; Saros & Anderson, 2015) and is found in many of New Zealand's low nutrient lakes (Reid, 2005). In Lake Ōpōrea the species assemblages shifted between *Discostella stelligera* and benthic Fragilariaceae suggesting fluctuations in the mixing depth, given that *Discostella stelligera* is highly sensitive to changes in stratification regimes (Wang et al., 2012; Saros & Anderson, 2015; Stone, Saros & Pederson, 2016). This was possibly driven by fluctuating Holocene temperatures as indicated in Holocene palaeoclimate records from other sites on the eastern South Island (Anderson et al., 2018; Hinojosa et al., 2021), although the imprecise age model from Lake Ōpōrea hinders further analysis across this time period. In Lake Ōtūroto, *Discostella stelligera* and *Discostella* spp. (< 5  $\mu\text{m}$ ) exhibited opposing fluctuations. The size difference between the taxa likely reflects differing ecological requirements and nutrient uptake, with *Discostella* spp. (< 5  $\mu\text{m}$ ) having a competitive advantage in lower nutrient (micro-oligotrophic) open water due to its smaller size (*sensu* Irwin et al., 2006; Litchman, Klausmeier & Yoshiyama, 2009; Winder, Reuter & Schladow, 2009).

In the shallow Lakes Kirihonuhonu and Emily, there was a diverse benthic assemblage before human arrival characterised by high relative abundances of *Pseudostaurosira*, *Staurosirella*, *Punctastriata* and *Staurosira* genera (benthic Fragilariaceae), which frequently dominate shallow lakes (Bennion, Fluin & Simpson, 2004; Spaulding et al., 2015). Species in these genera are 'generalists' as they have broad ecological tolerances (Kingsbury, Laird & Cumming, 2012; Edlund et al., 2017; Hobbs et al., 2017) making inferences about past lake ecology difficult. Both lakes were likely consistently shallow, as planktonic taxa were never a major component of either record. The lakes were probably low in nutrients, although there was some variability in  $\delta^{13}\text{C}$  for Lake Emily indicating fluctuating aquatic productivity (algae and macrophytes). Species fluctuations indicate that lake ecology still varied in the absence of major catchment modifications. These lakes are likely influenced by their extensive marsh and wetland habitats, and as water level fluctuated naturally, the surrounding area would be inundated increasing habitat availability for benthic and epiphytic diatoms (*sensu* Stone & Fritz, 2004).

#### 4.3 In-lake responses following changes in landscape vegetation

Native forest cover declined after the first evidence of Māori activity in both catchments and was followed by a transition to tussock grassland dominated landscape (Figures 5, 6; Poaceae). This

occurred elsewhere on the eastern South Island of New Zealand (McWethy et al., 2010; McWethy et al., 2014; Woodward et al., 2014 b). The extent of landscape change was likely influenced by the drier climate in this region, the lack of adaptive mechanisms to fire in native plants and the slow regeneration time of many species (Perry et al., 2012; Perry, Wilmshurst & McGlone, 2014; McGlone et al., 2017). It is likely the pollen from *Pteridium esculentum* was contemporaneous between Lakes Ōtūroto, Kirihonuhonu and Emily due to their proximity and, despite the lack of macrofossil targets, the age for the transition from the pre-human to Māori landscape periods, is reasonably constrained. The age model suggests wide scale forest reduction occurred in about 1390 CE.

**Lake Ōtūroto and Ōpōrea:** *Discostella stelligera* is the key species marking the ecological response in Lakes Ōtūroto and Ōpōrea, although the shifts differ between lakes. *Discostella stelligera* declines in Lake Ōtūroto and increases in Lake Ōpōrea following the first evidence of human activity. In Lake Ōpōrea *Discostella stelligera*, became the dominant taxon while benthic Fragilareaceae declined. *Discostella stelligera* can respond to increases in nutrients (Saros et al., 2014; Malik & Saros, 2016), such as those associated with anthropogenic forest clearance and subsequent nutrient mobilisation from erosion of sediment into the lakes (Köster et al., 2005; Costa-Böddeker et al., 2012; Beck, Medeiros & Finkelstein, 2016; Velez et al., 2021). This has been observed in other New Zealand lakes (McWethy et al., 2010; Short et al., 2022). It is unclear which nutrient(s) were limited in Lake Ōpōrea; however, *Discostella stelligera* can opportunistically respond to increasing nitrogen (Saros & Anderson, 2015; Perren, Axford & Kaufman, 2017). In Lake Ōpōrea, the ratio between planktonic *Discostella stelligera* and benthic Fragilariaceae increased following vegetation changes in the catchment. This suggests a decrease in water column transparency as phytoplankton growth enhanced by increasing nutrient concentrations in the water column, reduced light availability to the benthic zone (Bannister et al., 2019; Strock et al., 2019). The inferred increase in nutrients (through catchment erosion) is supported by the increasing  $\delta^{13}\text{C}$ , which is a proxy for increased aquatic productivity. In other locations, the changing benthic to planktonic ratio, has been interpreted as a change in lake levels (Hofmann et al., 2021), or mixing regime (Saros & Anderson, 2015; Strock et al., 2019) but there are no further indicators in the diatom record, that support these hypotheses. In Lake Ōpōrea, the increase in  $\delta^{13}\text{C}$  is probably reflective of nutrient input into the lake, and despite the tolerance of small Fragilariaceae to a broad array of ecological conditions (Bennion, Fluin & Simpson, 2004; Heathcote et al., 2014; Kingsbury, Laird & Cumming, 2012), it appears they were sensitive to light attenuation in Lake Ōpōrea.

In Lake Ōtūroto, there is a shift from *Discostella stelligera* to *Aulacoseira ambigua* indicative of nutrient enrichment. *Aulacoseira ambigua* has higher Si requirements than the smaller planktonic

diatoms (Rioual et al., 2007; Poister et al., 2012), and is a mesotrophic to eutrophic taxon (Siver & Kling, 1997; Poister et al., 2012; Siver et al., 2021). Vegetation modification, and subsequent erosional processes, likely increased the export of dissolved silica (DSi) and other nutrients, from the catchment into the lake, altering the natural Si fluxes (Struyf et al., 2010; Carey & Fulweiler, 2012; Nantke et al., 2021). This nutrient enrichment is shown by the increase in overall algal productivity indicated by higher  $\delta^{13}\text{C}$  values (Figure 5). It is unclear which nutrient(s) were limiting in Lake Ōtūroto, although in the high country region lakes are generally limited in phosphorus or co-limited by nitrogen and phosphorus (Kelly, Robertson & Allen, 2014). The increase in abundance of *Aulacoseira ambigua* is a response to forest clearance and the subsequent nutrient enrichment from detrital inputs (Bradbury, Cumming & Laird, 2002; Terasmaa et al., 2013; Gąsiorowski et al., 2021). Other studies suggest the abundance of *Aulacoseira*, is due to reduction in forest cover (Rühland, Smol & Pienitz, 2003; Rudaya et al., 2009) allowing for wind-induced turbulence to suspend the taxon in the water column. Taxa in the genus *Aulacoseira* are heavily silicified in comparison to other planktonic taxa, and therefore require turbulent conditions to maintain their presence in the photic zone (Rühland, Smol & Pienitz, 2003). The later, partial recovery of *Discostella stelligera*, and decline of *Aulacoseira ambigua* suggests, however, that an open catchment landscape, and therefore wind-induced turbulence, is not the primary driver of the abundance of *A. ambigua* in Lake Ōtūroto. Instead, it implies that export rates of DSi, and other nutrients, into the lake slowed as the stability of vegetation returned with the establishment of the grassland community.

**Lakes Kirihonuhonu and Emily:** Aquatic transitions occurred in Lakes Kirihonuhonu and Emily and are shown through the changing species composition in the benthic diatom assemblages. As the vegetation transitioned to grassland in the catchment of Lake Kirihonuhonu, the concentration of fragiliarioid taxa declined in favour of *Encyonopsis krammeri* and *E. subminuta*, with the latter not previously recorded in abundance. *Encyonopsis subminuta* is found in oligo-mesotrophic lakes (Rivera et al., 2018) in epiphytic and epilithic habitats (Cejudo-Figueiras et al., 2010; Hofmann et al., 2020), indicating that it thrives in shallow lakes (Novais et al., 2014; Cantonati et al., 2021). It is possible that *Encyonopsis krammeri* has similar resource affinities and it has been found in epilithic (Kennedy & Buckley, 2021) and epiphytic samples (Chapter 2, Figure 3) although water quality preferences of this taxon are not clear. In Lake Emily, oligotrophic taxa (*Stausirella cf. ovata*, *Stausirella canariensis*) decline in concert with detection of the first evidence of Māori activity, with an increase in taxa characteristic of more mesotrophic conditions (*Encyonopsis subminuta*, *Fragilaria cf. perminuta* and *Stausira* species; (Delgado et al., 2015; Rivera et al., 2018). The change to mesotrophic water conditions is further supported by an enriched  $\delta^{13}\text{C}$  signal, i.e. greater aquatic productivity. *Discostella*

*stelligera* is present in both lakes, increasing at the time of first Māori activity in Lake Emily but decreasing in Lake Kirihonuhonu. As shallow lakes generally record only small abundances of planktonic taxa (Hall & Smol, 2010) the trend of the taxon in these lakes is difficult to ascertain, which is furthermore hindered by the variety of factors that influence the abundance of *Discostella stelligera* (Saros & Anderson, 2015). It is likely, however, that *Discostella stelligera* is responding to the changing aquatic conditions.

Woodward et al. (2014 a, b) suggested there was greater runoff into the lakes, following forest reduction, which led to an increase in water yield (*sensu* Brown et al., 2005). This would have resulted in increased lake area and depth. Evidence of more water availability is provided through greater abundance of wetland and aquatic taxa, the submerged and emergent macrophytes: Cyperaceae, *Myriophyllum* spp. and *Isoëtes* spp. (Figure 6, Horrocks et al., 2000; Hawes et al., 2003; Kelly & Hawes, 2005; Hofstra & de Winton, 2016; Newnham et al., 2018). These taxa have been used elsewhere in New Zealand to infer the expansion of wetlands driven by forest reduction (McGlone, 1983; Wilmshurst et al., 2004; Woodward et al., 2014a). In the diatom record there was corresponding increase in epiphytic diatoms; *Encyonopsis krammeri* and *E. subminuta* supporting the idea of wetland expansion and increasing habitat availability driven by an inundation of surrounding habitat. Similarly, the *Discostella stelligera* in Lake Emily could reflect greater water depth knowing the preference for planktonic diatoms for open water conditions (*sensu* Hall & Smol, 2010).

#### 4.4 Implications of this study

##### 4.4.1 *Discostella stelligera* as an indicator of cultural nutrient enrichment

All lakes experienced aquatic transitions, but in Lakes Ōpōrea and Ōtūroto the aquatic transitions are observed predominantly through the changes in *Discostella stelligera*. In Lake Ōpōrea, the aquatic transition is characterised by the switch to *Discostella stelligera* dominance, and in Lake Ōtūroto, *Discostella stelligera* and *Discostella* spp. (< 5 µm) both decline as conditions favour *Aulacoseira ambigua*. While *Discostella stelligera* later recovers, *Discostella* spp. (< 5 µm) does not and neither do the benthic Fragilareaceae in Lake Ōpōrea. This suggests that *Discostella stelligera* is thriving in its optimal nutrient concentration. It appears the lakes were naturally microtrophic (TP: 1.8–4.1 mg/m<sup>3</sup>, TN: 34–73 mg/m<sup>3</sup>; Burns, Rutherford & Clayton, 1999). While the lakes became oligotrophic after the first evidence of Māori activity, the lakes can still be considered to be of a good ecological health.

This study, and others (McWethy et al., 2010; Short et al., 2022), suggest that *Discostella stelligera* in New Zealand is a useful indicator of cultural nutrient enrichment. Indeed, its presence in many lakes across New Zealand (Reid, 2005) has likely been influenced by human activity (e.g. Short et al., 2022).

However, it is also interesting to consider whether the inferred shifts in nutrient concentrations in these lakes, is a challenge to the well-defined concept of “cultural eutrophication”, which itself refers to excessive algal and plant growth as a result of anthropogenic activity (Smith & Schindler, 2009). While this is an established problem in many aquatic environments (Gruber & Galloway, 2008; Smith & Schindler, 2009), and is frequently associated with industrial agricultural intensification, e.g. Guiry et al. (2020), this study prompts consideration in redefining cultural eutrophication in lakes. Although the aquatic conditions following first Māori arrival never reached eutrophic water quality (TP: 20–43 mg/m<sup>3</sup>, TN: 337–725 mg/m<sup>3</sup>; Burns, Rutherford & Clayton, 1999), the measured diatom response and greater algal productivity ( $\delta^{13}\text{C}$ ) certainly indicate cultural eutrophication as a definition of anthropogenic mediated nutrient enrichment.

Associating cultural eutrophication with historically recent anthropogenic activity, can overlook long-term human impact on the environment (Bennion et al., 2011). There is an increasing recognition that intensification of human activity occurred long before the Industrial Revolution, with human influences detected in lake systems from the early to mid-Holocene, even though these may not have been the first human impacts in the landscape (e.g. Bradshaw et al., 2006; Bennike et al., 2021; Gąsiorowski et al., 2021). In this study, we unambiguously captured the first aquatic shifts associated with human activity, and the aquatic transitions observed are an example of early cultural eutrophication.

#### 4.4.2 How does the observed lake response compare to other studies nationally and globally?

One of the aims of this study was to further understand how aquatic systems respond to first human settlement. New Zealand is a prime location to address this question due to its recent occupation. The deforestation and landscape transformation of the Canterbury region is consistent with palaeoecological evidence from other landmasses with recent human settlement (Nogué et al., 2021). Landscapes were burned and opened, for the provision of ecosystem services, such as food and shelter, to humans (Rick et al., 2013; Castilla-Beltrán et al., 2021). In most other localities with recent (i.e. < 1000 years) human settlement, landscape transformation occurred rapidly, and vegetation became more open (Connor et al., 2012; Hiles et al., 2021; Nogué et al., 2021). These landscape transformations were the main drivers in the subsequent water quality response of many aquatic ecosystems, e.g. Lawson et al. (2007).

It is likely that many other New Zealand lakes experienced similar aquatic transitions to those recorded in the present study. Many New Zealand lakes are thought to be naturally low in nutrients (microtrophic–oligotrophic; *sensu* Abell et al., 2019) making them highly susceptible to localised

changes in vegetation and the subsequent release of nutrients through erosion. Spatial disparities in lake response to changes in landscape vegetation are likely to exist as there were differences in how the vegetation was cleared, the amount of vegetation cleared, and the size of human population (e.g. Tipa, 2013; Phillipps, McAlister & Allen, 2016). For example, it is likely that higher altitude lakes, such as those in the Southern Alps, were less affected by early human activity.

There are few studies that specifically address the ecological response of aquatic systems to human settlement because the longevity of human occupation prevents this (Dubois et al., 2018). In areas with recent human settlement, the focus has usually been on the timing of settlement or how the terrestrial landscape was transformed, e.g. Cabo Verde; (Castilla-Beltrán et al., 2019), Canary Islands (Nogué et al., 2013; de Nascimento et al., 2016), Azores (Connor et al., 2012; Raposeiro et al., 2021), Fiji and New Caledonia (Stevenson, Dodson & Prosser, 2001; Hope, Stevenson & Southern, 2009, see Nogué et al., 2021 for a comprehensive synthesis). In the studies examining lakes there is generally an increase in aquatic productivity following landscape clearance (Lawson et al., 2007), which is consistent with this study. However, the rates and magnitude are not always comparable, and neither are the indicators used. Some lakes experienced rapidly increasing lake productivity following human activity such as those in the Azores, Pico Island (Raposeiro et al., 2021) and Flores Island (Richter et al., 2022; Ritter et al., 2022), Faroe Islands (Gathorne-Hardy et al., 2007) and Iceland (Lawson et al., 2007; Richter et al., 2021). By contrast, others experienced little change, due to the small initial human population size and, or, because the main human activity did not occur near lakes; Samoa (Gosling et al., 2020), Azores; Corvo Island (Raposeiro et al., 2021), Greenland (Massa et al., 2012; Perren et al., 2012), Faroe Islands (Gathorne-Hardy et al., 2007). In the present study all four lakes underwent early aquatic transitions, making them one of the few examples, globally, where the unambiguous impact of first human activity has been readily detected in lake systems.

## 5 Conclusion

This study provides a new perspective on the initial effects of changing landscape vegetation on lakes. In this study, four lakes from Canterbury high country were analysed to determine their ecological response to the first changes in catchment vegetation. In all catchments, native forest transitioned into a landscape dominated by tussock grassland, with early and non-reversible responses recorded in the diatom assemblages contrasting with the notions that impacts by early populations on lakes are not easily detected (Dubois et al., 2018). This study indicates that nutrient enrichment in all four lakes: Otūroto, Kirihonuhonu, Emily and Ōpōrea was recorded before full scale vegetation turnover (Figure 8).



This study is an exemplar of how lakes respond to first human activity with respect to vegetation reduction. While there was a fundamental shift in the ecology of the study lakes, they remained oligotrophic and in what is conventionally seen as in good ecological health (*sensu* Stoddard et al., 2016). Furthermore, the complexity of lake responses is demonstrated by the change in diatom species composition between the shallow Lakes Kirihonuhonu and Emily when compared to the deeper Lakes Ōtūroto and Ōpōrea. In the shallow lakes, the benthic record became more diverse, likely as a response to both nutrient increases and habitat expansion, whereas the shifts in the deeper lakes were directly driven by increased nutrient availability in the water column.

This study provides unequivocal evidence for response by lakes to first human activity, rarely found elsewhere, and builds upon earlier evidence of major changes in lake ecology. The implication is that while there is no doubt that, at a global scale, lakes have been enriched with nutrients following industrial agricultural activity over the last few centuries, these impacts were, in fact, superimposed on a shifted baseline relative to their natural condition.

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## 8 Supplementary Information for Chapter 4 and Chapter 5

As the study lakes and methods for sediment core analysis from each lake were the same in Chapters 4 and 5, the supplementary information for both chapters was combined into one file.

### **Chapter 4: Initial human impacts on landscape vegetation drove nutrient change and aquatic transitions in lake ecosystems**

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### **Chapter 5: The legacy of anthropogenic activities in New Zealand's high country lakes.**

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## 1 Methods

### 1.1 Sediment subsampling

Four sediment cores were taken from each of the lakes in November 2019 (Figure 1) using a UWITEC Gravity corer, with a 95 mm diameter core barrel, before being packed with florist foam to prevent sediment movement during transport. Cores were cut into one metre increments for storage. The longest core was selected for all analyses (diatoms, pollen, sediment geochemistry) while the remaining cores were archived for future work and educational purposes. Each core was split lengthwise with one half being used for destructive analyses (pollen, diatoms, geochemistry and sedDNA (not used in this study)) and the other half used for computed tomography and other non-destructive analyses (not reported in this study). Cores were sampled at varying depths depending on the proxy sampled (Supplementary Table S1–S4).

**Table S1:** List of proxies, sample depth and number of samples from Lake Ōtūroto (Heron)

Proxy	Sample depth (cm)	Number of samples
<b>Length of core: 168 cm</b>		
Diatoms	0–10, 12–88 (every 2 cm), 89, 90–162 (every 2 cm), 163, 164, 165	91
Pollen and charcoal	1, 6, 11, 16, 18, 21, 23, 26, 29, 33, 39, 44, 49, 57, 64, 71, 76, 82, 86, 88, 89, 90, 99, 109, 119, 124, 139, 154, 165	29
Isotopes ( $\delta^{13}\text{C}$ , C:N)	0–12, 12, 16, 20, 23, 24, 28–76 (every 4 cm), 84, 85, 86, 88, 90, 94, 98, 106–162 (every 8 cm), 165	46

**Table S2:** List of proxies, sample depth and number of samples from Lake Kirihonuhonu (Emma)

Proxy	Sample depth (cm)	Number of samples
<b>Length of core: 76 cm</b>		
Diatoms	1–10, 12–72 (every 2 cm), 73, 74	44
Pollen and charcoal	1, 3, 5, 7, 9, 14, 16, 18, 19, 20, 21, 22, 24, 29, 34, 39, 49, 59, 69, 74	20
Isotopes ( $\delta^{13}\text{C}$ , C:N)	0, 1, 2, 4, 6, 8, 10, 12, 14, 16, 17, 18, 19, 21, 23, 25, 27, 31, 43, 51, 59, 67, 73	23

**Table S3:** List of proxies, sample depth and number of samples from Lake Emily

Proxy	Sample depth (cm)	Number of samples
<b>Length of core: 127 cm</b>		
Diatoms	0–9, 11–83 (every 2 cm), 84, 86, 88–126, 127	70
Pollen and charcoal	0, 5, 8, 13, 18, 23, 28, 33, 43, 53, 55, 57, 63, 67, 69, 71, 73, 82, 102, 122	20
Isotopes ( $\delta^{13}\text{C}$ , C:N)	1–9, 11–27 (every 2 cm), 28, 29, 33, 37, 41, 45, 49, 53, 57, 61–65, 69, 73, 81, 88, 96, 104, 112, 120, 127	42

**Table S4:** List of proxies, sample depth and number of samples from Lake Ōpōrea (Pearson)

Proxy	Sample depth (cm)	Number of samples
<b>Length of core: 173 cm</b>		
Diatoms	1–10, 12–88 (every 2 cm), 89, 91–171 (every 2 cm), 172, 173	92
Pollen and charcoal	1–21 (every 2 cm), 24, 27, 28, 30, 33, 36, 38, 41, 45, 51, 56, 61, 85, 97, 126, 156, 167, 174	28
Isotopes ( $\delta^{13}\text{C}$ , C:N)	1, 5, 9, 13, 16, 19, 20, 24, 26–30, 34, 38, 42, 46, 50, 54, 58, 62, 66, 70, 78, 86, 93, 101, 109, 117, 125, 133, 141, 149, 157, 173	36

## 1.2 Sediment chronology

Table S5: Lake Ōtūroto (Heron) numerical age data

Sub-bottom depth (cm)			Sample ID	<sup>210</sup> Pb age (yBP)		<sup>14</sup> C results						Biostratigraphic age (CalBP)	
Min	Max	Med		<sup>210</sup> Pb Mean	<sup>210</sup> Pb σ	NZA	F(Mod)	F(Mod) σ	CRA	CRA σ	δ <sup>13</sup> C		δ <sup>13</sup> C σ
168.4	168.4	168.4	Base of core										
162.4	165.8	164.1	HERON_LC1U_2B_76-77cm			71675	0.891	0.002	924	19	Not measured		
89	90	89.5	HERON_LC1U_2B_2-3cm			71674	0.917	0.002	698	19	-27.24	0.2	
20	21	22.5	<i>Rumex</i> emergence										93-88
13.5	14.5	14	<sup>210</sup> Pb_14cm	3	3.6								
12.5	13.5	13	<sup>210</sup> Pb_13cm	-2	3.3								
11.5	12.5	12	<sup>210</sup> Pb_12cm	-7	3.0								
10.5	11.5	11	<sup>210</sup> Pb_11cm	-13	2.8								
9.5	10.5	10	<sup>210</sup> Pb_10cm	-19	2.5								
8.5	9.5	9	<sup>210</sup> Pb_9cm	-24	2.2								
7.5	8.5	8	<sup>210</sup> Pb_8cm	-30	1.9								
6.5	7.5	7	<sup>210</sup> Pb_7cm	-35	1.7								
5.5	6.5	6	<sup>210</sup> Pb_6cm	-41	1.4								
4.5	5.5	5	<sup>210</sup> Pb_5cm	-47	1.1								
4	5	4.5	<i>Lindavia</i> emergence										-52
3.5	4.5	4	<sup>210</sup> Pb_4cm	-52	0.9								
2.5	3.5	3	<sup>210</sup> Pb_3cm	-57	0.6								
1.5	2.5	2	<sup>210</sup> Pb_2cm	-62	0.4								
0.5	1.5	1	<sup>210</sup> Pb_1cm	-66	0.1								
0	0	0	Top of core										-69

Table S6: Lake Kiriuhonuhonu (Emma) numerical age data

Sub-bottom depth (cm)			Name	<sup>14</sup> C results						Biostratigraphic age (CalBP)	
Min	Max	Med		Sample ID	NZA	F(Mod)	F(Mod) σ	CRA	CRA σ		δ <sup>13</sup> C
74.2	74.2	74.2	Base of core								
48.7	49.7	49.2	LEMMA_LC4U_1B_60-61cm	74159	0.6320	0.0021	3689	27	Not measured		
41.7	42.7	42.2	LEMMA_LC4U_1B_53-54cm	74158	0.7085	0.0022	2768	24	Not measured		
31.8	33.5	32.7	LEMMA_LC2U_1A_46.5-47cm	73224	0.8224	0.0020	1570	19	-8.8	0.2	
28.2	29.2	28.7	<i>Fuscospora</i> spp. Peak								
19.7	20.7	20.2	<i>Pteridium</i> increase								
6.7	7.7	7.2	<i>Rumex</i> and <i>Pinus</i> emergence								93-88
0	0	0	Top of core								-69

Table S7: Lake Ōpōrea (Pearson) numerical age data.

