A Paleoecological Investigation of Recent Cyanobacterial Blooms and their Drivers in Two Dune Lakes

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Abstract

Cyanobacteria have a major impact on many of Aotearoa New Zealand's lake ecosystems. Blooms of the prokaryotic organisms can cause hypoxia and fish kills, while their potential to produce a range of toxins pose a risk to social and cultural values. Cyanobacteria blooms are common in dune lakes along coastal Manawatū-Whanganui, with little information to guide the management of these globally-rare ecosystems. Setting appropriate targets for restoration programmes is therefore difficult, as cultural eutrophication effects cannot be disentangled from baseline conditions. Paleolimnology has been used within this thesis to reconstruct the environmental and in-lake changes of Lakes Alice and Wiritoa, two dune lakes of similar size that have different depths.

Surface water samples from Lakes Alice and Wiritoa were collected monthly between November 2021 and April 2022 AD, while surface sediment samples were collected in April 2022 AD. Metabarcoding analysis indicated the cyanobacterial communities within the surface sediment were very similar to the seasonal average water column communities, with some likely effects from accumulated settling, lake depth and length of the water sampling period. Sediment cores were collected from the depocenters of both lakes and analysed for pollen, trace metals, trace elements and autochthonous chlorophyll-a. Historic cyanobacterial communities in each lake were assessed via environmental DNA, offering taxonomic and quantitative insight into the changing structure of each lake's ecosystem. Both lakes have experienced significant environmental change with human settlement. Their catchments were likely covered in podocarp forest prior to human arrival, followed by significant deforestation during Māori settlement. European arrival then signals the onset of intensifying agriculture with ongoing deforestation and conversion of scrub to pasture. Increased cadmium concentrations in both lakes identify the onset of aerial superphosphate topdressing and intensive agriculture. Cyanobacterial communities in both lakes transition from the picocyanobacterial *Cyanobium* to bloom-forming, potentially toxigenic taxa including *Dolichospermum* and *Microcystis*; the most significant magnitude shift in cyanobacterial communities occurs with the onset of intensive agriculture in both lakes.

Nutrient reduction is likely key to reducing the impact of cyanobacterial blooms in Lakes Alice and Wiritoa, although in neither lake will nutrient reduction alone result in complete water quality restoration. Deforestation of the catchments was identified as an additional driver of potential cyanobacterial blooms. Additional unknown drivers or in-lake thresholds may be aggravating the cyanobacterial blooms seen today, and further research to identify these would be valuable. Both lakes likely have internal mechanisms that will maintain their elevated trophic status if external nutrient inputs are reduced, however these differ between the lakes due to their depth differences.

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Being part of the Lakes380 project has been an unforgettable experience, and further information is available at https://lakes380.com/. For any interested students – go for it!

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1 Chapter 1 - Introduction

Cultural eutrophication is one of the most pressing water quality issues facing Aotearoa New Zealand. Associated with agricultural land-use, eutrophication can quickly alter a lake's primary productivity and cause a cascade of effects (Abell, Özkundakci, Hamilton, & Miller, 2011; Conley et al., 2009). Nearly half of Aotearoa New Zealand's approximately 3800 lakes larger than 1 hectare in area are classified as in poor or very poor condition, while only 15% are in good or very good condition (Ministry for the Environment & Stats NZ, 2020a). Lake water quality has a strong relationship with catchment land-use; 70% of lakes in pastoral catchments are in poor or worse condition, compared with just under 20% of lakes in native forest (Ministry for the Environment & Stats NZ, 2020a). Furthermore, 36% of lakes are heavily impacted by exotic macrophytes or completely devegetated (Ministry for the Environment & Stats NZ, 2020a). Exotic fish are further disturbing lake ecosystems (de Winton, Dugdale, & Clayton, 2001). This has culminated in at least 37 lakes nationally flipping to a phytoplankton-dominant regime, a state that can be difficult to reverse (Schallenberg & Sorrell, 2009; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993).