Sub-bottom depth (cm)			Sample ID	<sup>14</sup> C results						Biostratigraphic age (CalBP)	
Min	Max	Med		NZA	F(Mod)	F(Mod) σ	CRA	CRA σ	δ <sup>13</sup> C		δ <sup>13</sup> C σ
173	173	173	Base of core								
120.2	121.2	120.7	PEARS_LC1U_2B_30-31cm	71790	0.4959	0.002	5634	26	-27.27	0.2	
56	58.1	57.1	PEARS_LC2U_1A_75.5-76cm	71789	0.5944	0.002	4179	23	-28.97	0.2	
28.2	30.3	29.2	PEARS_LC2U_1A_45-46cm	71788	0.8190	0.002	1604	21	-26.33	0.2	
26.7	27.7	27.2	<i>Pteridium</i> increase								
18.2	19.2	18.7	<i>Rumex</i> emergence								93-88
1.2	2.2	1.7	<i>Lindavia</i> emergence								-52-58
0	0	0	Top of core								-69

Table S8: Lake Emily numerical age data

Sub-bottom depth (cm)			Sample ID	<sup>210</sup> Pb age (yBP)		<sup>14</sup> C results						Biostratigraphic age (yBP)	
Min	Max	Med		<sup>210</sup> Pb Mean	<sup>210</sup> Pb σ	NZA	F(Mod)	F(Mod) σ	CRA	CRA σ	δ <sup>13</sup> C		δ <sup>13</sup> C σ
128	128	128	Base of core										
106.3	119.2	112.7	EMILY_LC3U_2A_31-32cm			74238	0.5123	0.0015	5373	23	-13.9	0.2	
106.1	115.7	110.9	EMILY_LC3U_2A_28-29cm			74237	0.5746	0.0016	4451	22	-28.5	0.2	
80.9	81.9	81.4	<i>Fuscospora</i> spp. Peak										
70.4	80.4	70.9	<i>Pteridium</i> increase										
28.4	29.4	28.9	EMILY_LC1U_1A_46-47cm			73344	0.9644	0.0023	291	19	-13.2	0.2	
27.4	28.4	27.9	<i>Rumex</i> emergence										93-88
20.5	21.5	21	<sup>210</sup> Pb_21cm	6	0.7								
19.5	20.5	20	<sup>210</sup> Pb_20cm	1	0.8								
18.5	19.5	19	<sup>210</sup> Pb_19cm	-4	0.8								
17.5	18.5	18	<sup>210</sup> Pb_18cm	-8	0.8								
16.5	17.5	17	<sup>210</sup> Pb_17cm	-12	0.8								
15.5	16.5	16	<sup>210</sup> Pb_16cm	-17	0.7								
14.5	15.5	15	<sup>210</sup> Pb_15cm	-22	0.7								
13.5	14.5	14	<sup>210</sup> Pb_14cm	-27	0.6								
12.5	13.5	13	<sup>210</sup> Pb_13cm	-31	0.6								
11.5	12.5	12	<sup>210</sup> Pb_12cm	-36	0.5								
10.5	11.5	11	<sup>210</sup> Pb_11cm	-39	0.5								
9.5	10.5	10	<sup>210</sup> Pb_10cm	-42	0.5								
8.5	9.5	9	<sup>210</sup> Pb_9cm	-44	0.4								
7.5	8.5	8	<sup>210</sup> Pb_8cm	-47	0.4								
6.5	7.5	7	<sup>210</sup> Pb_7cm	-50	0.4								
5.5	6.5	6	<sup>210</sup> Pb_6cm	-53	0.3								
4.5	5.5	5	<sup>210</sup> Pb_5cm	-55	0.3								
3.5	4.5	4	<sup>210</sup> Pb_4cm	-57	0.3								
2.5	3.5	3	<sup>210</sup> Pb_3cm	-60	0.2								
1.5	2.5	2	<sup>210</sup> Pb_2cm	-64	0.2								
0.5	1.5	1	<sup>210</sup> Pb_1cm	-67	0.1								
0	0	0	Top of core										-69

### 1.3 Sedimentary diatom analyses

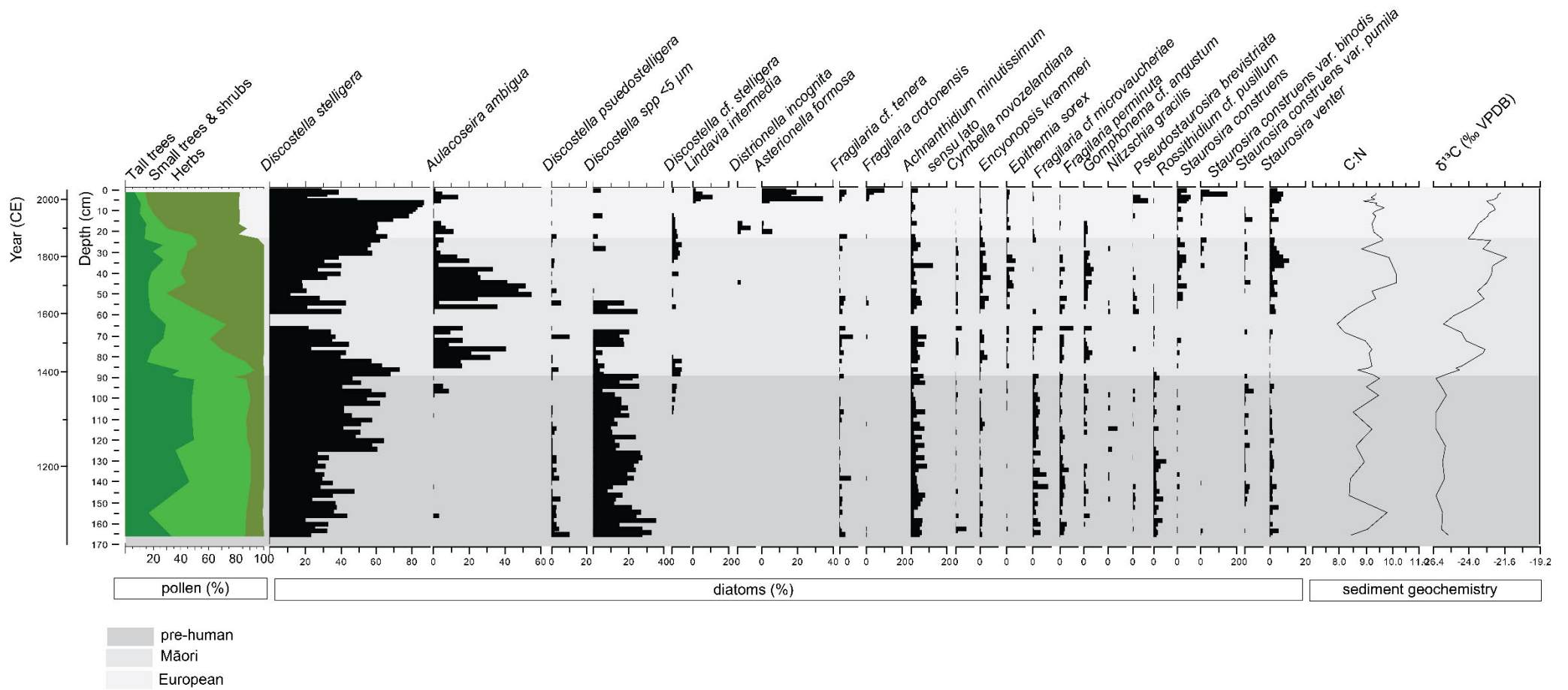
In Lakes Ōtūroto and Ōpōrea, smaller valves of *Discostella* spp. were difficult to identify under light microscope due to their small size and lack of discernible features. Scanning electron microscope analyses were inconclusive because some dissolution had occurred, and the samples were also difficult to clean. The taxon therefore was assigned a name reflecting its size; *Discostella* spp. < 5 µm. The difficulty of assigning an identity to small *Discostella* taxa is also noted in Davies et al. (2018) and Potapova et al. (2020).

In Lakes Ōpōrea, Kirihonuhonu and Emily *Staurosira venter* was separated into *Staurosira venter* morph 1 and morph 2. However, due to the low abundance of the taxon in Lake Ōtūroto, there was no separation of the species into their respective morphotypes.

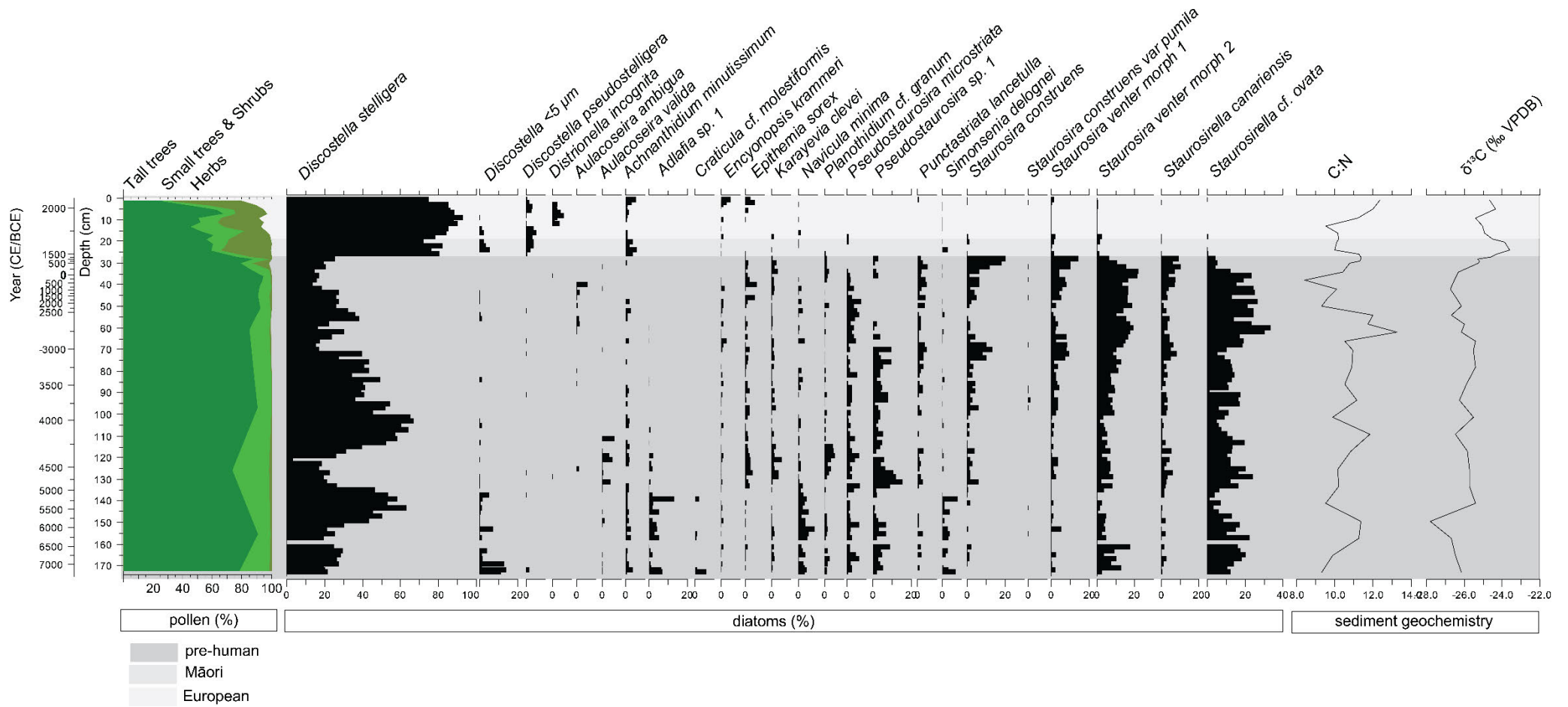
Samples from depths 60, 62 and 64 cm in Lake Ōtūroto were not included in the statistical analyses as only a few diatoms (max. 37) were recorded from 10 transects. The sample from a depth of 159 cm in Lake Ōpōrea was not included in any statistical analyses as there were only 8 diatoms recorded from 10 transects.

## 2 Results

### 2.1 Sedimentary diatoms, pollen and geochemistry

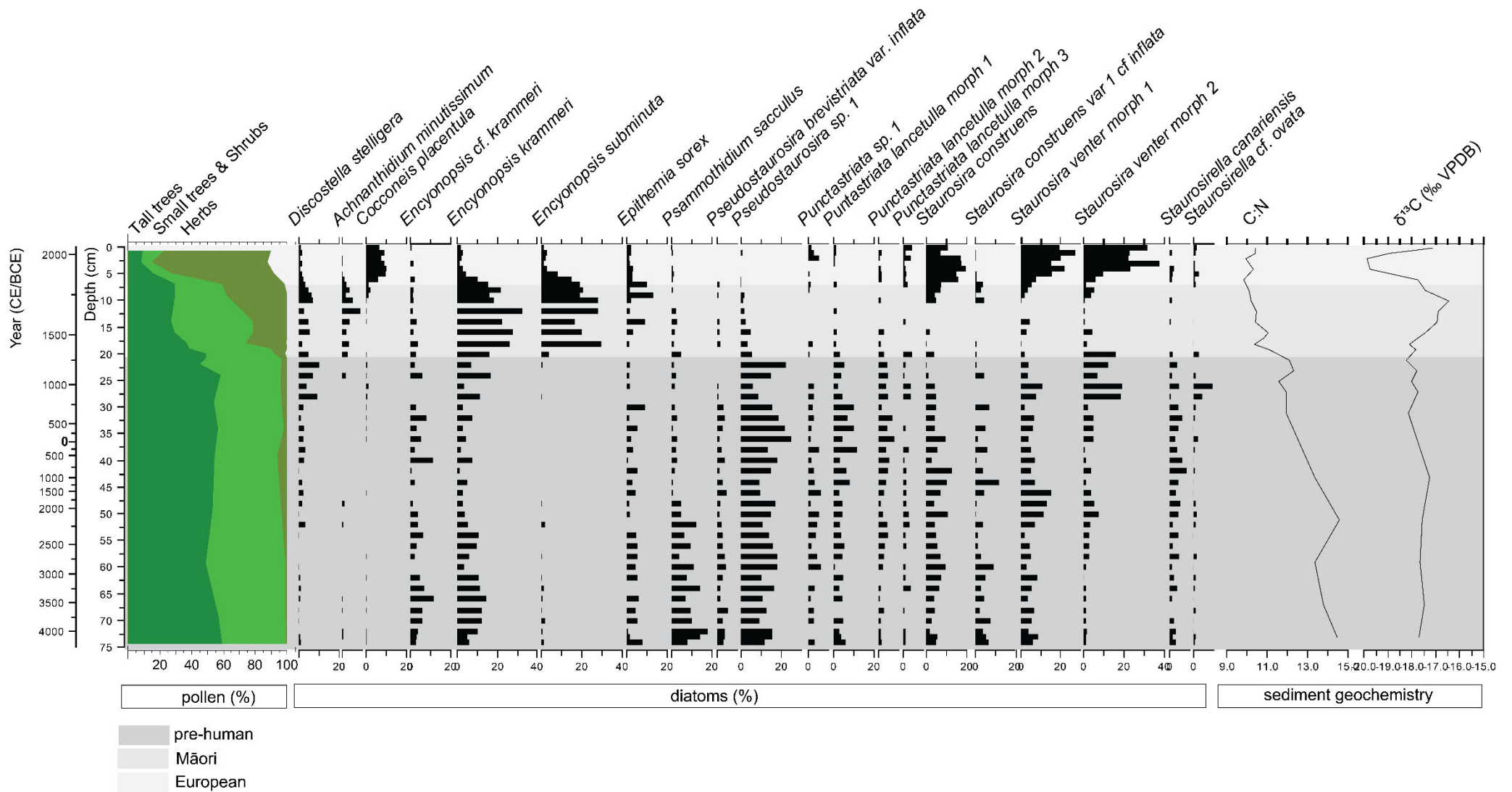


**Figure S1:** Diatom assemblage data, geochemistry and pollen habitat from Lake Ōtūroto. Diatom taxa at ≥ 5% abundance (in at least one sample) were included. The shading represents the occupation phase of the catchment.

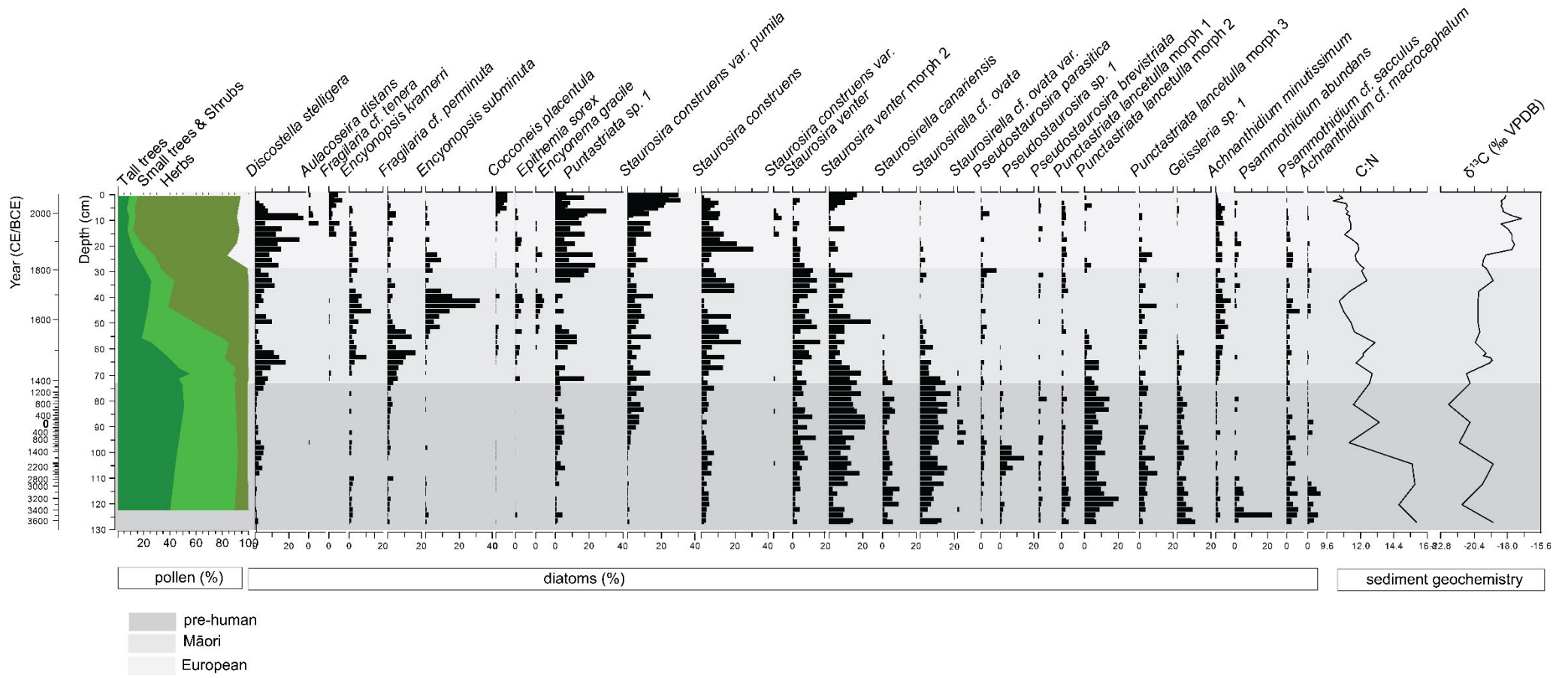


**Figure S2:** Diatom assemblage data, geochemistry and pollen habitat from Lake Ōpōrea. Diatom taxa at ≥ 5% abundance (in at least one sample) were included. The shading represents the occupation phase of the catchment.

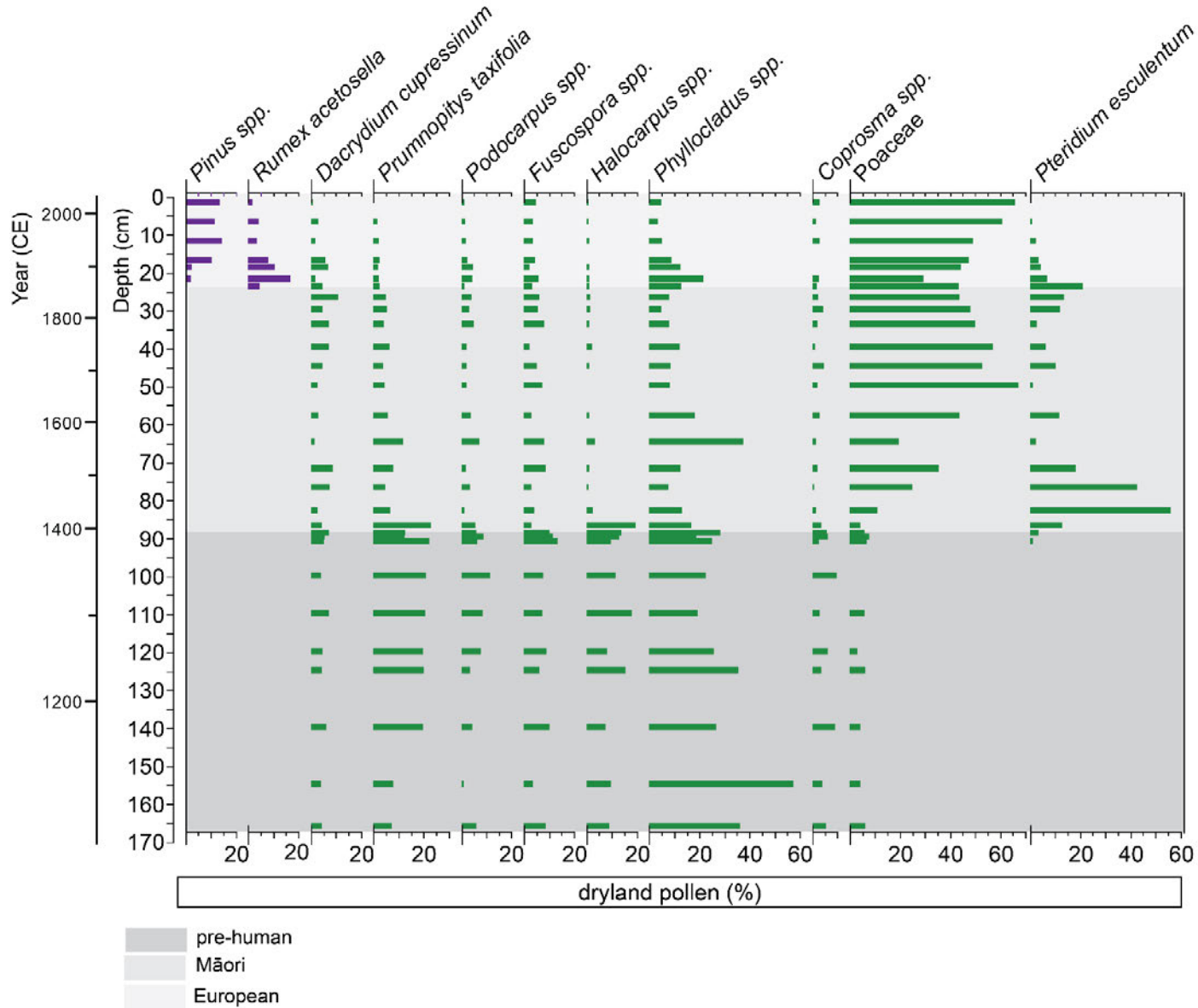




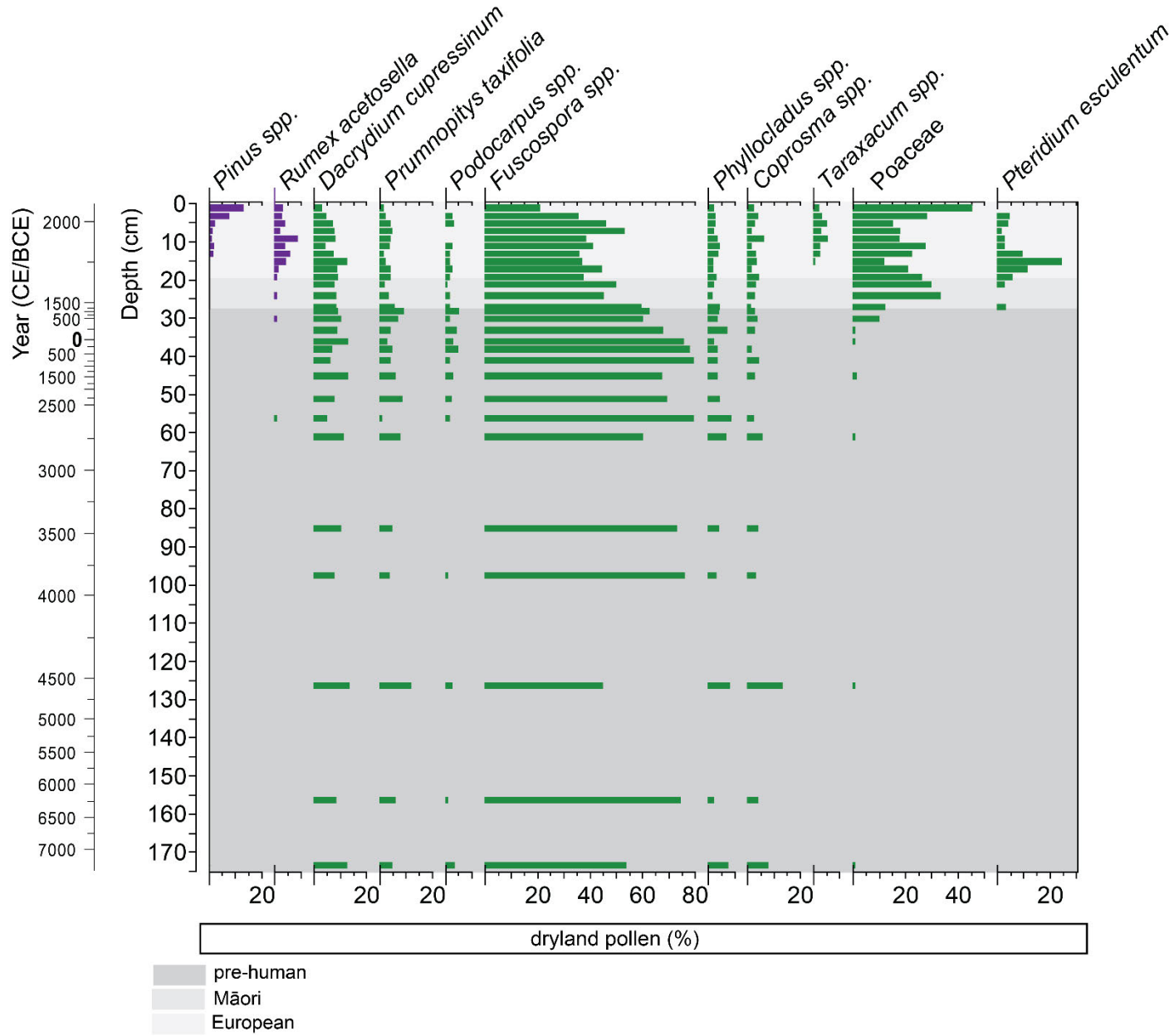
**Figure S3:** Diatom assemblage data, geochemistry and pollen habitat from Lake Kirihonuhonu. Diatom taxa at  $\geq 5\%$  abundance (in at least one sample) were included. A selection of aquatic and wetland pollen are shown. The shading represents the occupation phase of the catchment.