Cyanobacterial blooms are a symptom of eutrophication (Conley et al., 2009). Cyanobacterial blooms can significantly alter lake ecosystems, as turbidity increases and dissolved oxygen declines which can have detrimental impacts on flora and fauna (Drake, Kelly, & Schallenberg, 2011; Schallenberg & Sorrell, 2009). The ability of some cyanobacteria to produce powerful toxins is of further concern (Merel et al., 2013). These toxins are a risk to animal and human health either through consumption of the water or by contact with it (Merel et al., 2013; Wood, Hamilton, Paul, Safi, & Williamson, 2009). These cyanobacterial blooms jeopardise ecosystem services and public health (Merel et al., 2013; Paerl, 2017).

Despite high public support for action to improve water quality in Aotearoa New Zealand (Joy & Canning, 2021; Stewart-Harawira, 2020), lake managers face several challenges for creating management plans. Limited data availability for many lakes (Larned, Snelder, Whitehead, & Fraser, 2018; Verburg, Hamill, Unwin, & Abell, 2010) makes determining the causes of decline difficult, while establishing the baseline states of lakes after degradation has already occurred is challenging (Abell, Ozkundakci, Hamilton, van Dam-Bates, & Mcdowell, 2019; Battarbee & Bennion, 2011; Smol, 2008). The extent of eutrophication across the country means the reference lakes (i.e. those still in very good condition) are rare (Schallenberg, 2019). Paleolimnology – the study of chronologically-laid benthic sediments to reconstruct past environmental conditions – can provide data that helps with establishing informed environmental targets and helps with developing restoration plans (Schallenberg, 2019; Smol, 2008).

Lakes Alice and Wiritoa are two dune lakes in the Manawatū-Whanganui region. They have a similar surface area (12 ha and 22 ha respectively) but differ primarily in their depth – 3 m and 19 m at their deepest

points respectively (Land Air Water Aotearoa, 2023a, 2023b). Similar to many dune lakes along this coastline, both are eutrophic with frequent cyanobacterial blooms (Gibbs & Champion, 2013; Horizons Regional Council, 2019). These blooms contain potentially toxigenic taxa. The rarity of dune lakes globally makes intervention imperative, but that same rarity makes obtaining information on reference state systems difficult (Drake, Kelly, Schallenberg, Ponder-Sutton, & Enright, 2009; Wetzel, 2001). This Master's project used paleolimnological methods and molecular techniques to investigate how these two lakes have changed over time, the drivers of those changes, and if timelines of eutrophication response differ in dune lakes of different depths. Surface water sampling was used to establish the reliability of cyanobacteria DNA detections in the sediment core. This data will provide valuable insights on the how best to rehabilitate or restore methods water quality in Lake Alice and Lake Wiritoa (Gann et al., 2019; Short, Tibby, Vandergoes, Wood, Lomax, Puddick, Pearman, Howarth, Moy, & Šunde, 2022).

1.1 Objectives

1) *Compare the cyanobacteria community composition in the surface sediment and surface water in each lake for one summer season.*
   A key assumption of paleolimnological DNA investigations is that the taxonomic composition of sediment reflects the overlying water column. Verifying the sensitivity of sediment to changes in the surface water will provide insight into the reliability of sediment core DNA data.

2) *Use sediment cores to identify the cyanobacteria community composition in each lake, and investigate how it has changed over recent centuries.*
   The taxonomic composition of the cyanobacteria community within a water body can be indicative of both water quality, and the level of risk to both human and faunal populations which may access the water body. The historic taxonomic composition of the cyanobacterial community in the lakes will allow inference about baseline water quality and the extent of change relative to today.

3) *Compare the timelines of eutrophication between a shallow and deep dune lake in order to constrain possible driving mechanisms.*
   It is often assumed that shallow lakes are particularly vulnerable to anthropogenic impacts due to having low dilution capacity, but this is largely untested. Comparing paleolimnological proxies with cyanobacterial community composition can provide

information on both the key factors that drive poor water quality and how quickly any change has occurred.

1.2 Thesis overview

Chapter two provides a broad review of the literature for how land-use in Aotearoa New Zealand has changed, the relationship between lake eutrophication and cyanobacterial blooms, and the role that paleolimnology has and could play in lake management. Particular attention is given to how environmental DNA can detect cyanobacteria both in surface water and sediment cores. Chapter three presents a geographic and ecological context for Lake Alice and Lake Wiritoa, and the Manawatū-Whanganui dune lake system. Chapter four covers the methodologies used, and Chapter five presents the results. Chapter six describes the reconstructed environmental history of both lakes, and discusses how the cyanobacterial communities have changed over time. Chapter seven summarises the key findings and gives recommendations for future research.