**Figure S4:** Diatom assemblage data, geochemistry and pollen habitat from Lake Emily. Diatom taxa at  $\geq 5\%$  abundance (in at least one sample) were included. A selection of aquatic and wetland pollen are shown. The shading represents the occupation phase of the catchment.



**Figure S5:** Select pollen data from Lake Ōtūroto. The taxa shaded in purple were introduced to New Zealand following European colonisation.



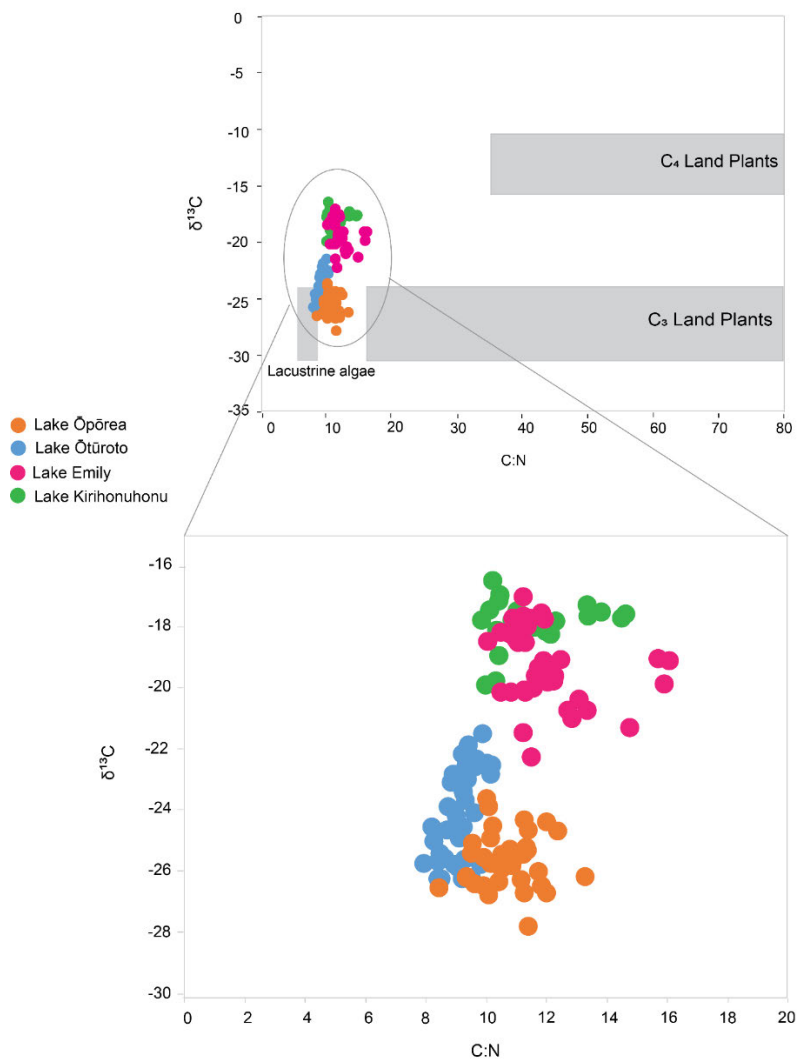
**Figure S6:** Select pollen data from Lake Ōpōrea. The taxa shaded in purple were introduced to New Zealand following European colonisation.



**Figure S7:** Select pollen data from Lake Kirihonuhonu. The taxa shaded in purple were introduced to New Zealand following European colonisation.



**Figure S8:** Select pollen data from Lake Emily. The taxa shaded in purple were introduced to New Zealand following European colonisation.



**Figure S9:** Biplot of sediment organic matter analyses showing  $\delta^{13}\text{C}$  and atomic C:N. Figure adapted from (Meyers, 2003).

### 3 References

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## Statement of Authorship

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Publication Details	Written in the format of an article in the <i>Journal of Paleolimnology</i> .

### Principal Author

Name of Principal Author (Candidate)	Julia Short		
Contribution to the Paper	Conceptual design, field work and sample preparation, diatom data collection and analyses, isotope data collection and analyses, data interpretation and statistical analyses (diatoms, pollen, isotopes) Producing figures, Manuscript production, writing and editing		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	19/7/22

### Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the thesis; and
- iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Signature		Date	4/8/22

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Contribution to the Paper	Producing data (Lake Oturoto isotopes), field work and collection of samples, manuscript editing and data interpretation		
Signature		Date	11/8/22

Name of Co-Author	Xun Li		
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Contribution to the Paper	Producing data (pollen)		
Signature		Date	12/08/2022

## Chapter 5

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### The legacy of anthropogenic activities in New Zealand's high country lakes

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## Abstract

Lakes are threatened by the increasing pressure of human activities with many degrading at an accelerating rate. In many regions of the world, freshwater degradation was exacerbated by European colonisation, and the introduction of European style agriculture. In New Zealand, lakes, especially those located in low to mid-altitude catchments, recorded changes in water quality after catchment deforestation following Māori settlement. The Canterbury high country (600–800 m.a.s.l.) was transformed from native forests to grassland-dominated vegetation approximately 600 years ago, and has more recently, in the last 150 years, been used for a variety of agricultural activities. The catchments of four lakes, located in this area: Ōtūroto, Kirihonuhonu, Emily and Ōpōrea were used for sheep farming following European colonisation. Diatom and sedimentary isotopes were examined from sediment cores collected from these lakes with the aim of identifying lake response to European activities, while data from water monitoring was used to complement the understanding of the diatom assemblages for the last 15 years. In contrast to the marked shifts recorded in all lakes after vegetation changes following Māori settlement, the response to European activity differed between sites. The shallow lakes, Lakes Kirihonuhonu and Emily, responded quickly to European catchment activity and continue to reflect increasing eutrophication, which is supported by trends in water monitoring data. In Lakes Ōtūroto and Ōpōrea which are larger and deeper, there was no major change after initial European settlement, and shifts in water quality only occurred 130 years later as culmination of continuing agricultural pressure. The diatom assemblages indicate that in these deeper lakes, nitrogen enrichment is now the main driver of species' distribution. There is increasing need to rehabilitate these lakes and their catchments, to ensure that they maintain their ecological and cultural values, and it is suggested that the lakes should be managed at a landscape scale, considering the interconnected freshwater landscape and mix of land use that co-occur in the lake's catchments.

## 1 Introduction

The degradation of lake ecosystems as a direct result of anthropogenic activity has been occurring for centuries (Jenny et al., 2016; Smol, 2019) but has accelerated since the 1950s, leading to shifts in the ecology and water quality of many lakes (Huang et al., 2022). Eutrophication of lakes, which is defined as the excessive growth of plants and phytoplankton due to nutrient enrichment, is one of the most pervasive and tangible anthropogenic effects on freshwater systems often interacting simultaneously with other stressors making it difficult to manage (Smith & Schindler, 2009; Le Moal et al., 2019; Birk et al., 2020). Furthermore, anthropogenic climate change is now a significant threat to lentic systems due to altered surface water temperatures and the mixing regimes of lakes (O'Reilly et al., 2015; Woolway & Merchant, 2019). The combination of these factors, in addition to the loss of freshwater biodiversity (Dudgeon et al., 2006) has resulted in an urgent need to effectively manage lake ecosystems (Albert et al., 2021). Conservation measures, such as nutrient abatement and native species management, however, have only increased in complexity as freshwater systems face multiple pressures (Jackson et al., 2016), while stakeholders often have differing values (Reid et al., 2019; Albert et al., 2021).

In New Zealand, lakes are greatly valued, with a wide range of ecosystems services associated with biodiversity, recreation, economy and human well-being (Weeks et al., 2016). For Māori, the indigenous people of New Zealand, lakes are integral to spiritual and cultural well-being (Te Aho, 2019; Stewart-Harawira, 2020). However, many of the country's lakes are in poor ecological health with loss of native biodiversity and declining water quality (eutrophic–supertrophic conditions), also affecting naturally low nutrient lakes (Ministry for the Environment & Stats NZ, 2020a). Nutrient concentrations are generally increasing in lakes throughout New Zealand (Abell et al., 2019; Ministry for the Environment & Stats NZ, 2020a). In response to this, and other issues associated with freshwater, New Zealand's government introduced the National Policy Statement for Freshwater Management (NPS-FM). Regional councils must meet set targets for nutrient and algal concentrations for lakes (Snelder, Larned & McDowell, 2018). When lakes do not meet a minimum standard, or “national bottom line”, action is required to improve water quality and lake health (Stephens et al., 2018; Ministry for the Environment & StatsNZ 2020b). Monitoring water quality has thus become an integral part of lake management in New Zealand, and consequently local government and agencies have been regularly monitoring a small selection of lakes (< 200) around the country, some for more than a decade (Larned et al., 2020; LAWA, 2021).

Monitoring water quality is necessary for management of lake systems, although understanding recent trends is often hindered by the long-term ecological degradation that has already occurred in many lakes. Therefore, methods that capture earlier anthropogenic influences are essential (Maberly & Elliott, 2012; Smol, 2019). Palaeolimnological techniques, using material preserved in lake sediments, can assist with understanding historic lake ecology and water quality. In particular, indicators like diatoms, can be used for reconstructing

past water quality. Palaeolimnological techniques have been used previously, in conjunction with long-term monitoring data, to detect causes of changing water quality in lakes and explore how recently observed changes compare with historic trends (Kämpf et al., 2012; Paterson et al., 2017; Wiltse et al., 2022). There are only a few palaeolimnological studies in New Zealand that specifically examine lakes responses to anthropogenic activities. Together they highlight that following the start of European agricultural practices in New Zealand, lakes experienced an increase in algal productivity (Woodward & Shulmeister, 2005; Augustinus et al., 2006; Woodward et al., 2014; Stephens et al., 2018), enhanced sedimentation (Woodward & Shulmeister, 2005; Schallenberg, Goff & Harper, 2012), greater salinisation (Woodward & Shulmeister, 2005; Schallenberg & Saulnier-Talbot, 2016) and degradation of macrophyte communities (Schallenberg & Saulnier-Talbot, 2016; Stephens et al., 2018). The timing of these changes, however, varies, with some lakes recording ecological changes within decades of the start of European activity (e.g. Woodward et al., 2014; Stephens et al., 2018), while in other lakes, ecology and water quality changed later, near to the mid-20<sup>th</sup> Century (e.g. Woodward & Shulmeister 2005; Augustinus et al., 2006; Schallenberg & Saulnier-Talbot, 2016).

The lakes in the Ōtūwharekai (Ashburton) and Selwyn-Waihora regions of the Canterbury high country in New Zealand have extensive ecological and cultural values especially for the *iwi* (Māori “tribe”) Ngāi Tahu. Lakes in this region were analysed in Chapter 4 to explore their response to changing vegetation following evidence of first Māori activity in the area. The results presented in Chapter 4 showed that the water quality of the lakes shifted rapidly, following the transformation of native forests to vegetation dominated by tussock grassland in approximately 1400 CE. Furthermore, this change was large enough to represent an aquatic transition (Dubois et al., 2018), yet, these lakes still had low nutrient concentrations (oligotrophic-mesotrophic) at the end of the pre-European period. However, there is limited data about how water quality changed after the commencement of European pastoral activities, later followed by 20<sup>th</sup> Century agricultural intensification. Regular monitoring of these sites has only occurred for the past 10–15 years and indicate that nutrient concentrations are increasing in both shallow and deep lakes (Bayer & Meredith, 2020). However, the increase in nutrients fluctuates, raising questions about the long-term structure, functioning and response of lakes to various catchment activities. This includes the legacy of historical pastoral activity as land use and intensity has varied in the region, and currently some catchment areas and lakes have more focus on conservation (*sensu* Robertson & Suggate, 2011).

Paleolimnological methods and water monitoring data can be complementary and given the availability of monitoring data for some lakes in the Canterbury region, the present study used these together to examine the ecological history of four lakes of varying depth and size. The present study sought to, 1) reconstruct the historic water quality of four lakes (two deep and two shallow) in the Canterbury high country from the start of European settlement, 2) compare diatom trends in each lake over the last 200 years, in combination with

monitoring data, and 3) to consider the implications of the results for lake management. This chapter focuses particularly on the trend of water quality in recent decades, and whether the timing of changes in water quality differed between sites, given their differing depths and size, and proximity. In comparison to the deeper lakes, it was hypothesised that the diatoms assemblages in the shallow lakes would be more marked in their response to the water quality changes, given the sensitivity of shallow lakes to land-use activities.

## 2 Methods

### 2.1 Study area

The Canterbury high country is located on the leeward side of the Southern Alps of New Zealand, an area subject to an orographic rain shadow (Macara, 2016). The four lakes are situated in inter-montane basins with Lakes Ōtūroto (Heron), Kirihonuhonu (Emma) and Emily in the Ōtūwharekai (Ashburton) region, and Lake Ōpōrea (Pearson) in the neighbouring inter-montane basin in the Selwyn-Waihora (Waimakariri district, approximately 60 km east) (Figure 1, Table 1). The high country experiences a mixture of pastoral, conservation and recreational uses, e.g. fishing and hiking. Trophic classification throughout the text follows the trophic level categorisation for New Zealand's lakes (Burns, Rutherford & Clayton, 1999). Dominant land cover types in the region are, 1) low productivity grassland, which refers to grassland that is not fertilised regularly or cultivated, and may include native tussock, *Chionochloa* spp., *Festuca* spp. and *Poa* spp. (Hewitt et al., 2012), and 2) high productivity grassland referring to regularly fertilised land that is generally used for animal production. Species include non-native *Lolium perenne* and *Dactylis glomerata* (Thompson, Grüner & Gapare, 2003).

Lakes Ōtūroto, Kirihonuhonu and Emily are also part of the Arawai Kākāriki Wetland conservation program overseen by New Zealand's government (Robertson & Suggate, 2011). Ōtūwharekai is the inter-montane basin complex in which these lakes are situated, and the wetlands (including the lakes) and the braided Rivers: upper Rangitata and South Ashburton, in this area, are of immense ecological and intrinsic value (Robertson & Suggate, 2011). The nationally important wetlands in this region are an example of an intact inter-montane wetland system that supports a variety of endemic and rare flora and fauna, e.g. *Oligosoma waimatense* scree skink and *Myosotis minutiflora* pygmy forget-me-not (Robertson & Suggate, 2011; Myers et al., 2013). Restoration and conservation efforts in the region have occurred since 2007 (Robertson & Suggate, 2011; Bayer & Meredith, 2020). All lakes, including Lake Ōpōrea, have ecological targets for TN, TP and algal biomass in the Canterbury Land and Water Regional Plan (Environment Canterbury Regional Council, 2017) as well as the National Policy Statement for Freshwater Management. Data from the water quality monitoring that occurs in these lakes is displayed in Figure 2.

**Table 1:** Physical and chemical attributes of each of the four study lakes. TN = Total Nitrogen, TP = Total Phosphorus. These values along with trophic level classification are the five-year average, of median values, from the late spring to early autumn sampling period (December–May). Data sourced from Bayer & Meredith (2020).

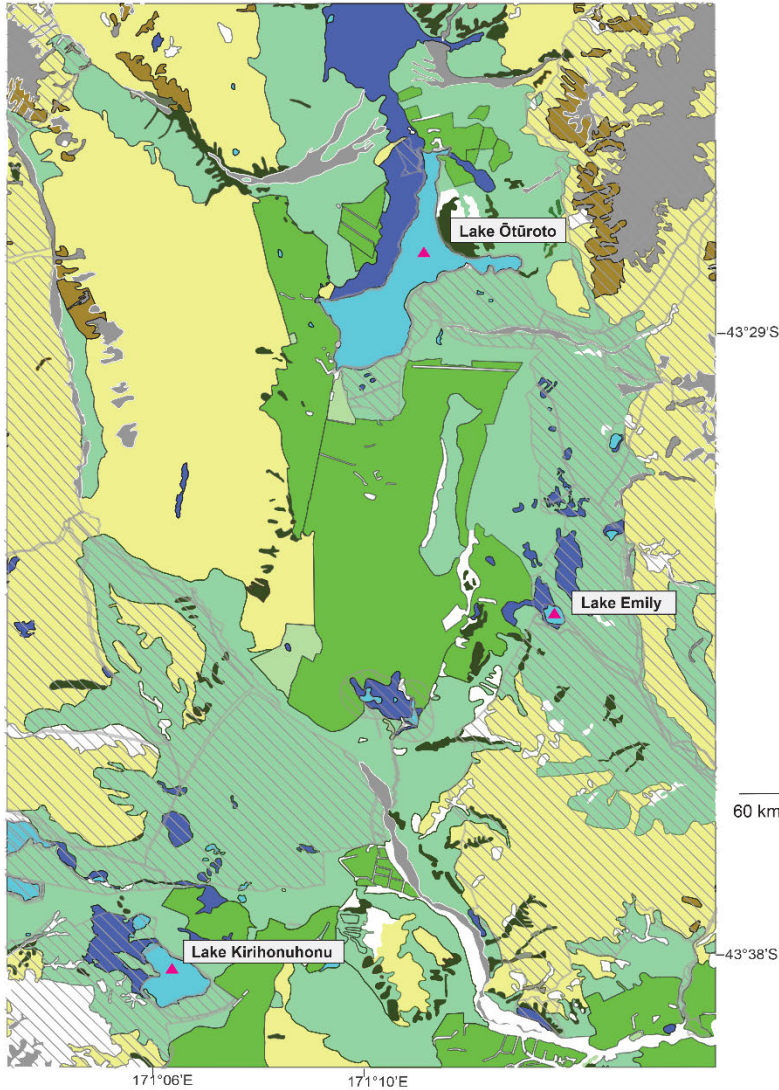
Lake	Ōtūroto (Heron)	Kirihonuhonu (Emma)	Emily	Ōpōrea (Pearson)
Region	Ōtūwharekai			Waimakariri
Location	43°29'16"S, 171° 9' 58"E	43°38'19"S, 171° 6' 23"E	43°33'10"S, 171° 13' 35"E	43°6'10"S, 171°46'41"E
River catchment	Upper Rakaia	Rangitata and Ashburton	Upper Ashburton, Lake Heron Basin	Upper Waimakariri
Max. depth (m)	36	3	2.5	17
Size (ha)	695	167	19	202
Catchment area (ha)**	11, 094	3, 560	241	1, 666
Trophic Level (2015-2019)	Mesotrophic TN: 156 µg/L TP: 5.6 µg/L	Eutrophic TN: 632 µg/L TP: 26.4 µg/L	Eutrophic TN: 430 µg/L TP: 21 µg/L	Mesotrophic TN: 268 µg/L TP: 14.8 µg/L
pH (November 2019)	8.3	9.1	N.A	8.7
Dominant catchment land cover	Non-native high and low productivity grassland	Non-native low productivity grassland, wetland, and swamp	Non-native Low productivity grassland, wetland, and swamp	Non-native low and high productivity grassland, <i>Discaria toumatou</i> scrub.
Conservation	Hakaterere Conservation Park: Sections of each catchment situated in this conservation park (Department of Conservation, 2013). Lake Ōtūroto is a Wildlife refuge*			Moana Rua Wildlife refuge* (Department of Conservation, 2022).

\*Important habitat for wildlife and prevents hunting and motorised boats and aims to minimise disturbance (*sensu* Bayer & Meredith, 2020).

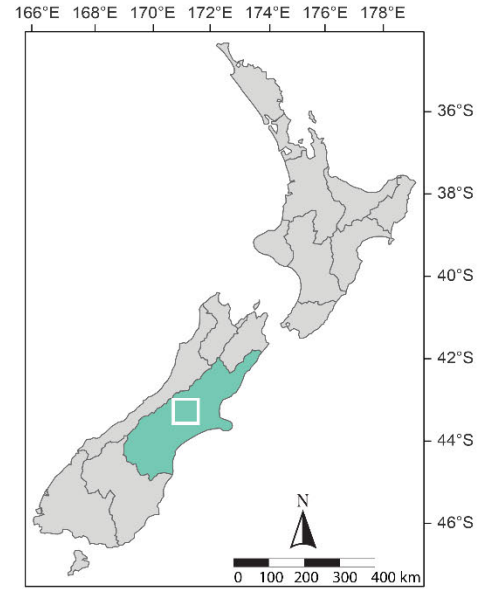
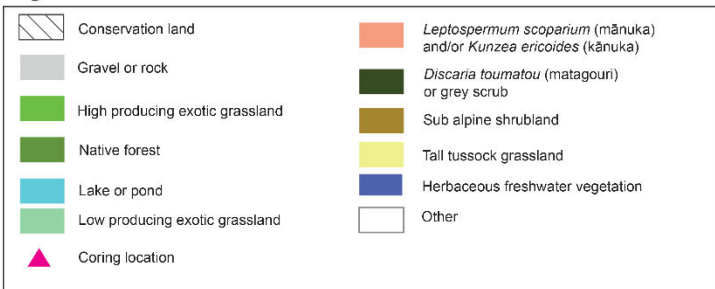
\*\* Data sourced from Kelly, Robertson & Allen (2014) and Kelly, Floerl & Cassanovas (2020).