2 Chapter 2 – Literature Review

Aotearoa New Zealand has approximately 3800 lakes larger than 1 hectare in area. Of these approximately 46% are eutrophic and at least 31% are still degrading (Ministry for the Environment & Stats NZ, 2020a). Cyanobacterial blooms are a symptom of eutrophication (Abell, van Dam-Bates, Özkundakci, & Hamilton, 2020; Conley et al., 2009). Cyanobacteria have a number of ecological adaptions that give them a competitive advantages over other phytoplankton in certain conditions – for example, they are very adept at uptake of excess nutrients enhancing their ability to proliferate in eutrophic water bodies (Cottingham, Ewing, Greer, Carey, & Weathers, 2015). These blooms can jeopardise both ecosystem functioning and produce high quantities of powerful cyanotoxins (discussed further in Section 2.3), risking public health (Merel et al., 2013; Paerl & Paul, 2012; Puddick, Thomson-Laing, & Wood, 2019). Despite high public support for action (Joy & Canning, 2021), the limited data availability on both the current states and historic states of many Aotearoa New Zealand lakes makes target-setting difficult (Abell et al., 2019; Schallenberg, 2019; Verburg et al., 2010). Paleolimnology is one method to gain these insights. With the use of new molecular tools, insight into the trends and drivers of cyanobacterial blooms are available with higher taxonomic resolution. As the National Policy Statement for Freshwater Management mandates more recovery and restoration planning, lake scientists can benefit from the integration of contemporary monitoring and paleolimnological analysis (Battarbee & Bennion, 2011; Ministry for the Environment, 2020).

2.1 History of Land-use Change

The landscape of Aotearoa New Zealand has undergone significant changes with human settlement. As water quality is deeply linked to what is happening on the land, understanding the scope of terrestrial change is crucial to understanding what is causing lake degradation (Abell et al., 2011; Drake, Kelly, & Schallenberg, 2011). Wider literature identifies pre-human times, the arrival of Māori around 1280 AD, colonisation by Europeans around 1820 AD, and agricultural intensification from 1950 AD until present as the four broad time periods in Aotearoa New Zealand's history (DeFries, Foley, & Asner, 2004; MacLeod & Moller, 2006; McGlone & Wilmshurst, 1999; Pool, 2015). The timing of these zones varies geographically (Newnham, Lowe, Gehrels, & Augustinus, 2018).

Paleoecological records suggest that the country was 85–90% forested prior to human arrival, with the remaining unforested areas largely being above the treeline (McGlone, 1989). Podocarp-broadleaved forest covered most of the country, with beech forest and scrubland in cooler, drier or more exposed areas (Alloway et al., 2007). The first wave of human settlement by Māori at likely took place around 1280 AD (Perry, Wilmshurst, McGlone, McWethy, & Whitlock, 2012; Wilmshurst, Anderson, Higham, & Worthy, 2008). The initial settler population was low (Perry et al., 2012), and is estimated to have reached around

100,000 nationally before European arrival (Pool, 2015). Māori undertook significant deforestation by burning after their arrival to allow travel, village construction and cropping (Baillie & Bayne, 2019). Furthermore, they undertook burning to encourage the growth of the successional species *Pteridium esculentum* (Bracken fern) as a key source of carbohydrate (Baillie & Bayne, 2019; McGlone & Wilmshurst, 1999). This burning was done relatively quickly, although it was less rapid in the humid northern and western regions (Newnham et al., 2018). Deforestation was also speculated to have been completed in stages, with repeated burnings creating a feedback loop that further discouraged forest regeneration (Perry et al., 2012; Wilmshurst, Higham, Allen, Johns, & Phillips, 2004). The Māori economy during this time was subsistence-based, with supplemental long-distance trade and exchange between tribes (Pool, 2015).