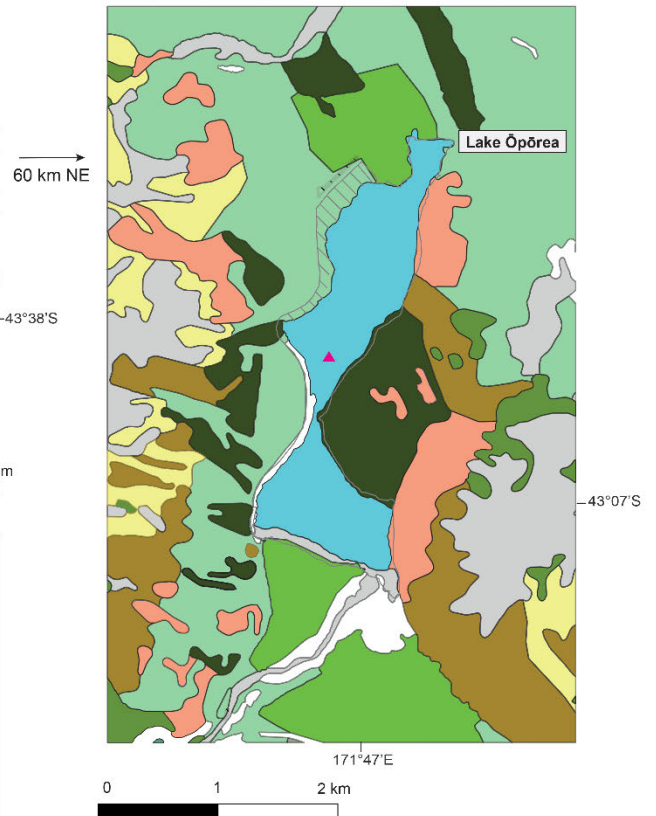
Ōtūwharekai region



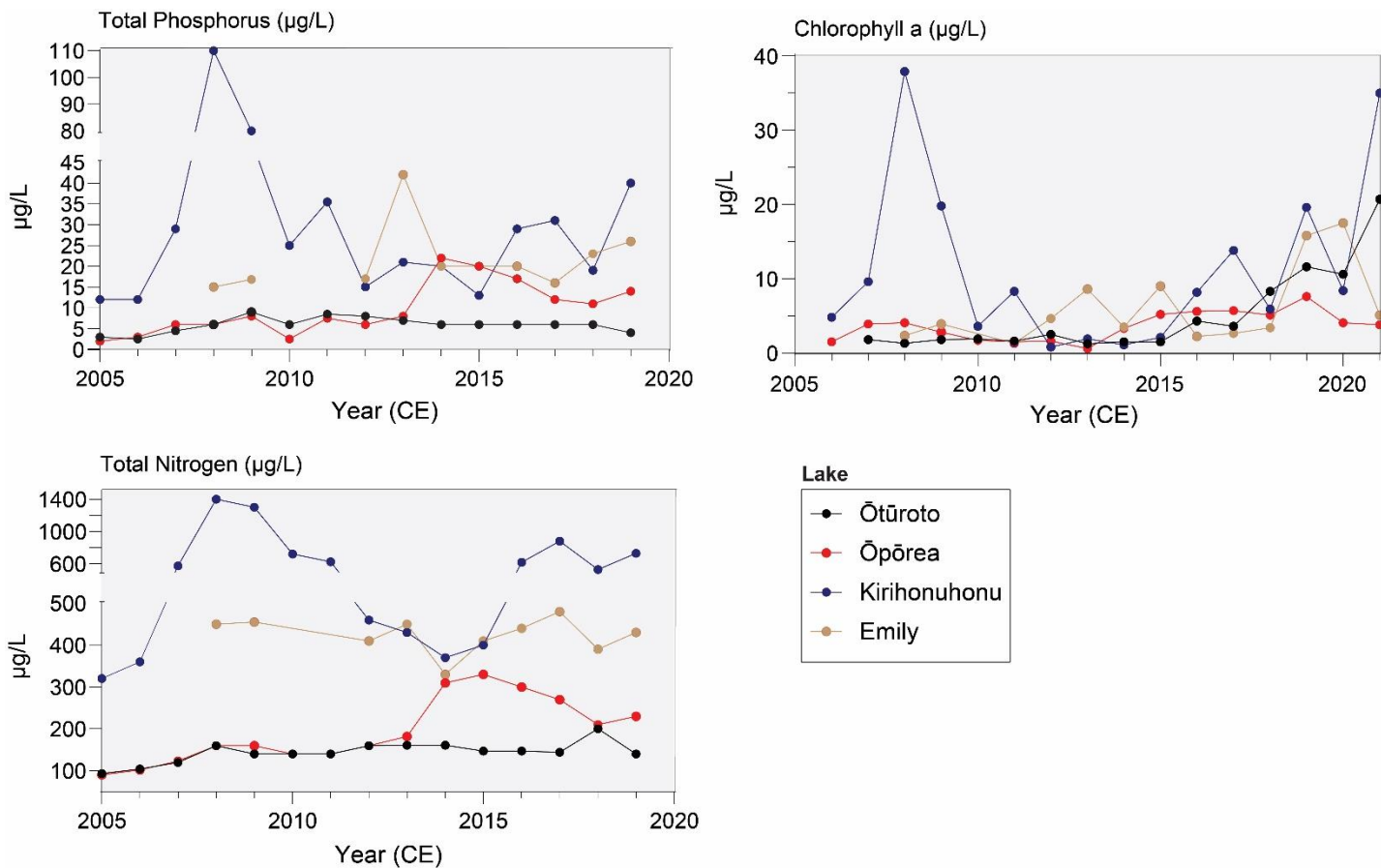
Legend:



Selwyn-Waihora region



**Figure 1:** The location of each lake with its respective land cover. Grey hatching covers areas afforded some conservation protection, which extends to all lake catchments except that for Lake Emily. Data sourced and adapted from: Manaaki Whenua – Landcare Research, New Zealand Land Cover Database Version 5.0 (January 2020) and Department of Conservation. Licenced for re-use under the CC by 4.0 licence.



**Figure 2:** Seasonal (December to March) median nutrient concentrations, and average chlorophyll *a* values from all lake sites. Data sourced from Bayer & Meredith (2020) and Environment Canterbury Regional Council, unpublished data. Note: There are data missing for some years.

## 2.2 Water quality

The methods for water monitoring and data collection for each lake are outlined in Bayer & Meredith (2020).

## 2.3 Sediment core sampling and subsampling

In November 2019, four sediment cores from each of the lakes were extracted (Figure 1) using a UWITEC Gravity corer, with a 95 mm diameter core barrel. Cores were packed with florists' foam to prevent movement of the sediment during transport. The longest core from each lake was split, with one half being used for pollen, diatom and geochemistry analyses and the other used for non-destructive analyses (not included in this study). Samples were analysed from varying depths (Supplementary Table S1–S4). A full description of the sampling resolution and methodology for all proxies is given in Supplementary Information.

## 2.4 Sediment chronology

The chronology for all lakes was established using numerical age constraints derived from a combination of  $^{210}\text{Pb}_{\text{ex}}$  dating, pollen biostratigraphy and  $^{14}\text{C}$  dating combined with Bayesian age-depth modelling. The sampling resolution of the sediment cores varied between lakes and was informed by availability of macrofossils, and the diatom and sediment stratigraphy. The full description of the methods can be found in Chapter 4.

## 2.5 Pollen analysis

Samples were processed following Faegri, Iversen & Giovannini (1989). Pollen was extracted from 0.25 cm<sup>3</sup> sediment taken at a variable sampling interval (Supplementary Table S1–S4), using 10% hot hydrochloric acid, acetolysis and 6- $\mu\text{m}$  sieving. Pollen concentrations were calculated by adding *Lycopodium* tablets (Lund University, Batch numbers: 1031, 140119321, 050220211 and 1031) to each sample. Pollen and spore identifications were made using: Large & Braggins (1991), Pocknall (1981a), Pocknall (1981b), Pocknall (1981c), Moar (1993), and reference collections of New Zealand pollen. Pollen data are presented as the relative frequency of a sum of 150 pollen grains, minimum, and includes the pollen of all dryland plants: trees, shrubs, herbs and *Pteridium esculentum*. *Pteridium esculentum*, is included as a dryland plant as the functional morphology of *P. esculentum*, particularly in a disturbed landscape, is similar to shrubland (McGlone, Wilmshurst & Leach, 2005). Wetland plants and fern spores were not included in the dryland pollen sum but are expressed as a proportion of that sum. Charcoal fragments were counted and presented as concentration per cm<sup>3</sup>.

Periods of each lake's ecological history referred to throughout this study, were assigned using the pollen and charcoal stratigraphy. The first sustained abundance of *Rumex acetosella* or *Pinus* spp., marks the start of European activity in the catchment. These taxa are not native to New Zealand, having been brought by European colonists. Similarly, *Pteridium esculentum*, in conjunction with increases in both Poaceae pollen and charcoal, mark the boundary of the first Māori activity in the Canterbury region.

## 2.6 Diatom analysis

For each sediment core, samples were extracted contiguously for the top 10 cm, and every 2 cm thereafter: Lakes Ōtūroto ( $n = 91$ ), Kirihonuhonu ( $n = 44$ ), Emily ( $n = 70$ ) and Ōpōrea ( $n = 92$ ). Sediment was treated in 15% hydrochloric acid to remove carbonates, and 25% hydrogen peroxide to remove organic matter, both in a water bath at 70°C for 3 hours (Battarbee et al., 2002). Samples were rinsed three times between each step with deionised water. A total of  $300 \pm 10$  valves were counted at x1000 magnification, on a Zeiss Axio A1 microscope, using Differential Imaging Contrast. Additional identification work for *Fragilariaceae* was completed on a Scanning Electron Microscope FEI Quanta 450 FEG, at Adelaide Microscopy. Diatom identifications were made using: Krammer & Lange-Bertalot (1986), Krammer & Lange-Bertalot (1988),

Krammer & Lange-Bertalot (1991a), Krammer & Lange-Bertalot (1991b), Vyverman, et al. (1995), Sonneman et al. (1999), Morales (2001), Knapp, Furey & Lowe (2006), Van de Vijver et al. (2008), Delgado et al. (2015), Reavie & Kireta (2015), John (2018), Rusanov et al. (2018), Wetzel & Ector (2021).

To assess the variability in diatom assemblages over time, a Non-Metric Multidimensional Scaling (NMDS) was calculated for all lakes, for the length of the whole record. The analysis was completed in R package *vegan* 2.6-2 (Oksanen et al., 2022) in R (R Core Team, 2021) on a Bray-Curtis dissimilarity matrix using taxa that occurred in at least  $\geq 2\%$  in three or more samples. Data were square root transformed prior to analysis to reduce the effect of abundant taxa. Taxa separated into morphotypes (e.g. *Punctastriata lancetulla* morphs 1, 2 and 3) were treated as individual taxa in data analysis. *Discostella stelligera*, *D. cf. stelligera*, *D. pseudostelligera* and *D. < 5  $\mu\text{m}$*  were merged as “*Discostella stelligera* complex” for presentation and discussion of data. This is consistent with other studies (Malik, Northington & Saros, 2017; Sivarajah et al., 2019) and reduces some of the uncertainty in identification of species belonging to *Discostella*.

## 2.7 Stable isotope analysis

Bulk organic C and N stable isotope compositions,  $\delta^{13}\text{C}$  and carbon (C) and nitrogen (N) concentrations were analysed from each lake to track past changes in aquatic productivity and organic matter provenance (Meyers & Teranes, 2002; Leng & Marshall, 2004). The resolution and number of samples varied between each lake (Supplementary Tables S1–S4).

The samples from Lake Ōtūroto ( $n = 47$ ) were measured at the Stanford University Stable Isotope Lab using a Thermo Delta V Advantage isotope ratio mass spectrometer coupled to a Thermo FlashSmart Elemental Analyzer via a ConFlo IV. Approximately 8 mg of freeze-dried, homogenised sediment was weighed into silver capsules and acidified *in situ* with 6% sulfurous acid to remove carbonate phases (Verardo, Froelick & McIntyre, 1990). An identical set of samples were weighed into tin capsules to measure the  $\delta^{15}\text{N}$  and obtain total carbon concentrations. One standard deviation of replicate pairs ( $n = 5$ ) for C (acidified) and N (unacidified) stable isotopes provide an indication of instrument reproducibility and is 0.04‰ and 0.05‰, respectively. Carbon isotope data are expressed using conventional  $\delta^{13}\text{C}$  notation relative to the PDB standard using USGS-40 as a reference.

Samples from Lakes Ōpōrea ( $n = 36$ ), Kirihonuhonu ( $n = 23$ ) and Emily ( $n = 42$ ) were analysed at the University of Adelaide. Samples were treated with 10% hydrochloric acid for 1 hour to ensure removal of the carbonates, triple rinsed with deionised water, freeze dried, and homogenised before analysis. Samples were combusted on Perkin Elmer 2400 Series II Elemental Analyser to establish elemental (TOC, N) concentration. Following this, samples were weighed using target masses (range 1–18 mg) reflecting the amount of TOC in each sample to optimise C mass for isotope analyses.  $\delta^{13}\text{C}_{\text{org}}$  values were measured on the carbonate-free sample aliquots

utilising a Nu Horizon IRMS coupled with an EuroVector EuroEA elemental analyser at the Mawson Analytical Spectrometry Services laboratories at the University of Adelaide. Data are expressed in the conventional  $\delta^{13}\text{C}$  notations relative to the PDB standard. Standardisation was based on in-house glycine ( $\delta^{13}\text{C}$ :  $-31.2\text{‰}$ ), glutamic acid ( $\delta^{13}\text{C}$ :  $-16.7\text{‰}$ ), and triphenylamine ( $\delta^{13}\text{C}$ :  $-29.2\text{‰}$ ) standards which have been calibrated against international standards (USGS40 & USGS41). Long-term precision is  $<0.2\text{‰}$  and replicates of individual samples generally lie within  $0.3\text{‰}$ . C/N ratios are presented as atomic weight following Meyers & Teranes (2002).

In all lakes,  $\delta^{13}\text{C}$  values were corrected for the Suess effect, using the formula from Verburg (2007) for sediment samples since  $\sim 1850$  CE. The Suess effect is the changing ratio of  $\delta^{13}\text{C}$  to  $^{12}\text{C}$  levels in the atmosphere, due to a depletion of atmospheric  $\delta^{13}\text{C}$  due from anthropogenic activity, and subsequently it affects the  $\delta^{13}\text{C}$  signal of sedimentary organic matter (Schelske & Hodell, 1995; Verburg, 2007).

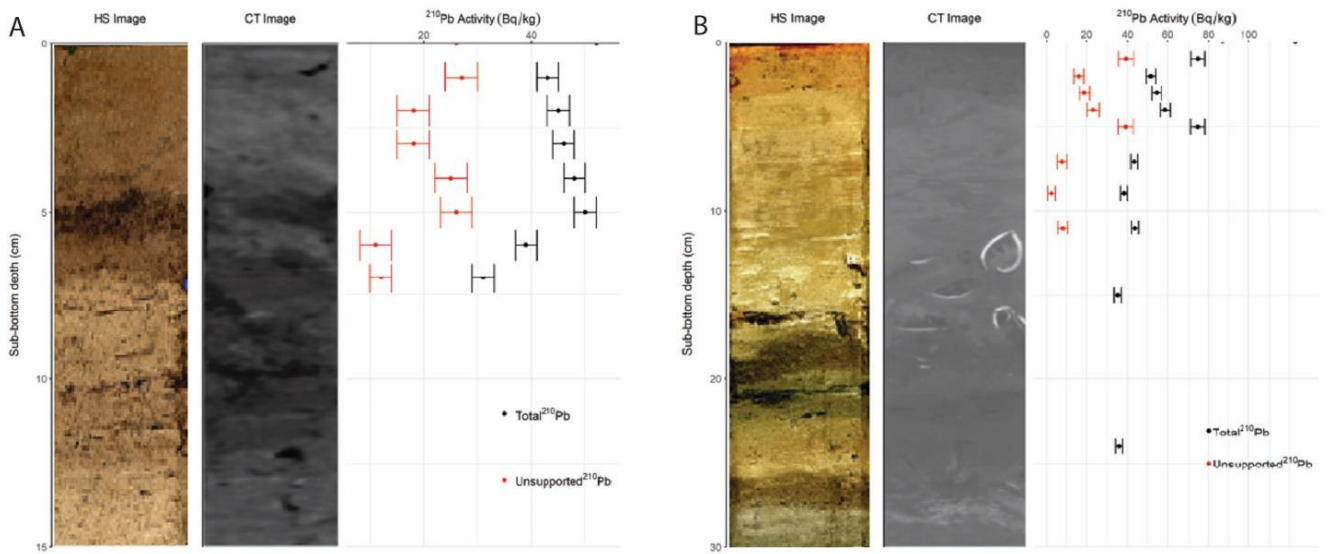
### 3 Results

The discussion of the results covering the pre-human period, and the period following evidence of first Māori settlement, of each lake record is found in Chapter 4. This chapter discusses the results for the chronology, pollen, diatoms and sediment geochemistry, for the post-European period.

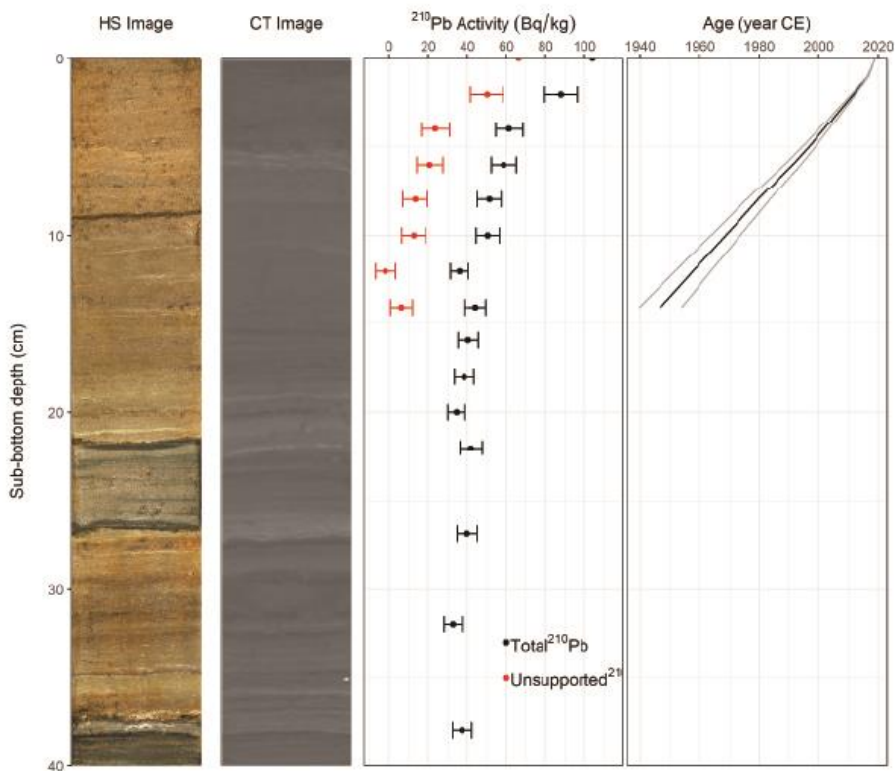
#### 3.1 Chronology

Results of the chronology for each lake, referring to the time before the start of European activity, including the  $^{14}\text{C}$  dates and use of integrated chronology between the sites, are discussed in detail in Chapter 4. The results herein discuss the chronology derived from  $^{210}\text{Pb}$  methods.

*Unsupported  $^{210}\text{Pb}$  age models:* The analysis of unsupported  $^{210}\text{Pb}$  provided mixed results for the four lakes. Non-monotonic downcore trends in unsupported  $^{210}\text{Pb}$  in Lakes Kirihonuhonu and Ōpōrea precluded accurate age-depth modelling and so no  $^{210}\text{Pb}$  derived age-depth models were produced for these cores. The unsupported  $^{210}\text{Pb}$  profiles appear to have been disturbed by sediment mixing caused by bioturbation, which can be observed as convoluted or homogenised bedding in the CT tomography (Figure 3). Bioturbation may be associated with burrowing by organisms, such as freshwater mussels (*Echyridella menziesi*; kākahi), the remains of which are present in the cores (Figure 3). There was no evidence of bioturbation in Lakes Ōtūroto and Emily, and unsupported  $^{210}\text{Pb}$  profiles exhibited more monotonic downcore trends (Figures 4 and 5). Unsupported  $^{210}\text{Pb}$  derived age-depth models from these lakes agreed well with independent age constraint from the invasive diatom *Lindavia intermedia* in the case of Lake Ōtūroto, and the first occurrence of *Rumex* spp. when age-depth model derived sedimentation rates were extrapolated to the relevant depth in each core. The age of first European activity at 95% Highest Probability Density Function (HPDF) range is listed in Table 2. The median age is referred to throughout while acknowledging the earliest part of the 95% HPDF range is too young for European arrival in Lake Emily.



**Figure 3:** Core image, sagittal slice through CT tomography, and total and unsupported  $^{210}\text{Pb}$  from Lakes Kirihonuhonu (a) and Ōpōrea (b). The remains of *Echrydella menziesi* (kākahi) are evident in Lake Ōpōrea (b).



**Figure 4:** Core image, sagittal slice through CT tomography, total and unsupported  $^{210}\text{Pb}$ , and the CRS derived age-depth model for Lake Ōtūroto.



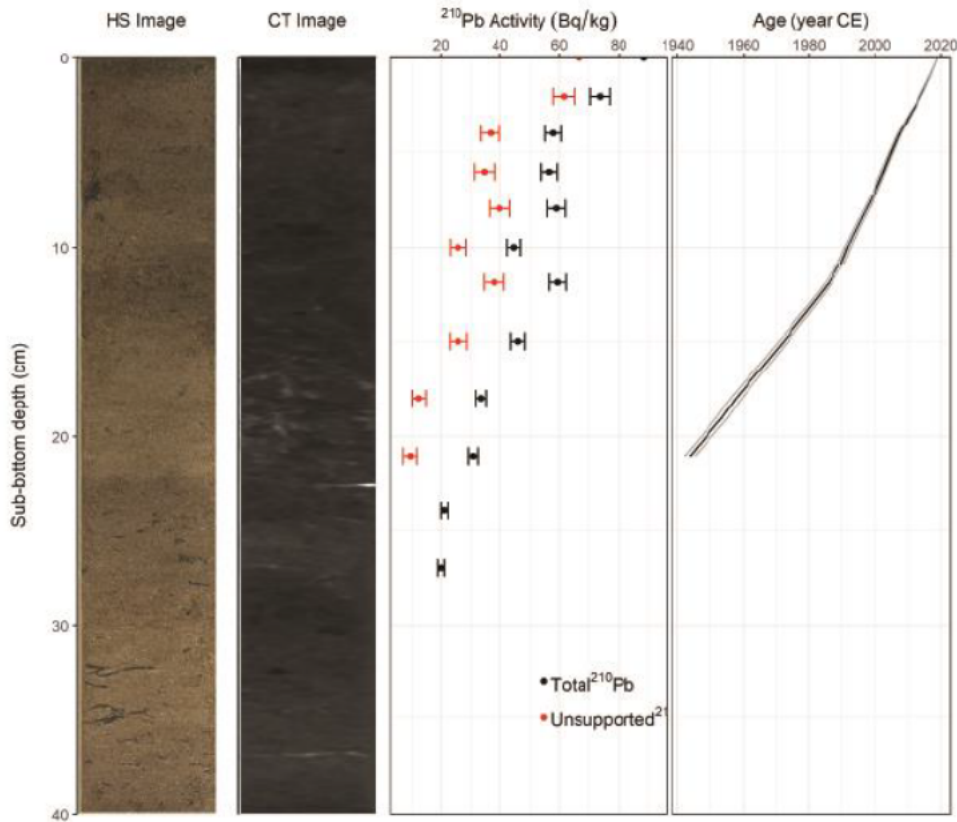


Figure 5: Core image, sagittal slice through CT tomography, total and unsupported  $^{210}\text{Pb}$  and CRS derived age-depth model for Lake Emily.

Table 2: The range of possible dates for the start of European activity (informed by *Rumex acetosella* or *Pinus* spp.) at 95% HPDF, and their corresponding depth.

Lake	Depth (cm)	Pollen stratigraphy	Start of European activity (Years CE) at 95% HPDF
Ōtūroto	23	<i>Rumex acetosella</i>	1857–1862
Kirihonhonu	7	<i>Rumex acetosella</i>	1850–1865
Emily	73	<i>Pinus</i> spp.	1712–1860
Ōpōrea	19	<i>Rumex acetosella</i>	1857–1862

### 3.2 Water quality

Monitoring of water quality has occurred since 2005 in Lakes Ōtūroto, Kirihonuhonu and Ōpōrea and from 2008 in Lake Emily. The TN and TP values have had a fluctuating increase over their monitored period in all four lakes (Bayer & Meredith, 2020) (Figure 2). To compare the values from the start of monitoring, the 5-year average of monitoring data was used to account for the longer term trend. Therefore, using the 5-year average

to 2019, Lake Ōtūroto seasonal median TN increased from 93 µg/L (2005) to 156 µg/L (2019) while TP increased from 3 µg/L to 5.6 µg/L (2019). In Lake Kirihonuhonu, the seasonal median TN increased from 320 µg/L (2005) to 632 µg/L (2019), while TP increased from 12 µg/L to 26 µg/L (2019). TN decreased from 450 µg/L (2008) to 430 µg/L (2019) in Lake Emily, although TP increased over the same period from 15 µg/L to 21 µg/L (2019). Lake Ōpōrea median TN increased from 90 µg/L (2005) to 268 µg/L (2019) while TP increased from 2 µg/L to 15 µg/L (2019) in the same period. Using the Mann-Kendall trend test, these trends were significant (Bayer & Meredith, 2020).

### 3.3 Pollen

**Ōtūroto, Kirihonuhonu and Emily:** *Rumex acetosella* was the first non-native taxon to be found in the sediment cores from Lakes Ōtūroto and Kirihonuhonu and it was introduced in approximately c. 1857 CE when the region was used for pastoral leases (Acland, 1946) (Figure 6, 7). *Pinus* spp. was the first non-native taxon found in the Lake Emily sediments. *Pinus* spp. were introduced when it became widely planted in the 1870s (Beattie & Star, 2010). Poaceae increases in abundance in the record from the ~1850s while other native taxa, e.g. *Prumnopitys taxifolia* (mataī), *Dacrydium cupressinum* (rimu), and *Phyllocladus* spp. were either present in small amounts or continue to decline. Finally, there is some charcoal in the early stage of the record for Lake Kirihonuhonu.

The wetland and aquatic pollen (as a proxy for macrophyte abundance) found in the records from Lakes Kirihonuhonu and Emily are presented as a sum of their habitat (Figure 7); however, the dominant species for each lake are *Myriophyllum* spp., *Isoetes* spp., *Typha* spp. and Cyperaceae in Lake Kirihonuhonu and *Isoetes* spp. and *Myriophyllum* spp. in Lake Emily (Supplementary Figures S3 and S4). In both lake records the abundances of aquatic taxa experience a decline, relative to the Māori period, especially in Lake Emily. The decline occurs immediately following the start of European activity (1860 CE–1880 CE). Conversely, the wetland taxa slightly increase, especially in Lake Kirihonuhonu following the first sign of European activity after c. 1857 CE.

**Ōpōrea:** *Rumex acetosella* appears in the record in approximately 1857 CE (Acland, 1946). Its occurrence aligns with an increase in charcoal which only starts to decline in the 1980s (Figure 6). *Fuscospora* spp., *Dacrydium cupressinum* and *Prumnopitys taxifolia* remain stable, while over time Poaceae steadily increases.

### 3.4 Diatoms

The NMDS of all phases of human activity in the four lakes reveal distinct diatom assemblages in each period (stress levels < 0.15) (Figure 8). The stress levels were lower than the general threshold of acceptance (0.2) and indicate the NMDS ordination results are suitable for interpretation (Clarke, 1993; Dexter, Rollwagen-Bollens & Bollens, 2018).