The second wave of human settlement was Europeans, beginning around 1820 AD, although low levels of contact began in the late AD 1700s (Pool, 2015). The signing of Te Tiriti o Waitangi in 1840 broadly entrenched the land-use regime shift from Māori to European practices (Ewers et al., 2006; MacLeod & Moller, 2006; Pool, 2015). European settlers continued deforestation but replaced the subsistence cropping with an intensifying industrial agriculture utilising imported cattle, sheep and plant species (Ewers et al., 2006; Pears, 1982; Rowarth, 2013). These supported both a substantial population increase (Pool, 2015), and brought about the advent of commercialised export agriculture (Blattman, Hwang, & Williamson, 2007; MacLeod & Moller, 2006; Rowarth, 2013). Acclimatisation Societies imported various exotic taxa such as trout (*Oncorhynchus mykiss* and *Salmo trutta*) and gorse (*Ulex europaeus*) for release into Aotearoa New Zealand to support food, recreation and ornamental objectives – there was a broad goal to change the Aotearoa New Zealand landscape to better imitate Europe (Pears, 1982).

European agriculture further intensified with the advent of aerial topdressing in the mid-20th Century, which allowed the application of fertiliser at a larger scale and quicker timeframe (MacLeod & Moller, 2006). Expansion of agriculture continued, reaching 60% of national land area during the 1970s AD (MacLeod & Moller, 2006). Farms diversified during the 1970s AD, before widespread conversion to dairying in the 2000s (MacLeod & Moller, 2006; Moller et al., 2008). Stock numbers and product yields broadly increased from earlier decades, supported by rapid increases in fertiliser applications and a 400% increase in irrigated areas over 40 years to the 2000s (MacLeod & Moller, 2006). This shift is broadly classified as a new era of Aotearoa New Zealand history that reaches to today – intensive agriculture (MacLeod & Moller, 2006; Rowarth, 2013; Stewart-Harawira, 2020).

The legacy of human interactions with the Aotearoa New Zealand environment can be seen in many ecosystems today. Currently, approximately 48% of indigenous vegetation cover remains in Aotearoa New Zealand (Cieraad, Walker, Price, & Barringer, 2015). This remaining cover is unevenly distributed by both spatially and ecologically (Cieraad et al., 2015). Indigenous forest cover has declined by around 70% from

pre-human levels nationally, with the remaining 20% concentrated in wet, cold and steep areas (Allen, Bellingham, Holdaway, & Wiser, 2013; Cieraad et al., 2015). This pattern reflects the priorities both Māori and Europeans placed on the land they chose to cultivate – flatter and warmer lowlands are favoured for clearance as they are more amenable to cropping and development (Baillie & Bayne, 2019; Ewers et al., 2006; McGlone, 1989). This may also reflect the ease of burning in different conditions, but this is still debated (Newnham et al., 2018). Wetlands are even more heavily affected, with an estimated 90% of wetland area lost nationally since human occupation started (Robertson, Ausseil, Rance, Betts, & Pomeroy, 2019). Furthermore, 60% of the remaining wetland area is likely experiencing moderate to severe degradation (Ausseil, Lindsay Chadderston, Gerbeaux, Theo Stephens, & Leathwick, 2011).

As land cover has changed, so too have the activities on that cleared land. Today, approximately 40% of the total land in Aotearoa New Zealand is classified as exotic grassland pasture, while 8% is exotic forest and 2% is utilised for horticulture and cropping (Ministry for the Environment & Stats NZ, 2021). Pastoral land-use has also changed over time, with dairy replacing sheep and beef farms (Ministry for the Environment & Stats NZ, 2021). Sheep and beef livestock numbers have declined consistently since 2000, while dairy cattle numbers have declined since their peak around 2015 (Ministry for the Environment & Stats NZ, 2021). This has coincided with an increase in phosphorus, nitrogen and potassium fertiliser sales within the same time period, suggesting that more is being produced on less area (Ministry for the Environment & Stats NZ, 2021). Urban areas occupy only 1% of total land area, but contain over 80% of our 5 million people (Ministry for the Environment & Stats NZ, 2021). This population is a 50-times increase from Māori subsistence levels in just over 700 years.