**Ōtūroto:** From approximately 1860 CE, the diatom record is dominated by planktonic *Discostella stelligera* comp. (Figure 6). The rest of the record is characterised by species primarily belonging to genera *Staurosira* and *Pseudostaurosira*. In the most recent sediments, since the 1990s, *Discostella stelligera* comp. noticeably declines and is replaced with a diversity of planktonic taxa: *Aulacoseira ambigua*, *Asterionella formosa* and *Lindavia intermedia*. There is also a small proportion of *Staurosira*.

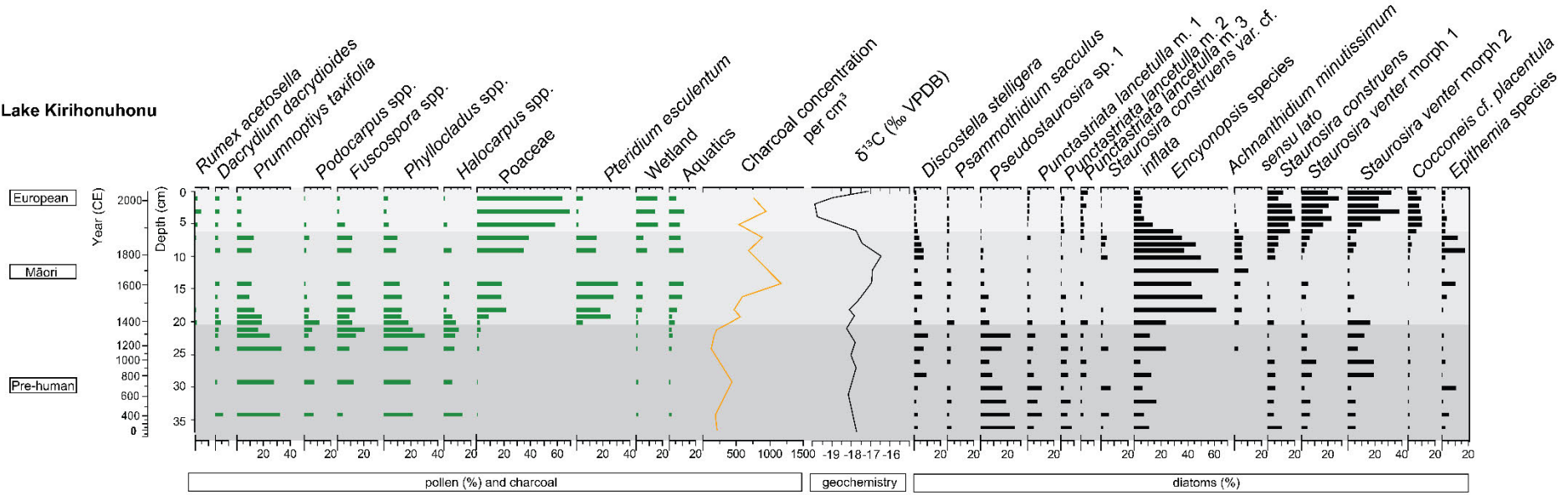
**Kirihonuhonu:** *Encyonopsis krammeri* and *E. subminuta*, decrease in abundance (when compared to their abundance before European activity, with *Staurosira venter morphs 1* and *2*, *Staurosira construens*, and epiphytic *Cocconeis cf. placentula* becoming the dominant taxa (Figure 7) from approximately 1857 CE–1890 CE onwards. Also present are small assemblages of *Discostella stelligera* and Fragilareaceae.

**Emily:** *Discostella stelligera* comp. was the dominant planktonic taxon and from approximately 1860–1880 CE onwards it increased while in same period, *Punctastriata* sp. 1 and *Staurosira* species both declined. There was also the presence of some *Aulacoseira* and *Encyonopsis* species. The rest of the diatom assemblage comprised dominant taxa belonging to Fragilareaceae: *Punctastriata* sp. 1 and *Staurosira* species (*S. construens*, *S. cf. construens var. pumila*). Since approximately 1990 CE *Punctastriata* sp. 1 and *Staurosira* have increased, along with *Cocconeis cf. placentula*, while *Discostella stelligera* comp. has declined (Figure 7).

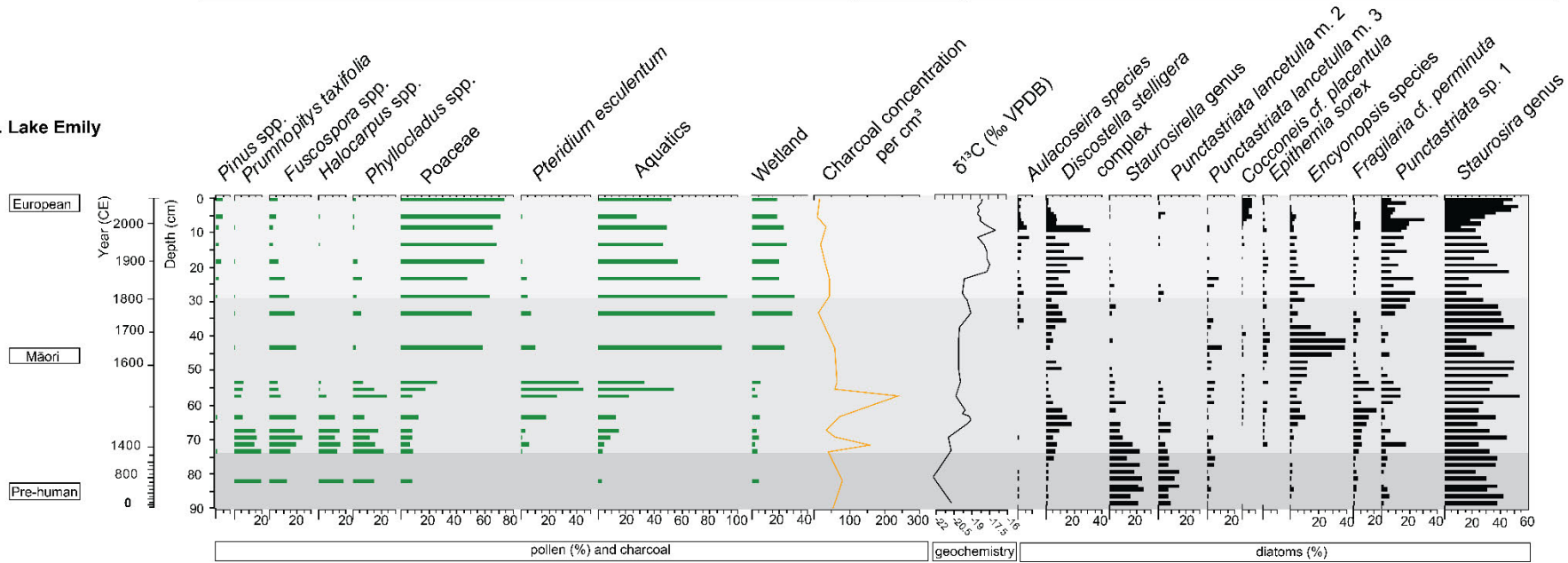
**Ōpōrea:** The diatom record of Lake Ōpōrea does not markedly shift after European activities commence in the catchment. *Discostella stelligera* comp. is still the dominant taxon throughout the European period (Figure 6). In the upper most sediments since approximately 2005 CE there are the appearances of other diatom taxa, in smaller abundance: *Epithemia sorex*, *Encyonopsis krammeri*, *Achnanthydium minutissimum* and *Distrionella incognita*.



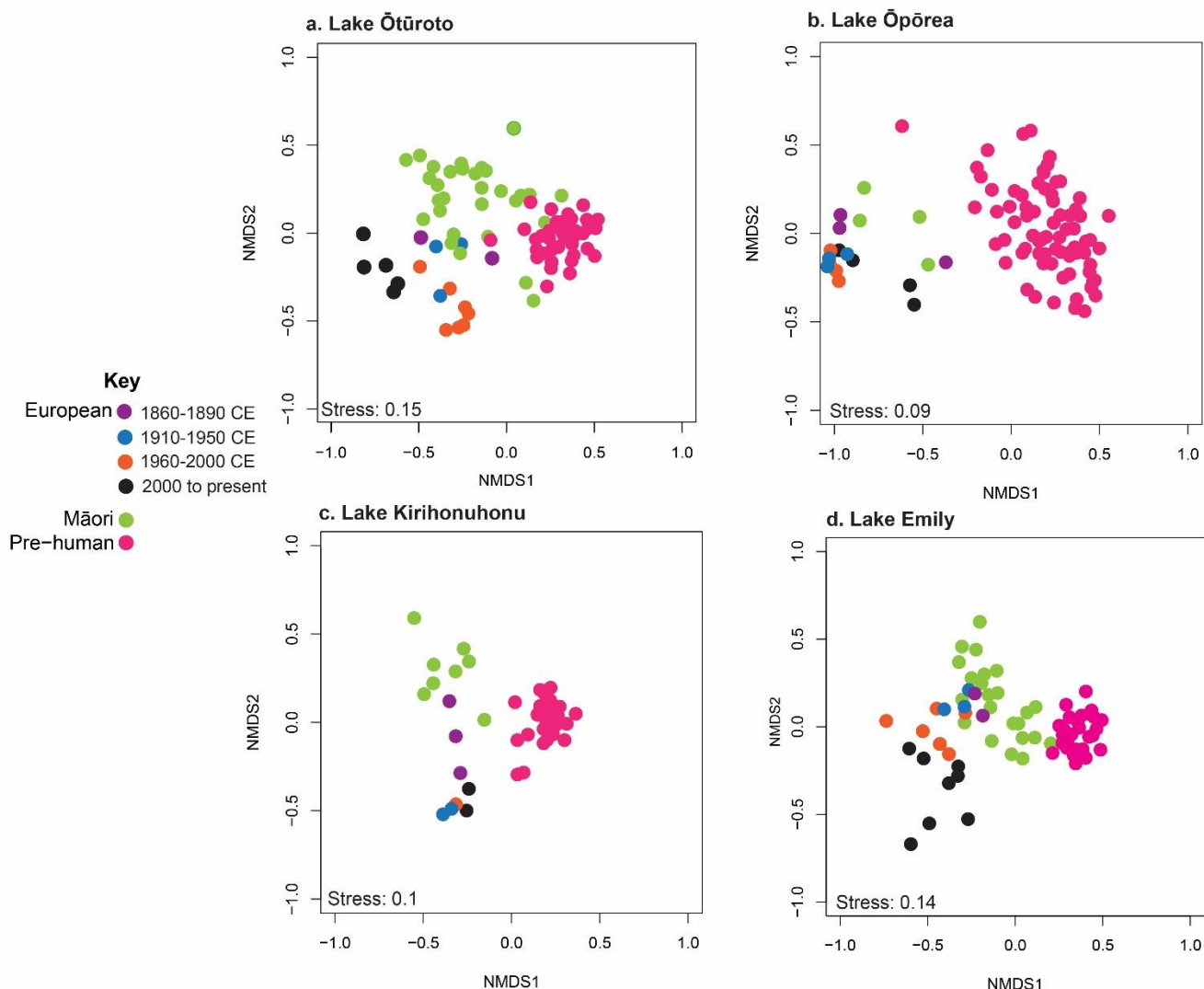
a. Lake Kiriuhonuhonu



b. Lake Emily



**Figure 7:** Pollen, charcoal, isotope and diatom data from (a) Lake Kiriuhonuhonu and (b) Lake Emily. Only key pollen and diatom taxa are shown.  $\delta^{13}\text{C}$  is expressed as parts per million Vienna Pee Dee Belemnite (VPDB). The shading corresponds with the different occupation phases of each lake's catchment, listed on the left.



**Figure 8:** NMDS of diatoms assemblages from the four study lakes. Each sample is colour coded according to the occupation phase of the catchment. The samples since the start of European activity, have been colour coded to according to specific time periods since the ~1850s. These time periods were selected using the age of each sample, however there are gaps in the range due to the low resolution of the sediments.

### 3.5 Sediment geochemistry

Following the commencement of European activity in the region,  $\delta^{13}\text{C}$  values declined in all lakes while C:N values were mostly stable. The C:N ratio in all lakes is generally  $\leq 12$  (Supplementary Figure S9), except for occasional higher values in Lake Ōpōrea, and therefore  $\delta^{13}\text{C}$  is interpreted as a signal of aquatic productivity (opposed to allochthonous terrestrial material), from both the algal and submerged macrophyte communities (Heyng et al., 2012; Anderson et al., 2018; Evans et al., 2021). In Lake Ōtūroto before human activity,  $\delta^{13}\text{C}$  was largely stable. Following an increase in  $\delta^{13}\text{C}$  after catchment clearance from approximately 1400 CE,  $\delta^{13}\text{C}$  declined in approximately 1860 CE.  $\delta^{13}\text{C}$  values, however, remained higher relative to the pre-human section of the record (Figure 6). In Lake

Ōpōrea before any human activity in the catchment, values fluctuated in both variables (Figure 6, Supplementary Figure S2). The greatest shift in  $\delta^{13}\text{C}$  occurred in 1580 CE with a peak  $\delta^{13}\text{C}$  of -23.6, as the lake became more enriched (Figure 6). Up to the present day,  $\delta^{13}\text{C}$  has declined but remains more enriched relative to the pre-human section of the record.

For Lake Kirihonuhonu, both variables were relatively stable, with only minor fluctuations, although C:N does gradually decline throughout the entirety of the record towards  $< 10$  at present (Figure 7, Supplementary Figure S3).  $\delta^{13}\text{C}$  started to increase in approximately 1400 CE but by the time of European activity commenced, had already started declining.  $\delta^{13}\text{C}$  has only increased in the uppermost sample from the early 2000s. In Lake Emily, C:N and  $\delta^{13}\text{C}$  historically fluctuated, but C:N declined towards the present day when values are 10–11 (Figure 7, Supplementary Figure S4). After peaking in approximately 1990 CE,  $\delta^{13}\text{C}$  values gradually decline towards the present.

## 4 Discussion

### 4.1 Summary of the key results

Lakes Ōtūroto, Kirihonuhonu, Emily and Ōpōrea all experienced further changes in water quality in response to the start of European agricultural activities in the Canterbury region. Multivariate analysis (Figure 8) shows there were distinct diatom assemblages during each of the occupation phases (pre-human, Māori and European) of each lake, identifying the legacy of anthropogenic influences on these lakes. The changes recorded in the Canterbury lakes are on a similar scale to other freshwater systems in the Southern Hemisphere where the effects of European colonisation, and subsequent land use practices, are well documented through palaeo-ecological studies (e.g. Haberle et al., 2006; Velez et al., 2021; Long et al., 2021). In these other studies, colonists' agricultural and industrial activities resulted in significant shifts in water quality, and ecology, of both lacustrine and riverine systems. For the four lakes in this study, while substantial changes in water quality also occurred, different rates of change were observed among the lakes. The main difference between each lake, was the timing of the changes in water quality, the point in the sediment record at which the nutrient level classification (using Burns, Rutherford & Clayton, 1999) were inferred to have increased as a direct result of European activities in the catchments.

The diatom assemblage data and multivariate analyses indicate that the deep Lakes Ōtūroto and Ōpōrea were resilient to early European activity, and only recorded a sustained deterioration in water quality from the 1990s and early 2000s. In contrast, within decades of first European activity, Lakes Kirihonuhonu and Emily experienced rapid changes in water quality. The rapidity of their response was, to a degree, expected given the sensitivity of shallow lakes to activities in their catchments (*sensu* Scheffer & van Nes, 2007). However, the trend in the diatom assemblages (e.g. gradual increasing

dominance of *Staurosira* taxa in both lakes) and multivariate analyses imply that initial response to European activities was not the sole cause of their current eutrophic state, but rather these lakes were continuing on a trajectory of sustained nutrient enrichment that had started prior to the first European activity in the region. It is necessary to acknowledge, however, the diatom assemblage data do not directly reflect the ecological changes associated with introduced and invasive fauna and flora.

In all four lakes, changes in water quality pre-date the start of monitoring. The monitoring data, however, are useful in providing an indication of the dominant trends in nutrient concentrations and show an upward trajectory in both TN and TP in all lakes over the last 15 years. Furthermore, using the trophic level classification from Burns, Rutherford & Clayton (1999), the monitoring data indicate the lakes are shifting into different nutrient classes, i.e. from oligotrophic to mesotrophic and eutrophic. The diatom assemblages in all lakes corroborate the 15 years of monitoring data with the present taxa indicative TN enrichment in Lakes Ōtūroto and Ōpōrea, and excessive eutrophication in Lakes Kirihonuhonu and Emily.

#### 4.2 Catchment vegetation change in response to European activity

The pollen records indicate that pastoral activities contributed to the further anthropogenic expansion of grassland (Figures 6, 7). Fire events were recorded in the records of Lakes Kirihonuhonu and Ōpōrea as fire was used to clear the landscape and promote new growth for sheep grazing (Peden, 2006). The species composition of the grasses will have changed, as non-native species were deliberately introduced by Europeans as they were better for sheep grazing (McIntyre, 2007). The pollen record does not allow for full separation of species, due to the difficulty in identifying grass pollen and they are therefore classified under Poaceae. Pollen evidence indicates that native tussock grassland (which comprises *Chionochloa* spp., *Festuca* spp. and *Poa* spp.) reached its maximum extent and was abundant in all catchments before Europeans arrived (Mark & McLennan, 2005) in approximately 1850 CE (Peden, 2006; Star, 2008). Pastoral activity (predominantly sheep farming) started in approximately 1857 CE when pastoral stations were first leased (Acland, 1946; Bayne et al., 2019).

#### 4.3 Lake water quality following European arrival

**Lakes Ōtūroto and Ōpōrea (deep lakes):** *Discostella stelligera* comp. is the primary indicator of water quality in the deeper Lakes Ōtūroto and Ōpōrea. In these lakes, *Discostella stelligera* comp. is an indicator of cultural eutrophication (Chapter 4), which is defined as anthropogenic driven nutrient in these lakes, opposed to eutrophication of the lakes. This is due to its increasing abundance as a response to nutrient enrichment following evidence of first Māori fires in Lake Ōpōrea, and decline as *Aulacoseira ambigua* (a taxon with higher nutrient requirements) was favoured in Lake Ōtūroto.

*Discostella stelligera* comp., later recovered, however, in Lake Ōtūroto, and as such, prior to European activity, the taxon is inferred to be persisting in its ecological niche in both lakes. *Discostella stelligera* comp. continued to dominate in the decades following the start of European farming, meaning that there were seemingly no large changes in water quality. Nutrient enrichment, however, would not necessarily drive a decline in abundance in *Discostella stelligera* comp. as its response to nutrients (N in particular) (Saros & Anderson, 2015), such as those from agricultural practices, and can be prolific. Furthermore, the taxon, is also found in abundance in mesotrophic lakes in the region, meaning there is a range of water quality in these lakes to which it is suited (Chapter 2). Hence, it is difficult to assess the difference in nutrient status between the two occupational phases of each catchment, although  $\delta^{13}\text{C}$  indicated there was little change in aquatic algal productivity. Furthermore, the relationship between nutrients, temperature and light availability (Saros & Anderson, 2015; Malik & Saros, 2016) can result in differing influences on the abundance of the taxon. For example, increasing nutrients cause an opportunistic response in *Discostella stelligera*, when light levels are high (Saros et al., 2014; Malik & Saros, 2016), while similarly, *Discostella stelligera* can favour increasing temperatures, and subsequent shallower mixing depths (Saros et al., 2016). However, the small and unprecedented abundances of other taxa; *Aulacoseira ambigua* and *Asterionella formosa* in Lake Ōtūroto, and *Distrionella incognita*, *Asterionella formosa* and *Achnantheidium minutissimum* in Lake Ōpōrea, suggest some small-scale response to anthropogenic pressures, given the higher nutrient preferences of these taxa (Wolfe, Baron, & Cornett, 2001; Tibby, 2004; Rioual et al., 2007).

The first major sign of major water quality changes in the European period is the decline in abundance of *Discostella stelligera* comp. at approximately 1990 CE in Lake Ōtūroto and 2005 CE in Lake Ōpōrea. This is likely to be the result of a large increase in nutrient concentrations, as a culmination of the trajectory of TN concentrations in these lakes exceeding the optima for *Discostella stelligera* comp. (Chapter 2). This trend in *Discostella stelligera* comp. pre-dates the start of water quality monitoring in Lake Ōtūroto, although possibly coincides with start of monitoring in Lake Ōpōrea. In Lake Ōtūroto, after the decline in *Discostella stelligera* comp. from approximately 1990 CE, taxa suited to N enrichment (*Asterionella formosa*; Wolfe, Van Gorp & Baron, 2003; Saros et al., 2005; Arnett, Saros & Mast, 2012), or P limitation (*Lindavia intermedia*; Interlandi, Kilham & Theriot, 1999; Kilroy et al., 2021; Novis et al., 2017) become prevalent. The monitoring data (Figure 2, Bayer & Meredith, 2020) are generally consistent with the change in diatoms assemblages, which together indicate an increase in TN concentrations. Although there is no obvious shift in planktonic taxa in Lake Ōpōrea, increasing TN is also likely the dominant driver in the decline of *Discostella stelligera* comp. in this lake.

The increasing nitrogen concentration is associated with land use and catchment activities. Lakes Ōtūroto and Ōpōrea's catchments are used for a mixture of farming (low and high producing non-native grassland), conservation and recreational activities such as trout fishing and non-motorised boating. Low intensity pastoral land use, which comprises 20–26%, of the catchments (Kelly, Floerl & Cassanovas, 2020) and sheep grazing can increase nitrogen loadings in New Zealand lakes (Galbraith & Burns, 2007; Weaver et al., 2017). Areas of both catchments (< 10%, Kelly, Floerl & Cassanovas, 2020) have high-producing, non-native grassland which would contribute greater nitrogen (Joy et al., 2022). The remainder of the catchments of both lakes comprise wetland and native shrubland (Figure 1). The increase in TN loading to these lakes is also reflected in trends of nitrogen in New Zealand, which is rising in many freshwater ecosystems (Julian et al., 2017; Snelder, Larned & McDowell, 2018; Abell et al., 2019; Armoudian & Pirsoul, 2020) as a result of increasing application of nitrogen fertilisers (STATS NZ, 2021). It is expected that without appropriate management to halt or reduce nutrient increases, the diatom flora will continue to shift in both lakes to reflect more eutrophic conditions. The monitoring data available indicate that the abundant diatoms in seasonal phytoplankton data are *Lindavia intermedia*, *Fragilaria* spp. (possibly *F. crotonensis*) and *Asterionella formosa*, which are all associated with high TN values (Chapter 2, Table S1 and S2, Environment Canterbury Regional Council, unpublished data). However, to assess the trends in diatom populations, monitoring should also occur in the winter as in comparison to other phytoplankton, few diatoms appeared in the summer monitoring period. In Canterbury and other lakes in New Zealand, diatom concentrations peak in autumn and winter (Hamilton et al., 2010; Bayer, Schallenberg & Burns, 2016). In addition, anthropogenic climate warming will exert its influence, contributing to changing species composition as a result of shallower mixing depths (Bayer, Schallenberg & Burns, 2016). Further investigation of these lakes should also include regular analyses of diatoms and other algae from the littoral zone as a means of anticipating water quality changes throughout the lakes, as littoral areas can be the first to experience changes in lake environments (Rimet, Bouchez & Tapolczai, 2016; Cantonati et al., 2021).

**Lakes Kirihonuhonu and Emily (shallow lakes):** The diatom and isotope records indicate that water quality in both shallow lakes declined long before monitoring began, probably within decades of the commencement of European pastoral activities. Their shallow depth makes them particularly susceptible to changing activity in their catchments (*sensu* Scheffer & Van Nes, 2007) and the diatom assemblages indicate that a change in water quality occurred in the range of 1857 CE–1890 CE (Lake Kirihonuhonu) and 1860 CE–1880 CE (Lake Emily) (Figure 7). The enrichment of Lakes Kirihonuhonu and Emily is likely due to a combination of burning, introduction of sheep grazing and subsequent manure run-off, the increased intensity in land-use and sediment erosion. While the direct cause is



difficult to ascertain, European activity in the region is well documented (e.g. Acland, 1946; Peden, 2006; McIntyre, 2007).

For both lakes, C:N values indicate that sedimentary organic matter is becoming increasingly algal (Supplementary Figure S9). The changes in diatom flora of Lakes Kirihonuhonu and Emily were still indicative of shallow lake environments (Fragilareaceae genera; *Staurosira*, *Pseudostaurosira* and *Punctastriata*), although there were differences in species composition between the two lakes (Figure 7). Species in these genera have broad ecological tolerances and can be abundant in shallow lakes (Bennion, Fluin & Simpson, 2004; Fluin, Tibby & Gell, 2009; Kingsbury, Laird & Cumming, 2012; Edlund et al., 2017; Hobbs et al., 2017). In addition, it is likely that many of the taxa can withstand low light availability, such as that associated with lake eutrophication and suspended sediments, although, they may be suspended in the water column through wind mixing and obtain light in the photic zone (Bachmann, Hoyer & Canfield, 2000; Jones et al., 2014; Giles et al., 2018). Wind-driven suspension of sediments further contributes to internal nutrient cycling, which is thought to be an important feedback mechanism contributing to the current eutrophic conditions in Lake Kirihonuhonu (Waters et al., 2020). It is likely that similar processes operate in Lake Emily, due to its size, position in the landscape and the lack of sheltering vegetation.

Following the initial changes to water quality (after the commencement of European activity), Lake Kirihonuhonu diatom assemblages remain stable (Figure 6), despite the increasing nutrient concentrations in recent years and its current eutrophic-supertrophic classification (Figure 2, Bayer & Meredith, 2020). The stability of the diatom assemblages is particularly important and suggests these taxa (*Staurosira construens* and *Staurosira venter* morph 1 and 2) can withstand constant eutrophic, low-light conditions, that exclude other species (*Encyonopsis* spp.). This follows a general pattern where the availability of light decreases as nutrient concentrations increase (Vadeboncoeur et al., 2003; Liboriussen & Jeppesen, 2006). There was a decline in  $\delta^{13}\text{C}$  which started prior to the commencement of European activity in Lake Kirihonuhonu, however in recent sediments,  $\delta^{13}\text{C}$  had been corrected for the Suess effect (Verburg, 2007). The decline in values possibly indicates  $\delta^{13}\text{C}$  depletion caused by methanotrophic bacteria (e.g. Hollander & Smith, 2001; Hofmann et al., 2021) driven by eutrophication-induced anoxia (*sensu* Jenny et al., 2018). Methanotrophic bacteria interfere with  $\delta^{13}\text{C}$  of the DIC reservoir in lakes and can deplete the isotopic signal in the sediment (Hollander & Smith, 2001; Heyng et al., 2012). Periods of anoxia occur in Lake Kirihonuhonu (Waters et al., 2018), but due to its shallowness, only for short periods.

In Lake Emily, *Discostella stelligera* comp. initially increased after the European activities, which is unusual in shallow lakes as they do not often support large proportions of planktonic species (Hall &

Smol, 2010). Another large change in water quality, occurred again in the early 1990s, following a peak in the *Discostella stelligera* comp. and the start of the depletion in  $\delta^{13}\text{C}$ , similar to Lake Kirihonuhonu. The depletion of  $\delta^{13}\text{C}$  is possibly driven by the same mechanism as Lake Kirihonuhonu, although it is uncertain whether Lake Emily experiences temporary periods of anoxia. Interestingly the timing of the decline in *Discostella stelligera* comp. coincides with the decline of the same taxon in Lake Ōtūroto. However, since the early 2000s Lake Emily's sedimentary record has high abundances of *Staurosira* species. This has also been documented in a lowland, hypertrophic lake on the North Island (Short et al., 2022). The sequential stages of changing water quality in Lake Emily indicate continual response to nutrient loading while the increasing abundance of benthic Fragilariaceae are consistent with their inferred ability to withstand low-light environments. Indeed, it is possible these taxa (benthic Fragilariaceae, *Staurosira*) will be found in other New Zealand lakes, especially eutrophic-hypertrophic shallow lakes.

Lastly, the macrophyte populations for Lakes Kirihonuhonu and Emily are an important component of their ecological status and management, as shallow lakes usually support a healthy macrophyte population (*sensu* Jeppesen et al., 2014). Lake Kirihonuhonu has experienced both extensive recruitment and loss of macrophytes (Schallenberg & Sorrell, 2009; Bayer & Meredith, 2020) in recent years. The recruitment of macrophytes was used as an example of a regime shift (Schallenberg & Sorrell, 2009), and is unique when compared to other lakes in New Zealand where regime shifts are usually characterised by macrophyte loss (Schallenberg & Sorrell 2009). The fluctuations in macrophytes for Lake Kirihonuhonu, is possibly captured in the uppermost decline of aquatic pollen (Figure 7). Lake Emily has also experienced a decline in aquatic pollen throughout the whole European period, but there has been no documented loss of macrophyte beds (Figure 7). In theory, epiphytic diatom taxa should assist with the interpretation of historic macrophyte cover. However, they provide conflicting evidence in these lakes. There is an unprecedented increase of *Cocconeis cf. placentula*, an epiphytic taxon, in these shallow lakes, even as aquatic pollen is declining. This is likely due to its broad ecological tolerance to nutrient concentrations (Jahn, Kusber & Romero, 2009; Rojas & Hassan, 2017). In New Zealand, it is also found to withstand a wide range of nutrient conditions (Kilroy et al., 2017). Despite its appearance, however, the abundance of *Cocconeis cf. placentula* is markedly lower in comparison to other epiphytic taxa belonging to *Encyonopsis* and *Staurosira*. Species in these genera were not only found growing in these lakes on submerged macrophytes and attached periphyton (Chapter 2, Figure 3,) but also appeared to have rapidly proliferated following wetland expansion (*Isoetes* spp., *Myriophyllum* spp. and Cyperaceae) as a result of first Māori activity (Chapter 4, Figure 6). It is clear, then, that both the diatom assemblage and macrophyte communities of Lakes

Kirihonuhonu and Emily have been subject to the cumulative effects of declining water quality, and the epiphytic diatom taxa reflect higher nutrient concentrations.

#### 4.4 The magnitude of changing lake ecology and future management considerations

The diatom assemblages in all four lakes shifted considerably in response to European pastoral activities in their catchments. Lakes Kirihonuhonu and Emily changed in the first few decades, while the main water quality change in Lakes Ōtūroto and Ōpōrea occurred from the mid-late 20<sup>th</sup> century (approximately 100–130 years later). Given the relationship between nutrient load and lake volume, deeper lakes can withstand a degree of perturbation as greater water volume increases their ability to absorb increases in nutrient loads (*sensu* Carpenter & Cottingham, 1997) whereas shallow lakes are more susceptible to nutrient enrichment (Scheffer & Van Nes, 2007). Therefore, the later response of the deeper lakes was probably a combination of cumulative anthropogenic pressure combined with greater use of fertilisers (StatsNZ, 2021). This later response in Lakes Ōtūroto and Ōpōrea matches global trends of freshwater degradation as the 1950s and onwards was a period of increasing intensity of agricultural inputs and subsequent environmental degradation (Huang et al., 2022). The sequence and timing of changes in water quality in the European period contrast with the shifts that transpired after the first evidence of Māori activity, where the lakes responded synchronously (Chapter 4). It appears that the most significant change in water quality, using diatom assemblages and a changepoint analysis, occurred following Māori arrival in the landscape (Figure 8, Chapter 4). The four lakes did not respond synchronously, and this is likely to be a result of the difference in resilience of each lake to withstand continual perturbations (*sensu* Holling, 1973; Carpenter et al., 2022).

This study highlights how the water quality in a suite of Canterbury lakes has changed in response to nutrient enrichment, in both the recent decades and immediately following the start of pastoral activities. Lakes Ōtūroto and Ōpōrea are currently mesotrophic while Lakes Kirihonuhonu and Emily are eutrophic. One of the main foci of this study was to examine the current use, and legacy, of agriculture and its effects on these lakes. Part of each lake's catchment is conservation estate managed by the Department of Conservation (Figure 1), and so, for example, in Lake Kirihonuhonu, areas of pastoral land were converted to conservation estate in 2000 CE (Robertson & Suggate, 2011; Bayer & Meredith, 2020). While parts of the catchment of the Ōtūwharekai lakes are conservation estate, farming still occurs in other areas and consequently, the nutrient loads of the lakes continue to exceed the limit outlined in regional water plans (Kelly, Floerl & Cassanovas, 2020) as well as national policy guidelines. The diatom assemblages reflect these nutrient loads. All lakes require a reduction in catchment loads of TN: 'low' (< 33%, Lake Ōtūroto, Lake Emily), 'moderate' (33–66%, Lake Ōpōrea) and 'high' (67–99%, Lake Kirihonuhonu) to meet the objectives in the Canterbury Land and

Water Regional Plan (Environment Canterbury Regional Council, 2017; Kelly, Floerl & Cassanovas, 2020). The same is required for TP in Lake Kirihonuhonu (high, 67–99%), and Lakes Emily and Ōpōrea (moderate, 33–66%). These required reductions in nutrient concentrations, exist irrespective of catchment size, given the substantial size differences between each lake (Table 1), and it is likely that land use activity is the dominant control of the nutrient loads. Furthermore, given the recent increasing trends in TN, TP and algal biomass (Figure 2, Bayer & Meredith, 2020) in Lake Ōtūroto and the trajectory of other lakes in the region, higher targets for nutrient reductions (currently < 33% for TN) (Kelly, Floerl & Cassanovas, 2020) may be needed for Lake Ōtūroto. While nutrient concentrations of these lakes increased following Māori arrival with the greatest change of the past, continuing agricultural activities in the region are driving these lakes to a nutrient state (mesotrophic to supertrophic) that is undesirable for these systems. The diatom stratigraphy of these lakes show this to be a gradual process which commenced 30–50 years ago in the deeper lakes but occurred more rapidly, at least 150 years ago, in the shallow lakes, meaning it is not a recent occurrence. It is obvious that nutrient concentrations have been rising for a long time, and that anthropogenic activities have influenced these systems.

The management of the lakes in this region, including current and historic nutrient loading can be facilitated by considering the landscape–lake connection; that is, the lakes and the surrounding landscape are inextricably linked. Current ecological theories address the inherent hydrological connectivity that exists between freshwater systems – lakes, rivers, streams, and wetlands, in a landscape, and the connection between freshwater and the surrounding terrestrial environment (Soranno et al., 2010; Heino et al., 2021). Hence, a lake and its catchment do not function, and should not be managed, in isolation, but rather as an entire system (Soininen et al., 2015; Fergus et al., 2017; Paerl et al., 2018). In the Canterbury region, particularly the Ōtūwharekai lakes, historic glaciation of the landscape created many of the interconnected freshwater features. Most lakes in the region drain into the Ashburton or Rakaia rivers, but are fed by small streams, wetlands and kettle lakes that traverse the landscape (Environment Canterbury Regional Council, 2017, Figure 1). Hence, activities beyond the boundaries of these catchments, given the variety of different land uses (Figure 1) will influence nutrient concentrations (*sensu* Wadworth-Watts et al., 2014) within the catchments. For example, there are areas which are classified as conservation land, but are adjacent to agricultural areas, such as the catchments of Lake Ōtūroto and Lake Kirihonuhonu.

## 5 Conclusion

The Canterbury region of New Zealand has experienced significant changes in the both the landscape and its uses since c. 1400 CE, which have subsequently affected the water quality and ecology of lakes in the region. The ecology of these lakes has been shaped by two phases of human activity, the first

Māori settlement and then later European-style agriculture. While the water quality in the lakes changed following early clearance of vegetation in the catchment, the advent of European pastoralism exerted additional pressures, driving further nutrient enrichment. Palaeolimnological methods have complemented water quality monitoring and places the start of nutrient enrichment in the shallow lakes soon after European arrival, while the deeper lakes have been noticeably shifting since the 1990s.

In summarising the diatom assemblage data, diatom species of tolerant of a wide range of water quality (Fragilariaceae) dominate the shallow Lakes Kirihonuhonu and Emily. Conversely, planktonic taxa, representative of, or tolerant to, N enrichment, are abundant in Lakes Ōtūroto and Ōpōrea. Currently, all lakes are in trophic categories (mesotrophic to eutrophic) that are not in keeping with the socio-ecological values of these sites with sustained eutrophication of the shallow Lakes Kirihonuhonu and Emily, and continual but increasing enrichment of Lakes Ōtūroto and Ōpōrea. Active management of these lakes and their catchments is critical if the region is to continue to support *iwi* and stakeholder values.

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## **Chapter 6**

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Conclusions and future work

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## 1 Conclusions

The overarching aim of this thesis was to examine the effects of anthropogenic land use on the water quality in a selection of New Zealand's lakes. This was achieved primarily through the analysis of diatom assemblages from five sediment cores. Interpretations of the longer diatom records were aided by diatom data from habitat and surface sediment samples from the centre of a selection of lakes in the Canterbury region (Chapter 2). There were two study locations, the first a single lake on the North Island of New Zealand, in the Manawatu-Wanganui region (Chapter 3), while the second was in the Canterbury high country on the South Island of New Zealand (Chapter 4 and 5). The palaeolimnological records were all supported with pollen data, representing historic vegetation communities in each lake's catchment, chronology to provide age constraints on timing of changes, and sediment geochemistry – although the methods varied between the study regions. The specific aims of the thesis were to:

1. Identify periods of significant changes in water quality in a selection of New Zealand's lakes through the last ~1000 years, a period which includes, and is just before the first human (Māori) arrival in New Zealand,
2. Analyse the differences in response of lakes to first Māori and European activities, and
3. To examine how palaeolimnology can be used to contribute to future lake management, using examples from lakes that are of i) cultural significance to *iwi* (which loosely translates to "tribe"), and ii) are important for national and local governments.

New Zealand, as argued through the thesis, is an ideal location to assess the scale and effects of anthropogenic activities on lakes, due to its relatively short period of human settlement. As the anthropological history of the country only covers approximately 750–800 years, there was a reasonable assumption in that palaeolimnological records would be able to capture, in the sediments and interpretation of the proxies, an understanding of the pre-human and "natural" state of lakes. With this time span, there is a greater likelihood of obtaining higher resolution records, while sedimentary dating techniques also benefit from the shorter time scale. These factors combined should provide a detailed reconstruction of lakes before human activity commenced, which is essential for understanding how the water quality shifted in lakes in response to various anthropogenic activities. The five palaeolimnological records in Chapters 3–5: Lakes Oporoa, Ōtūroto (Heron), Ōpōrea (Pearson), Kirihonuhonu (Emma) and Emily, suggest that the natural water quality state, interpreted from the diatom assemblage data, was of microtrophic to oligotrophic conditions, i.e. low nutrients. It is possible that these conditions are the natural state, i.e. without human influences, for many other lakes in New Zealand especially those at higher altitudes.

### 1.1 Changes in lake water quality in response to Māori activities.

The nutrient status of each lake, inferred from the palaeolimnological records, was either microtrophic or oligotrophic prior to human arrival. These conditions existed when all catchments were stable and forested with native trees and shrubs. In all lake records, *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Podocarpus* spp., *Fuscospora* spp., *Phyllocladus* spp. and *Halocarpus* spp. were the dominant taxa before Māori arrival (approximately 1620 CE in Lake Oporoa's catchment and 1400 CE in the Canterbury high country). The corresponding diatom flora consisted of low nutrient taxa, namely *Discostella stelligera* and a variety of species from Fragilariaceae belonging to genera *Staurosira*, *Staurosirella*, *Pseudostaurosira* and *Punctastriata*. There was reasonable stability in all diatom records (except for in Lake Ōpōrea), while any observed changes were attributed to natural factors, including variation in climate.

Changes in pollen composition signalled the start of Māori activity in all lake catchments in both regions. The appearance of *Pteridium esculentum* and an increase in Poaceae and charcoal concentration occurred in approximately 1620 CE in the Lake Oporoa catchment, and 1400 CE in the Canterbury high country (Ōtūwharakei and Selwyn-Waihora regions). In all lakes, the response in water quality, as reflected through diatom assemblages was rapid and probably occurred within decades of the first Māori activity. The diatom assemblages changed to reflect nutrient enrichment in different ways, although *Discostella stelligera* was a key indicator taxon in both study regions. In Lake Oporoa (Chapter 3, Study region 1), *Discostella stelligera* increased alongside *Staurosirella cf. ovata*, likely as a direct response to increasing nutrients following sedimentary erosion. Lake Oporoa became mesotrophic to eutrophic. In the Canterbury high country, the lakes responded simultaneously to the changes in catchment vegetation (Chapter 4, Study region 2). In Lake Ōtūroto, *Discostella stelligera* declined as nutrient enrichment favoured *Aulacoseira ambigua*, whereas in Lake Ōpōrea, *Discostella stelligera* proliferated as benthic Fragilariaceae declined. These lakes probably became oligotrophic-mesotrophic. In Lakes Kirihonuhonu and Emily their response to first Māori activities were reflected through a diversification of benthic Fragilariaceae and unprecedented appearances of *Encyonopsis* taxa and *Fragilaria cf. perminuta*. These changes signalled the start of mesotrophic conditions. Not only were the shifts in diatom ecology in the Canterbury high country significant enough to represent aquatic transitions, but the trends in *Discostella stelligera* are a signal of cultural eutrophication.

In the context of water quality response to first human activities, the increase in trophic status of these lakes is similar to what has occurred elsewhere around the world (see Chapter 4). In New Zealand, however, there is a distinct advantage in that there is little ambiguity created by the possibility of earlier Māori settlement, and it is generally accepted to be 750–800 years ago. Uncertainty about the

timing of human settlement is a problem in other localities that have late human-settlement histories, where there is still ambiguity about the exact timing of settlement, e.g. Easter Island (Rull, 2021), Madagascar (Douglass et al., 2019), Azores (Raposeiro et al., 2021). Furthermore, this study can be used to conceptualise what happened in lakes in response to first human settlement, and the likely trajectory of water quality in lakes, especially in locations where first human activity occurred thousands of years ago. For example, the two waves of human migration into New Zealand can be readily distinguished by the different phases of changing water quality in the lakes, but this is rarely possible in lakes with longer human histories. European colonisation and subsequent activities further contributed to the change in water quality, impacting lakes that were already fundamentally altered from their natural conditions. While similar changes in water quality is likely to have happened elsewhere, the longevity of human activity on most landmasses means that compromise, in the sense of being able to understand natural water quality, must be made. Therefore, a benchmark of water quality, with a rehabilitation goal in mind, is already far removed from natural conditions, i.e. rehabilitation using a point prior to the Industrial Revolution (Bennion et al., 2011), or before acceleration of decline in water quality (*sensu* Hering et al., 2010; McNellie et al., 2020). It is necessary, therefore, to try and identify the magnitude of changes between the waves of human activity, especially in the Canterbury region, and from this, decide whether a realistic rehabilitation or restoration goal can be achieved.

## 1.2 The changes in water quality in response to European land-use activities.

The responses of lakes to land use activities after European colonisation of New Zealand (c. 1830) differs between sites in their timing of changes and the trajectory to their current trophic levels. In Lakes Ōtūroto and Ōpōrea there were no immediate changes in the diatom assemblages, and thus water quality, in response to colonial settler activities. It was inferred that at this stage *Discostella stelligera* was thriving in optimum conditions and therefore any nutrient enrichment that would have occurred through pastoral activities is “absorbed” as the continuing dominance of *Discostella stelligera* (Chapters 4 and 5). These two deep lakes only became mesotrophic from the 1980s–1990s which corresponds with changing agricultural practices and enhanced fertiliser use. There is complexity in this region in understanding the different land uses as to some degree, large sections of each catchment are designated as conservation land.

There were, however, similarities in trajectories of nutrient enrichment between Lakes Oporoa (Chapter 3) and Lakes Kirihonuhonu and Emily (Chapter 5). Following the first stages of European pastoral activities, these shallow lakes recorded distinct shifts in their diatom assemblages. Lake Oporoa rapidly transitioned into a eutrophic system dominated by *Aulacoseira granulata* var.

*angustissima* and *Fragilaria* species and, from the 1960s, *Stephanodiscus hantzschii*. Lake Kirihonuhonu became seemingly stable with an abundance of *Staurosira* and *Staurosirella* probably indicating early eutrophic conditions, while in Lake Emily *Discostella stelligera* suddenly proliferated and then declined along with *Encyonopsis* as *Staurosira*, *Staurosirella* and *Cocconeis* became abundant. This too reflects a shift from mesotrophic to eutrophic water quality. Furthermore, in all three lakes their enrichment history continued to be similar, with an acceleration of declining water quality since the 1950s resulting from the intensification of agricultural activities, a situation which reflects patterns in many parts of the globe. The rapidity at which these shallow lakes responded, and their continuing trend of declining water quality is an artefact of their shallow depths and small catchments. Currently, all three lakes are eutrophic, although supereutrophic and hypereutrophic conditions have been recorded, which is in keeping with the global context in that shallow lakes are some of the most “at-risk” freshwater systems (*sensu* Ramstack Hobbs et al., 2016; Jeppesen et al., 2014). Their degradation has spurred studies and management activities aimed at rehabilitating or restoring their “pre-impact” water quality, or ecology, so that ecosystem services continued to be provided. In New Zealand, shallow lakes are disproportionately affected by anthropogenic activities (*sensu* Abell et al., 2019, Ministry for the Environment & StatsNZ, 2020) especially those located in lowland regions, and agricultural catchments.

### 1.3 Palaeolimnology and its contribution to lake management

The final aim of this thesis was to examine how palaeolimnological records could be used for lake management and rehabilitation. Palaeolimnology has long been synonymous with lake management as it allows for the identification of an array of water quality conditions. The case study of Lake Oporoa in Chapter 3 was the most instructive example in showing how palaeolimnology can be used for lake rehabilitation. Palaeolimnological data were analysed alongside the wishes of Ngāti Hauiti *iwi* to identify a time period where water quality supported cultural values of the lake. The diversity in proxies analysed in this study revealed the ecological history of Lake Oporoa and the complementary insights from oral history provides a globally unique example of the benefits of palaeolimnology combined with Indigenous knowledge and desires in the management of lake systems. In New Zealand (and the wider Oceania region) it is necessary to work with Indigenous people to effectively manage and provide opportunities for rehabilitation of lakes and other freshwater systems.

The Canterbury high country lake histories presented in Chapters 4 and 5, have some management activities, primarily through regular water quality monitoring and the designation of land as conservation estate. There is awareness from local and national government alike about the need for managing these systems (Robertson & Suggate, 2011; Bayer & Meredith, 2020), because water

monitoring data, in comparing data of the first sampling year (2005) to the 5-year sampling average (2019) indicate the trajectory of the lakes is still that of increasing nutrient concentrations. However, there is already some improvement in TN and TP levels, especially in Lake Ōpōrea. Palaeolimnology makes a valuable contribution to understanding these lakes, since the diatom assemblages indicated that increasing nutrient concentrations pre-date the start of monitoring. This is particularly relevant for Lake Ōtūroto and Lake Ōpōrea which are considered to have only recently shifted from oligotrophic to mesotrophic conditions (2017 and 2014 respectively; Bayer & Meredith, 2020). This is in contrast to Lakes Kirihonuhonu and Emily which became enriched soon after first European activity with a rapid change in diatom assemblages (shifting benthic Fragilariaceae) probably signifying mesotrophic to eutrophic conditions. A key outcome from a management perspective, is that Lakes Ōtūroto and Ōpōrea can withstand moderate landscape perturbations and still have water quality at a level where catchment nutrient controls are likely to be effective in contributing to the improvement of water quality. Controlling the loading of nutrients into lakes has been successful in some European sites, resulting in a return to low-nutrient conditions, i.e. re-oligotrophication, although it needs to be acknowledged that this process can take from years to decades to occur (Jeppesen et al., 2005; Jochimsen, Kümmerlin & Straile, 2013; Sabel et al., 2020). In contrast, the data suggest that management of Lakes Kirihonuhonu and Emily is more complex, as nutrient concentrations have long been elevated, and diatom assemblages reflect species with tolerances to a wide range of water quality, which means it will be difficult to ascertain, using diatoms, whether management strategies are working. Finally, in managing these lakes there needs to be consideration of the other water bodies (rivers, ponds, kettle holes, streams and wetlands) that comprise this landscape. The glacial history of this landscape means that water features are likely to be more interconnected while simultaneously they exist in catchments that have both conservation and pastoral activities. While the interconnectedness of the landscape has been acknowledged, to some extent, in regional council plans (Environment Canterbury Regional Council, 2017), there ought to be greater focus on understanding the hydrology and flows of nutrients through the landscape.

## 2 Limitations and suggestions for future work

It was not possible to develop precise age models since there were few terrestrial macrofossils preserved in the sediment cores from the Canterbury lakes. This was despite the fact that four cores were collected from each site and more than one core was analysed for preserved macrofossils. Consequently, the potential basal age range for Lakes Ōpōrea, Emily and Kirihonuhonu, spans 2–3 thousand years. Furthermore, the lack of chronology prevented some statistical approaches, such as rate of change analysis, or sedimentation rate from being used. This meant identifying the time of accelerated changes in water quality, and sedimentation, as a result of lake productivity, was hindered

as these techniques require more robust chronology (Birks & Birks, 2008; Mottl et al., 2021). In a similar vein, the upper sediments of Lakes Ōpōrea, Emily and Kirihonuhonu showed evidence of an irregular depositional profile of  $^{210}\text{Pb}$ , either because of sediment mixing or porosity and subsequent redistribution of radionuclides through sediments (*sensu* Abril & Gharbi, 2012; Barsanti et al., 2020) and therefore it was difficult to precisely compare trends from the sedimentary records in context of land-use change.

While the  $^{210}\text{Pb}$  dating age model was independently validated using *Pinus* spp. or *Rumex* spp. and *Lindavia intermedia*, future palaeolimnological studies would benefit from applying  $^{239+240}\text{Pu}$  and, or,  $^{137}\text{Cs}$  dating techniques to refine the chronologies from the mid-1950s onwards (Leslie & Hancock, 2008). This would also contribute to understanding the depositional profile of  $^{210}\text{Pb}$  in these lakes and further constrain the age in the most recent sediments. These techniques use radionuclide fallout from atmospheric weapons testing in the 1950s, with peaks of  $^{239+240}\text{Pu}$  occurring at known times, i.e. mid-1950s, 1964 and ~1968 (Hancock et al., 2011).  $^{239+240}\text{Pu}$  dating methods have already been used effectively in palaeolimnology (Zhang et al., 2022) and New Zealand is a suitable location to use radionuclide fallout (Hancock et al., 2011; Froehlich et al., 2019) although has not yet been applied extensively. The chronology methods using Pu are possibly superior to  $^{137}\text{Cs}$ , as  $^{137}\text{Cs}$  has lower detection limits, especially in the Southern Hemisphere, and a shorter half-life, of 30 years in comparison to the thousands of  $^{239+240}\text{Pu}$  (Hancock et al., 2011). However,  $^{137}\text{Cs}$  dating is also advantageous in complementing a  $^{210}\text{Pb}$  profile (Kirchner, 2011) and can be detected in sediments from 1955 onwards (Leslie & Hancock, 2008).