2.2 Eutrophication of Aotearoa New Zealand's Lakes

With the growing population of people, pressure on lakes is increasing. Lakes in Aotearoa New Zealand have limited natural biodiversity, yet provide important habitats and connectivity for native fish species (Schallenberg et al., 2013). They also provide important nutrient cycling, hydrological, provisioning and cultural ecosystem services (Schallenberg et al., 2013), and can support terrestrial fauna (Drake et al., 2011).

Lakes are especially susceptible to and indicative of anthropogenic pressures and land-use change. Most lakes are fed through streams or groundwater inflows and are therefore sinks that accumulate the characteristics of their catchments (Pearman et al., 2022; Wetzel, 2001). This sink dynamic is further emphasised by the lower flushing capacity of most lakes, as inflowing water and what it carries is held in the basin for a longer timeframe (Wetzel, 2001). Stratification of the water column along a temperature gradient then underpins many lake ecosystems, with the presence or absence of seasonal mixing determining the spatial and temporal distribution of oxygen, nutrients and biota throughout the lake

(Burns, Schallenberg, & Verburg, 2014; Shade, Chiu, & McMahon, 2010). Lakes can therefore concentrate and compound human impacts more than lotic systems.

2.2.1 Eutrophication

Eutrophication results from the excess supply of nutrients to a lake (Paerl, 2017; Wetzel, 2001). Natural eutrophication can occur without any human involvement, typically fueled by ontogeny, catchment geology and high ecological utilization (Abell et al., 2019; Horie, 1981; Smol, 2008; Vincent & Vincent, 1982; Wetzel, 2001). Cultural eutrophication is anthropogenic and broadly associated with nitrogen and phosphorous fertilizer in agricultural land-use both globally and in Aotearoa New Zealand (Conley et al., 2009; Gibbs, Roygard, Patterson, Brown, & Brown, 2022). After entering a lake through lotic, sub-surface and overland flows, nitrogen and phosphorous can quickly be utilised by phytoplankton and increase primary productivity (Paerl, 2017; Xu et al., 2019). As more lakes are identified as being affected by cultural eutrophication, the imperative grows ensure management decisions maintain or improve ecological integrity and ecosystem services (Abell et al., 2019; Schallenberg et al., 2013).

Increasing the primary productivity of a lentic ecosystem beyond its natural variation can have significant consequences. Phytoplankton blooms result in large dissolved oxygen swings through respiration that can suffocate aquatic fauna (Wetzel, 2001). Macrophyte communities can collapse as they are shaded out by algae, reducing the habitat available for zooplankton, macroinvertebrates and fish (Drake et al., 2011; Kelly & Schallenberg, 2019). Excess nutrients not taken up by phytoplankton and plants can be bound to lake sediments, particularly if transported into the system via erosion (Gibbs et al., 2022; Waters, Webster-Brown, & Hawes, 2021). These sedimentary nutrient stores can then be released into the water column either continuously or during hypolimnetic hypoxia, further fueling primary productivity (Gibbs et al., 2022; Paerl, 2017; Waters et al., 2021). Eutrophication can also be aggravated by other anthropogenic pressures. Wetland drainage and catchment deforestation can reduce nutrient attenuation, alter hydrological regimes and increase light availability (Clarkson, Ausseil, & Gerbeaux, 2013; Woodward, 2013), while exotic fish can release nutrients by disturbing sediments and graze the remaining macrophyte beds (de Winton et al., 2001). Climate change promotes both warmer water temperatures and longer summer stratification (Paerl & Huisman, 2009). These interacting pressures and lake processes can create feedback loops which result in the entrenchment of a new eutrophic state, whereby a lake "flips" from macrophyte-dominated to algae-dominated (Hilt, 2015; Schallenberg & Sorrell, 2009; Scheffer, Carpenter, Foley, Folke, & Walker, 2001). This process is depicted in Figure 2.1, with a eutrophied state encouraging the release of nutrients that prevent a return to oligotrophic conditions.