Secondly, it would have been beneficial to have additional autecological information for the diatom taxa recorded in the record from all lakes. While some of these issues were discussed in context of their chapters, especially with regards to the broad ecological tolerances of the benthic Fragilariaceae, as well as the problems associated with developing optima and tolerances for diatom taxa (*sensu* Juggins, 2013), this is still preferable to a lack of data. Much of the understanding of taxon responses to water quality parameters, or the physical characteristics of lakes, e.g. plant coverage, still relies on evidence from outside New Zealand. This is not a problem unique to New Zealand, and indeed other palaeolimnological studies would improve with the addition of autecological data of diatoms from the region of study (*sensu* McGowan et al., 2018; Kennedy & Buckley, 2021). However, in the context of this thesis, ideally, there should be a systematic study of the lake sites to build a data set with associated variables that influence a taxon's presence. For the habitat samples, for example it is likely there is habitat specificity for some of the attached taxa especially with different macrophytes (Rojas & Hassan, 2017, Chapter 2). Therefore, it would be advantageous to sample different habit types (e.g. submerged, emergent and sprawling macrophytes, pebbles, boulders and sand) in the littoral zone

and around the perimeter of the lakes, or along a depth gradient towards the pelagic zone (e.g. Hofmann et al., 2020). Simultaneously, water chemistry data and physical characteristics could be collected.

Interpretations of diatom assemblage data could be improved using trait-based approaches. A trait-based approach focuses more on diatom growth forms and their responses to resources or disturbances, i.e. light and physical disturbance, with the trait determining their environmental surrounds, not taxonomic identity (Soininen & Teittinen, 2019). In this context diatoms can be assigned an ecological guild: “low-profile”, “high-profile” and “motile” which is determined by their response to resource and disturbance measures, and to some extent, substrate preference (Passy, 2007). Trait-based approaches have been used in both palaeolimnological and limnological studies (Leira, Filippi & Cantonati, 2015; Benito et al., 2018; Velez et al., 2021), although consideration and uptake of this approach is not as extensive as expected, given the value of the data that it provides. In New Zealand and the lakes presented in this thesis, trait-based techniques could be applied to the habitat samples and to the sedimentary diatom record. Using these approaches could enhance the interpretation of longer records providing information about historic factors associated with physical disturbance, and light. Additionally, these approaches can separate taxa into ecological guilds at a genus level which is of benefit for taxa that can only be identified to this level (e.g. *Pseudostaurosira* sp. 1 and *Punctastriata* sp. 1.)

### 3 Concluding statement

New Zealand has a remarkable diversity of lakes, spanning an array of geomorphic types and providing numerous associated ecosystems services. They are an integral part of New Zealand’s freshwater landscape and cultural values, but unfortunately, are subject to continual anthropogenic impacts and management challenges. The long-term palaeolimnological records from five New Zealand lakes in this study show that > 750 years of anthropogenic activity in New Zealand has left its mark in the form of changing water quality in these lakes, driven to water conditions that surpass the natural state of these lakes. Ultimately the challenges for lake management in New Zealand, and elsewhere, is balancing the ecological requirements of lake ecosystems, so they can remain in a healthy ecological state, with the anthropogenic demands placed on these systems. Fortunately, there is considerable interest and awareness of the plight of freshwater from *iwi*, local councils throughout the country, and New Zealand’s national government, who together aim to understand historical lake conditions, monitor changes in lake ecology and to manage and remediate lakes. The palaeolimnological data presented in this thesis has contributed to this process and builds upon existing data sets, to further understand the effects of anthropogenic activities on New Zealand’s lakes.

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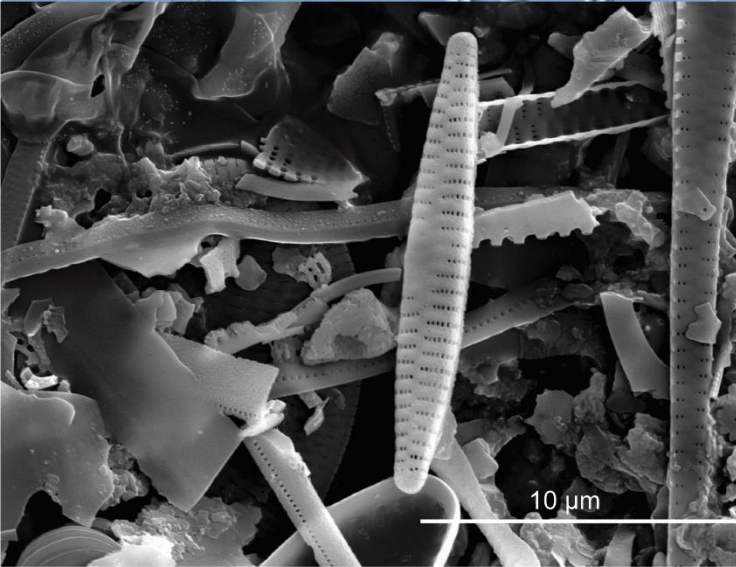
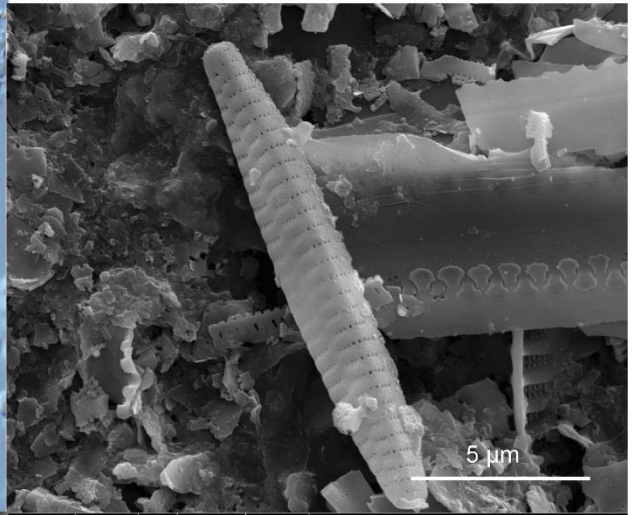
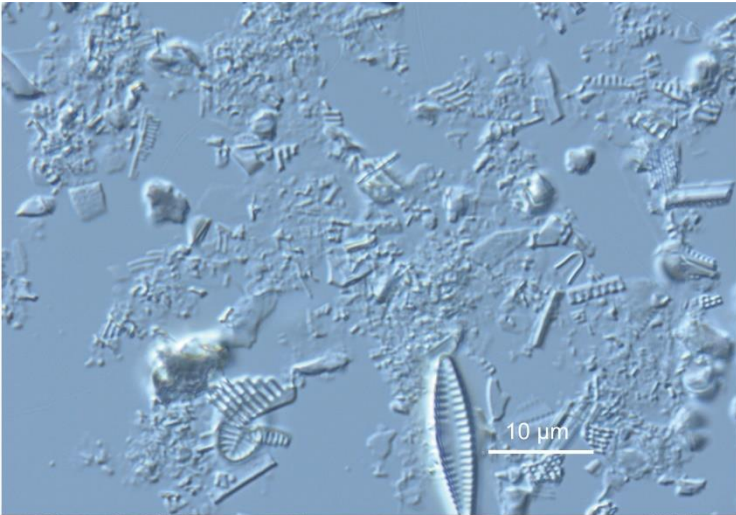
## **Appendix 1**

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Images of select diatom taxa, with a focus on benthic Fragilariaceae

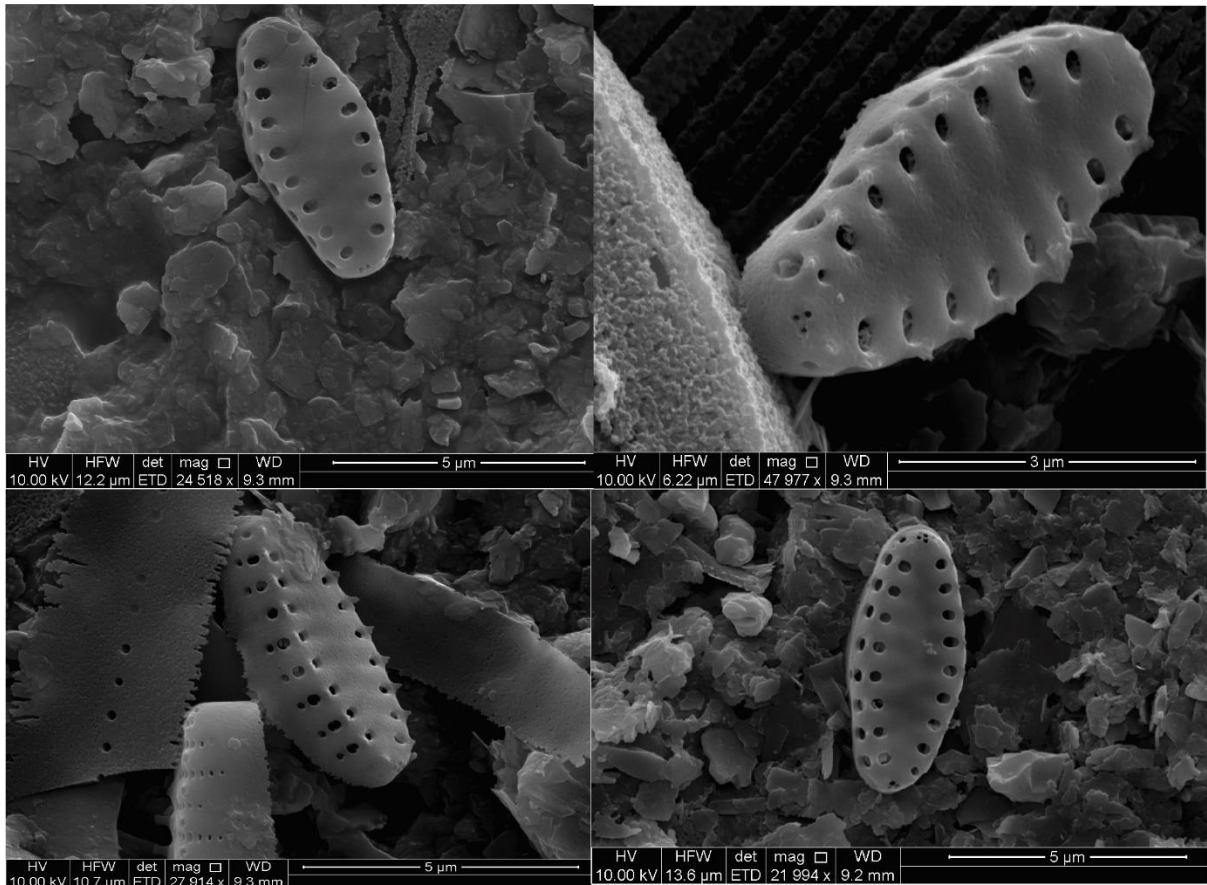
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These images and measurements were taken alongside the diatom analysis for all lakes, Lakes Oporoa, Ōtūroto, Ōpōrea, Kirihonuhonu and Emily. A FEI Quanta 450 FEG Scanning Electron Microscope (SEM) was used at Adelaide Microscopy to assist with identifying taxa belonging to Fragilariaceae.



*Fragilaria cf. perminuta*

Length: 24–25 μm  
Width: 2.5–3.5 μm  
striae: 14–16/10 μm

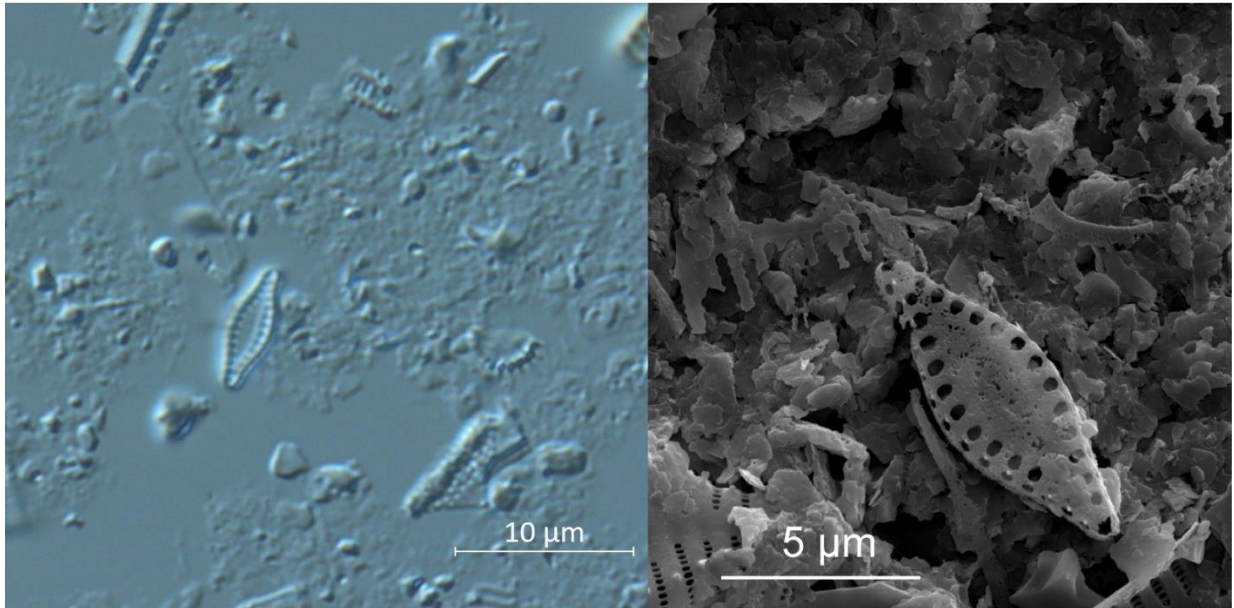


*Pseudostaurosira* sp. 1

Length: 6.5–7.5 μm

Width: 2.8–3.2 μm

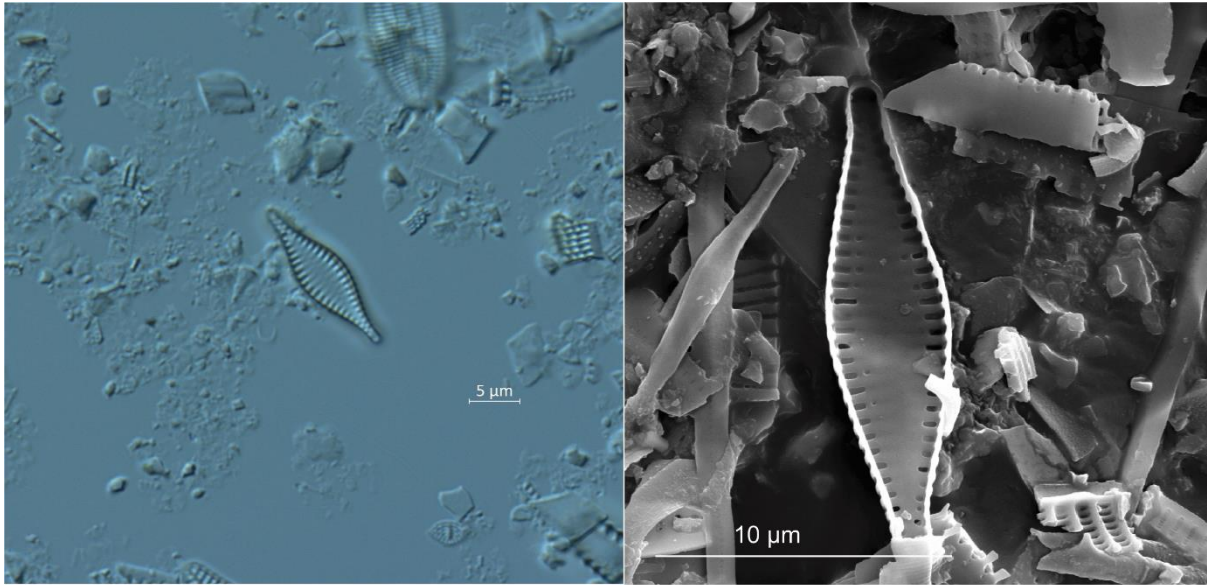
striae: 16/10 μm



*Pseudostaurosira microstriata*

Length: 6.5–7.5 µm  
Width: 2.5–3.5 µm  
striae: 20–22/10 µm



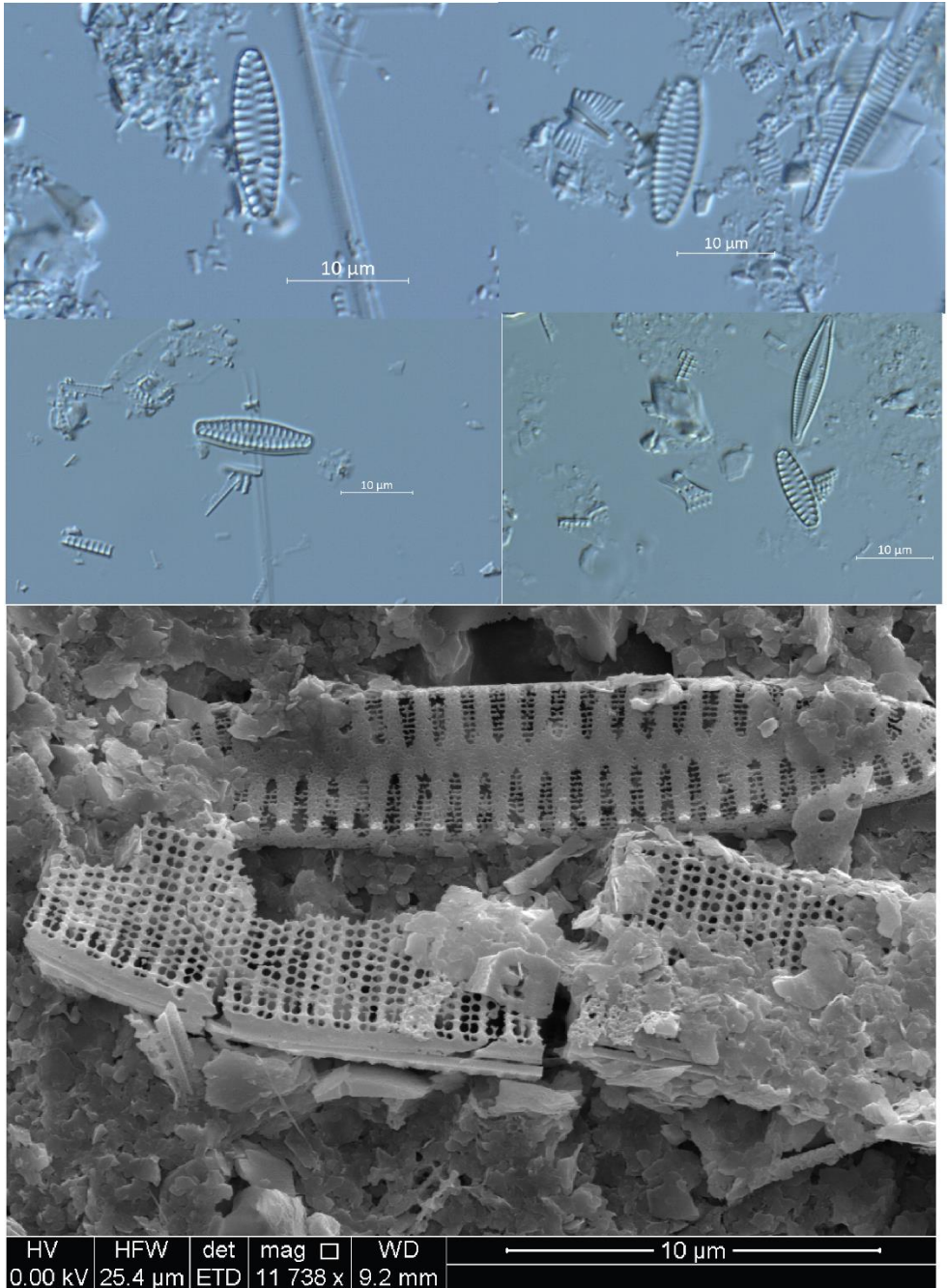


*Pseudostaurosira parasitica*

Length: 9.5–10.5  $\mu\text{m}$

Width: 4.0–4.2  $\mu\text{m}$

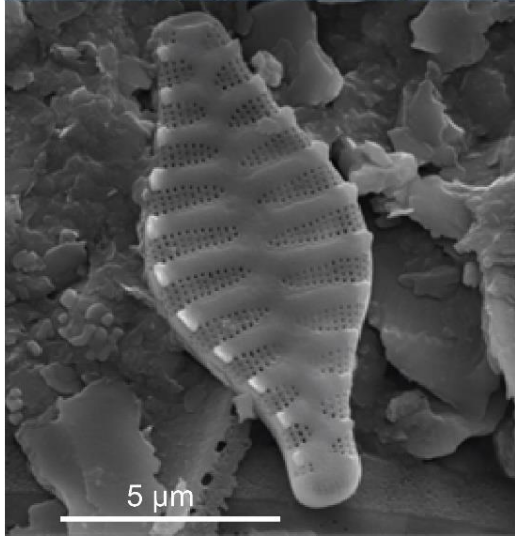
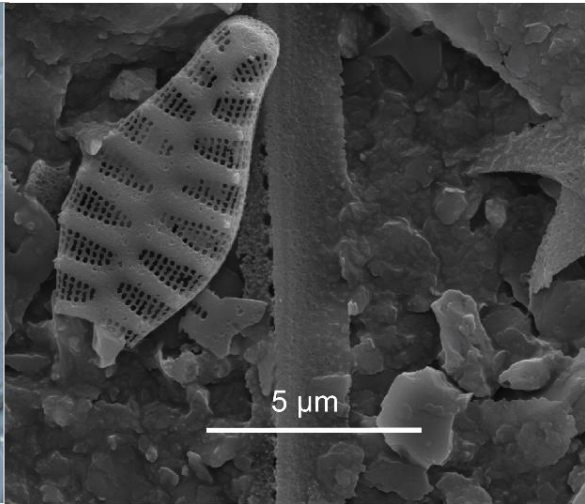
striae: 18/10  $\mu\text{m}$



*Punctastriata sp. 1*

Length: 10–15 µm  
Width: 3–4.5 µm  
striae: 12–14/10 µm



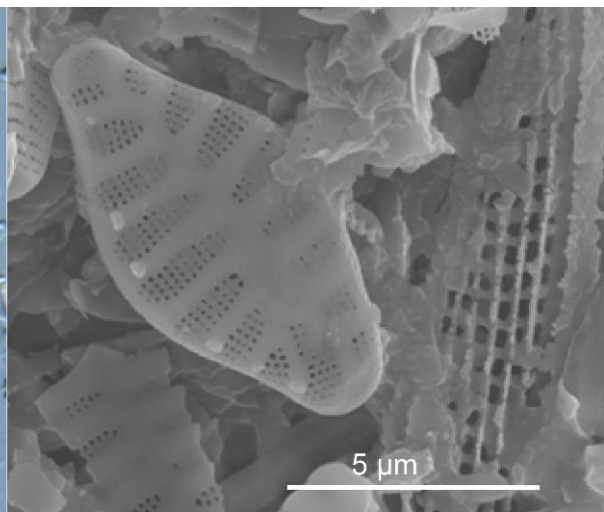


*Punctastriata lancetulla* morph 1

Length: 4.4–6.2 μm

Width: 1.9–2.8 μm

striae: 10/10 μm

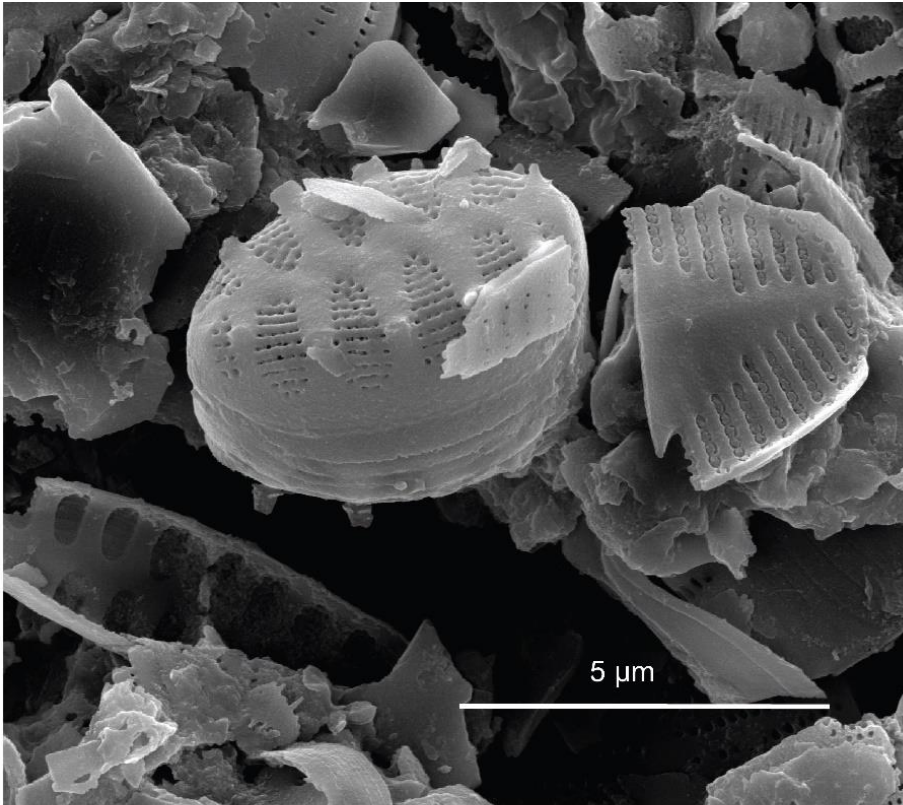


*Punctastriata lancetulla* morph 2

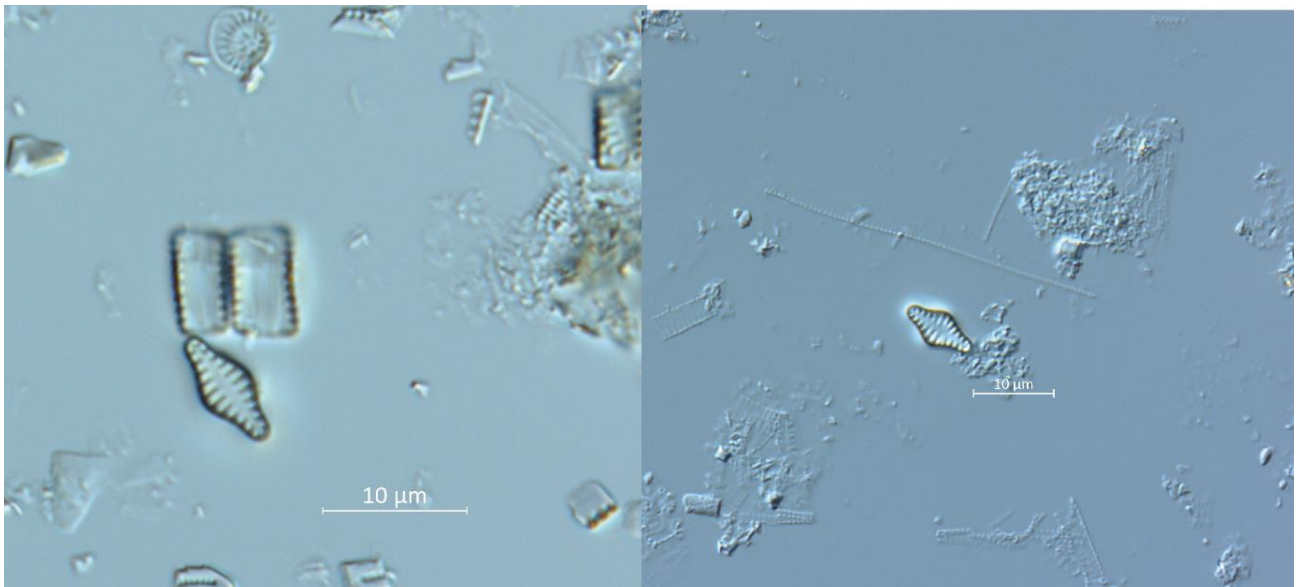
Length: 6–12 μm

Width: 4–5 μm

striae: 10–12/10 μm



*Punctastriata lancetulla* morph 3



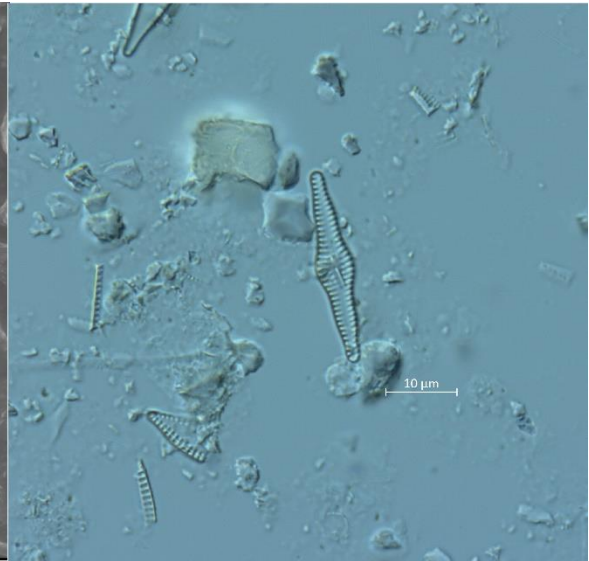
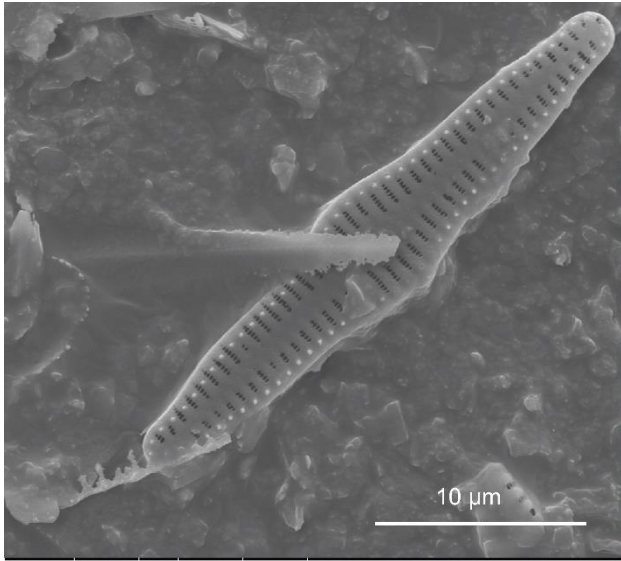
*Staurosira construens*

Length: 8–15 μm

Width: 4–5 μm

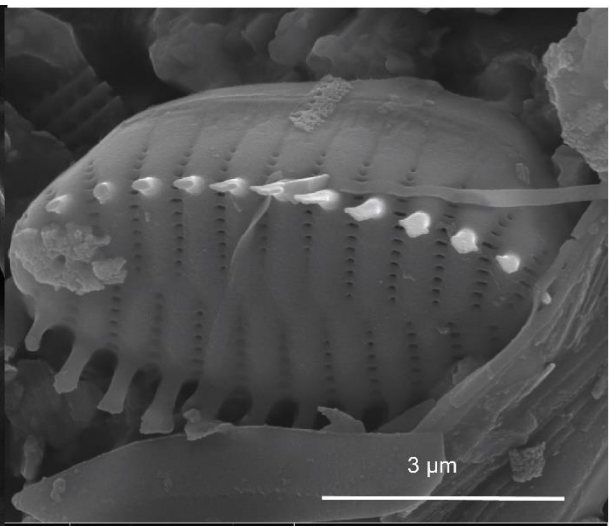
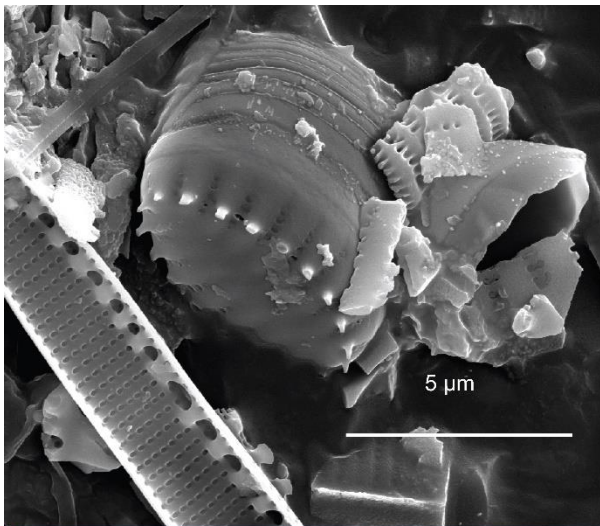
striae: 14–16/10 μm





*Staurosira construens* var. *cf. inflata*

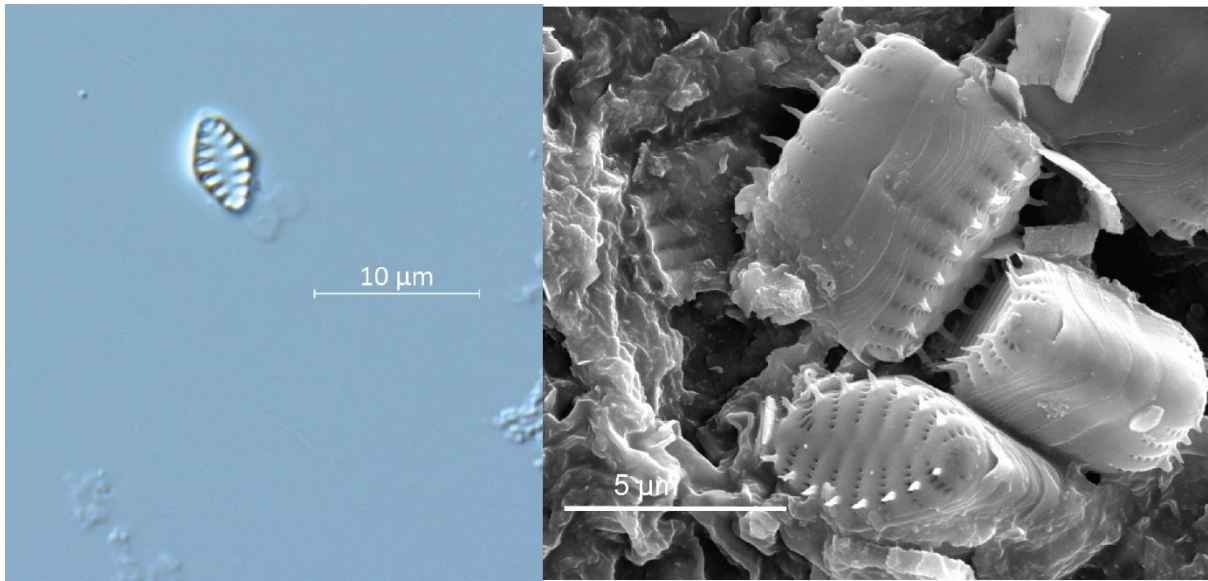
Length: 27–30  $\mu\text{m}$   
 Width: 5.5–6.5  $\mu\text{m}$   
 striae: 16/10  $\mu\text{m}$



*Staurosira* cf. *construens* var. *pumila*

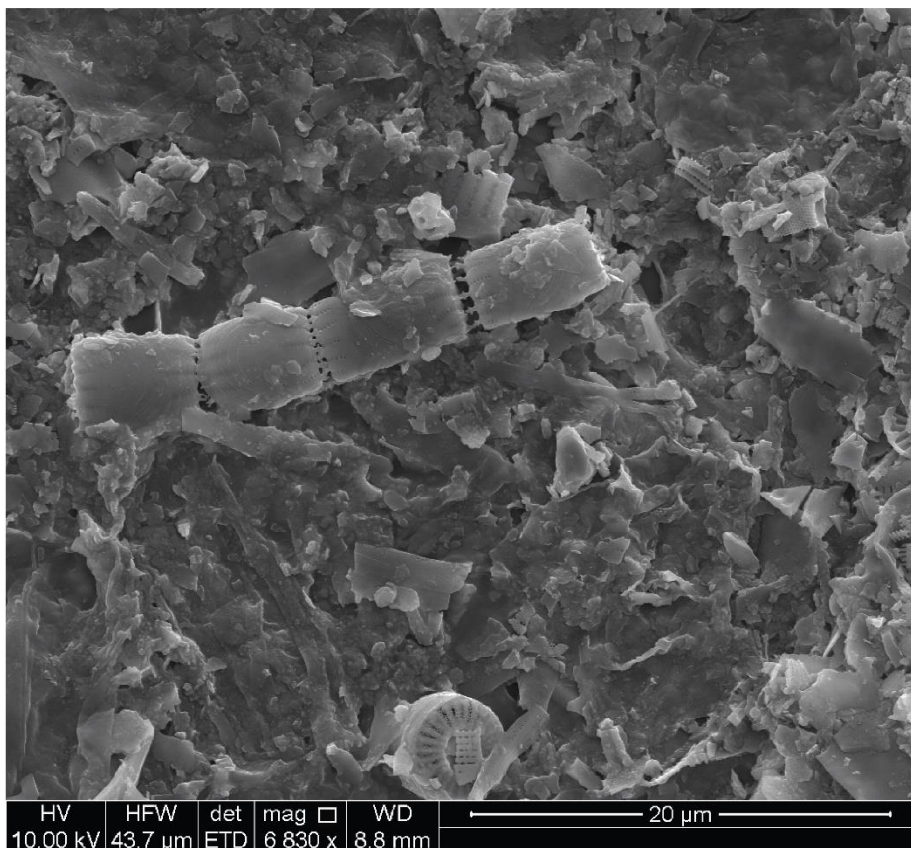
Length: 8–12  $\mu\text{m}$   
 Width: 3.5–5  $\mu\text{m}$   
 striae: 14/10  $\mu\text{m}$





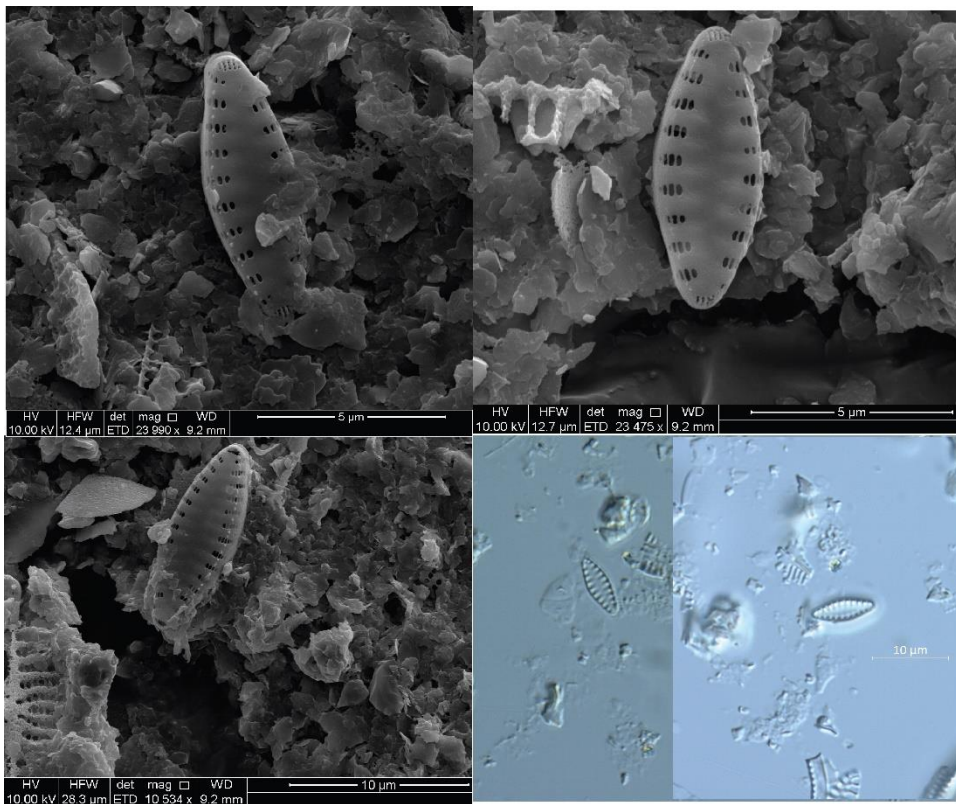
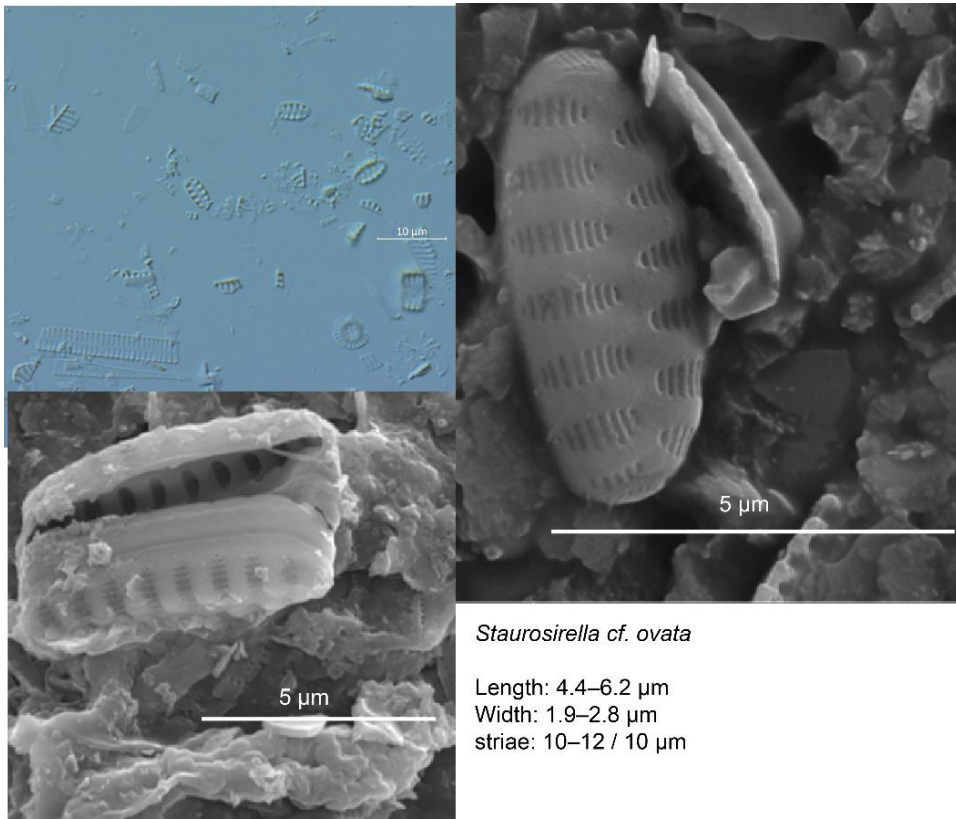
*Staurosira venter* morph 1

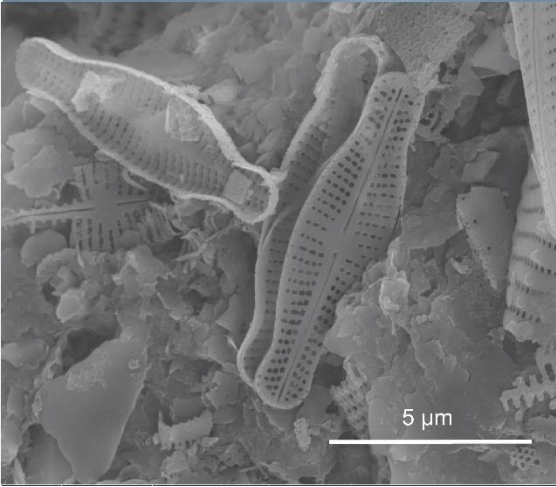
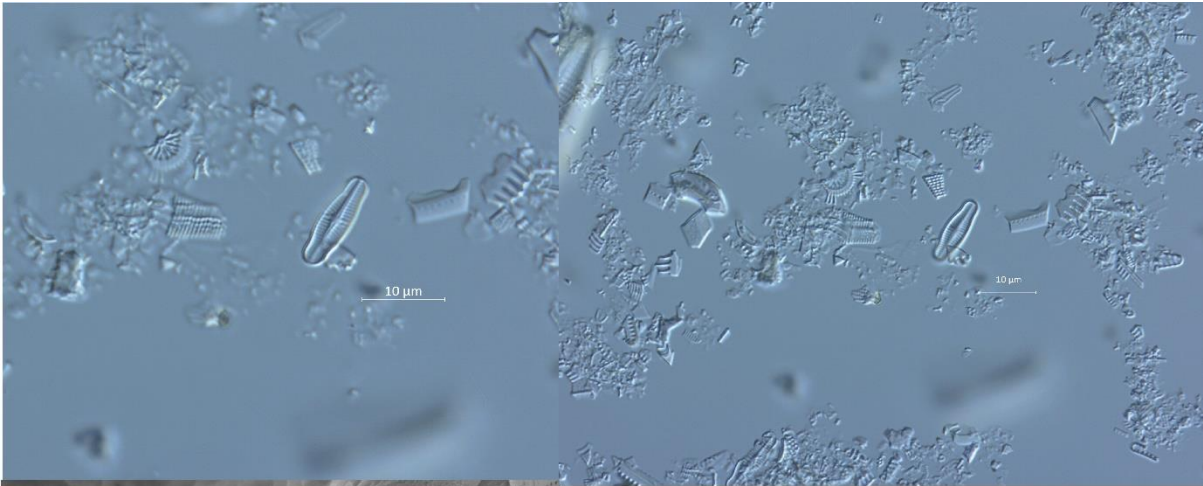
Length: 4–8 μm  
 Width: 2.3–5 μm  
 striae: 12-14/10 μm



*Staurosira venter* morph 2







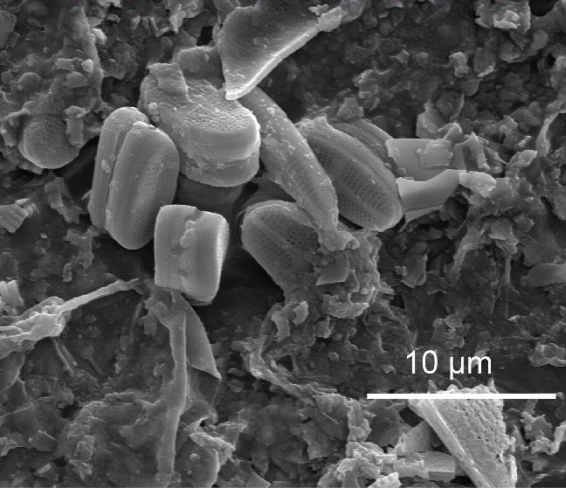
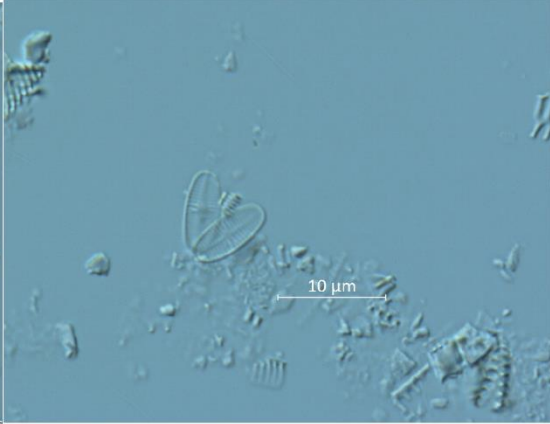
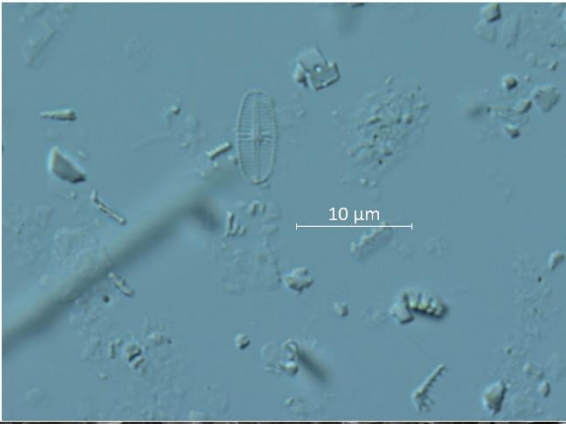
*Achnanthyidium cf. macrocephalum*

Length: 12–13 µm  
Width: 2.5–3.5 µm  
striae: 20–22/10 µm



*Psammothidium abundans*

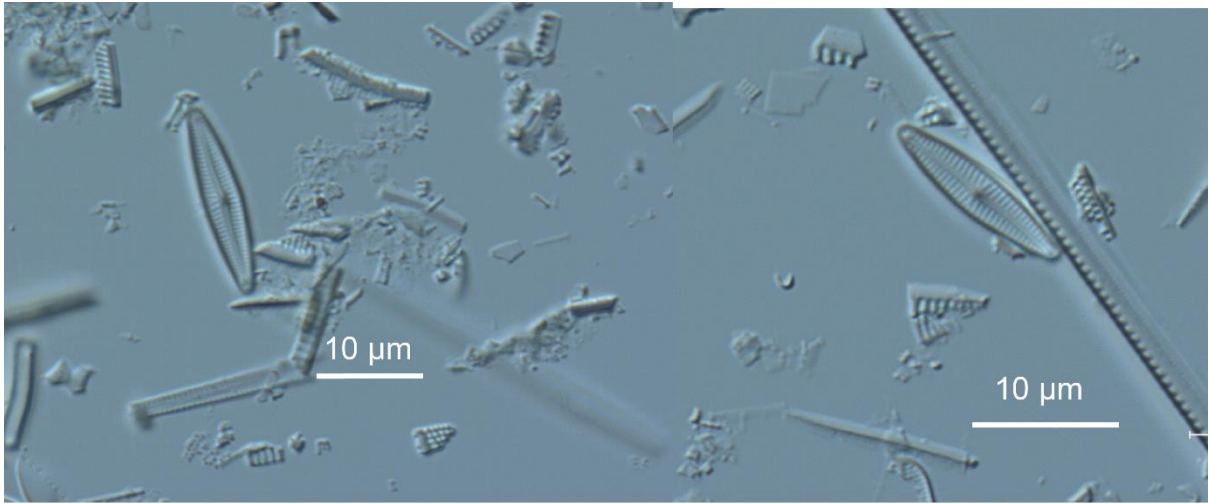
Length: 9–15 µm  
Width: 4–4.5 µm  
Striae: 28 / 10 µm



*Psammothidium sacculus*

Length: 7–8 μm  
Width: 2.5–3.5 μm  
striae: 28–30 /10 μm





*Encyonopsis krammeri*

Length: 9.5–18 µm  
Width: 2.5–3.8 µm  
Striae: 24–28 / 10 µm



*Encyonopsis subminuta*

Length: 12–19 µm  
Width: 3–4 µm  
Striae: 22–26 / 10 µm