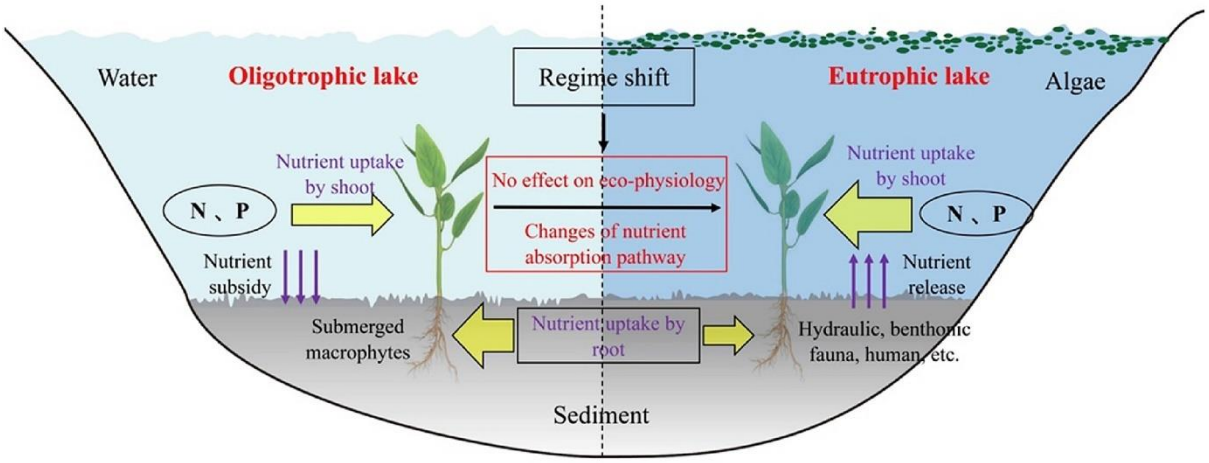

Figure 2.1 *A summary of altered nutrient pathways within a previously oligotrophic lake affected by eutrophication. Reproduced from Xu et al. (2019).*

Eutrophic lakes are recognized in Aotearoa New Zealand as having shorter and weaker food webs (Kelly & Schallenberg, 2019). Turbidity associated with algal blooms is linked with the collapse of macrophyte beds in shallow lakes nationally, with additional pressure from introduced coarse fish contributing to eutrophic maintenance (de Winton et al., 2001). Increased sediment delivery to lakes has been associated with higher turbidity (Drake et al., 2011), more anoxia (Waters et al., 2021), smothering of macrophytes (Schallenberg et al., 2013) and higher smelt egg mortality (Rowe & Taumoepeau, 2004). Internal phosphorous loading fuels algal blooms (Gibbs et al., 2022) with complicated release mechanisms (Waters et al., 2021). Regime shifts away from macrophytes are estimated to have occurred in 37 of Aotearoa New Zealand's studied lakes (Kelly & Schallenberg, 2019). Overall, Aotearoa New Zealand's eutrophic lakes have less resilience, less native species and less macrophyte cover.

2.2.2 Managing human impacts on lakes

As the extent of threat to Aotearoa New Zealand lentic ecosystems from anthropogenic pressures becomes more apparent, public support has grown for greater intervention (Joy & Canning, 2021; Stewart-Harawira, 2020). The trophic status of lakes nationally is primarily measured through the Trophic Level Index (TLI), adapted from the United States of America to account for Aotearoa New Zealand's unique mix of nitrogen-limited, phosphorous-limited and co-limited lakes (Abell et al., 2020). The TLI utilises total nitrogen, total phosphorous and chlorophyll-a to evaluate lake on its nutrient availability and phytoplankton productivity (Burns, Rutherford, & Clayton, 1999). Modelled TLI scores show that 46% of lakes in Aotearoa New Zealand have poor or very poor water quality, compared to 15% having good to very good water quality (Ministry for the Environment & Stats NZ, 2020a). Further insight is available into ecological integrity through the Lake Submerged Plant Index (LakeSPI), which assesses lakes according to their proportional amounts of native and exotic submerged plants (Clayton & Edwards, 2006; Schallenberg et al., 2013). Surveys over 20

years in 295 lakes have indicated that 36% were in a poor or de-vegetated state, compared to 34% in excellent or high condition (Ministry for the Environment & Stats NZ, 2020a). Mātauranga Māori approaches to monitoring such as the Cultural Health Index are increasingly being used as well, although their application can be uneven nationally (Harmsworth & Awatere, 2013; Stewart-Harawira, 2020).

Translating this monitoring information to lake management strategies, however, can be challenging. Despite the recognised need to localise strategies to each lake, 95% of lakes in Aotearoa New Zealand have only one year or less of monitoring data (Verburg et al., 2010). This lack of information is further challenged by most limnological research focusing on eutrophication effects in shallow lakes (Hilt, 2015; Özkundakci & Lehmann, 2019). Lakes can also naturally shift between trophic states over time, such as Lake Biwa in Japan and Lake Naivasha in Kenya (Harper, 1992; Horie, 1981); high primary productivity may therefore be a natural stage rather than human degradation (Harper, 1992). Disentangling both the extent and drivers of ecosystem change is therefore difficult (Schallenberg, 2019). In the absence of this critical information, blanket targets such as those set in the National Policy Statement for Freshwater Management are frequently used without the guarantee that these are achievable in every lake (Abell et al., 2019; Ministry for the Environment, 2020; Schallenberg, 2019).

A further complicating factor in lake management is hysteresis. Shallow lakes have frequently been observed to switch between alternative equilibria of clear, macrophyte-dominant conditions and turbid, algal-dominant conditions in response to both stochastic and threshold events, such as droughts or nutrient accumulation (Scheffer, 2001; Scheffer et al., 1993). Hysteresis can then maintain the lake within the clear or turbid state via internal feedbacks that resist a return to the previous state (Mehner et al., 2008; Scheffer, 2001). Macrophyte cover is suspected to be a key regulating factor within shallow lakes (Scheffer, 2001), with numerous shallow lakes both within Aotearoa New Zealand and internationally observed to enter a turbid state when devegetated (Schallenberg & Sorrell, 2009; Scheffer et al., 1993). Hysteresis has historically been theorised to not occur within deep lakes, as their limited littoral zones relative to lake area suggest lesser impacts from macrophytes on turbidity (Milan et al., 2022; Scheffer, 2001). This has changed in recent years, with stratification and its associated benthic phosphorous release instead been proposed as a hysteretic mechanism for deeper lakes, but this remains largely unexplored (Carpenter, Ludwig, & Brock, 1999; Mehner et al., 2008; Milan et al., 2022). If hysteresis is occurring within a lake, significant intervention is then required to return to clear conditions, with nutrient levels often needing to be reduced below the levels that previously forced the shift to a turbid state (Scheffer & Carpenter, 2003). Evaluating the effectiveness of intervention strategies is then challenging, and multiple strategies such as water level or fish stock management are necessary alongside significant nutrient reductions (Mehner et al., 2008; Schallenberg & Sorrell, 2009; Scheffer, 2001).

2.3 Cyanobacteria and Water Quality

Cyanobacteria are prokaryotes that comprise some of the oldest known life forms on earth, with their earliest ancestors being linked to the Great Oxygenation Event (Rasmussen, Fletcher, Brocks, & Kilburn, 2008; Reynolds, 2006). Although often referred to as "blue-green algae", they are not true eukaryotic algae (Reynolds, 2006). They are oxygenic, and their photosynthetic apparatus is speculated to form the basis for chloroplasts in eukaryotes (Raven & Allen, 2003). While most cyanobacteria in lakes are planktonic, some benthic species can occur in shallower basins, littoral areas and oligotrophic systems (Cantonati & Lowe, 2014; Quiblier et al., 2013; Smith et al., 2012). Genera such as *Cyanobium* and *Synechococcus* with cells less than 3 µm in size are classified as picocyanobacteria (Jasser & Callieri, 2016; Sieburth, Smetacek, & Lenz, 1978). Unicellular, colonial or filamentous morphologies can all occur within lakes (Reynolds, 2006). There is some evidence that some species form colonies in response to stressful conditions, and colonial forms can be more resistant to predation (Visser, Ibelings, Mur, & Walsby, 2005; Xiao, Li, & Reynolds, 2018). As key components of the photosynthetic phytoplankton within a lake by biomass, cyanobacteria directly contribute to the primary production of a lake (Garcia-Pichel, Belna, & Sus, 1995; Stockner, Callieri & Cronberg, 2000). Unlike green algae, however, cyanobacteria are largely unpalatable to usual predators such as herbivorous fish (Gulati & Demott, 1997; Sellner, 1997). Instead, their primary predators within a lake are typically bacteria, amoeba, protozoans and a limited suite of zooplankton (Bauer & Forchhammer, 2021; Dryden & Wright, 1987; Gustafsson & Hansson, 2004).

A unique characteristic of cyanobacteria is their toxin production. Cyanotoxins are produced as secondary metabolites (Kardinaal & Visser, 2005). The main known chemical structures are cyclic peptides (microcystins, nodularins) and alkaloids (anatoxin-a, cylindrospermopsins, saxitoxin, guanitoxin and lyngbyatoxin-a) and lipopolysaccharides (Chorus & Welker, 2021; Wood, Holland, et al., 2006; Wood, Maier, et al., 2017). Both toxic and non-toxic varieties of a species can co-exist within a colony, with toxins only produced in cells with the appropriate genetic architecture (Kardinaal & Visser, 2005). Within Aotearoa New Zealand, the most commonly occurring phytoplankton genera that produce cyanotoxins are *Microcystis*, *Cuspidothrix*, *Nodularia* and *Raphidiopsis* (formerly *Cylindrospermopsis*), however more have been observed as toxigenic overseas (Puddick, Kelly, & Wood, 2022). Furthermore, while many effects and producers of cyanotoxins are known, there are likely other compounds and effects still unknown (Chorus & Welker, 2021). The ecological role of cyanotoxins is still unclear, though they likely perform multiple roles including allelopathy against other phytoplankton and macrophytes, and protection against grazing (Fernando, Gerald, Mario, Miroslav, & John, 2008; Gross, 2003; Jang, Ha, & Takamura, 2007). Cyanotoxins can operate in a range of mechanisms when ingested, with common pathways targeting the liver, skin and nervous system (Merel et al., 2013). Symptoms after exposure can include respiratory failure, haemorrhage, rashes and gastrointestinal issues depending on the types of toxins present (Chorus, 2001;

Merel et al., 2013; Pearson, Mihali, Moffitt, Kellmann, & Neilan, 2010). Most cyanotoxin is contained within the cell, and so the greatest exposure risk comes from consuming the whole cell (Codd, Morrison, & Metcalf, 2005; Wood et al., 2009). As a result, larger fauna such as livestock, dogs and people are more at risk of cyanotoxin exposure as they drink water or consume filamentous mats (Codd et al., 2005; Wood et al., 2009).

Cyanobacteria are strong competitors against other phytoplankton taxa. They are broadly more tolerant of warmer temperatures than diatoms and green algae, with many species reaching optimal growth conditions above 25°C (Reynolds, 2006). Especially warmth-tolerant species such as *Dolichospermum circinalis* can be considered sentinels of climate change in lakes (Puddick et al., 2022). Some species have high sulphide tolerances, and can perform anoxygenic photosynthesis with sulphide as an electron donor (Cohen, Jørgensen, Revsbech, & Poplawski, 1986). While cyanobacteria utilise chlorophylls for photosynthesis, additional accessory phycocyanin, allophycocyanin and phycoerythrin pigments give them a further competitive edge (Merel et al., 2013). These phycobilin pigments are stored within phycobilisomes, and enable cyanobacteria to utilise more of the visible light spectrum for photosynthesis, give them their characteristic blue colour, and allow photoacclimation to changing light levels (Lee, 2018; Schallenberg, Pearman, Burns, & Wood, 2021). Some taxa such as *Dolichospermum* have gas vesicles that allow vertical migration in the water column to access light in the epilimnion and nutrients further down, while negatively buoyant taxa such as *Oscillatoria* settle out to the sediment (Visser, Ibelings, Bormans, & Huisman, 2016). Some cyanobacteria genera can overcome nitrogen limited conditions by differentiating their photosynthetic vegetative cells into heterocytes, which fix atmospheric nitrogen as ammonia for utilisation in the filament (Howarth, Marino, & Cole, 1988; Reynolds, 2006). These cells form under nitrogen-limited conditions and have thick glycolipid membranes ensure a low oxygen environment to protect the contained nitrogenase (Bothe, Schmitz, Yates, & Newton, 2010). When growth conditions become further unfavourable, akinetes can be formed in genera such as *Aphanizomenon*, *Gleotrichia* and *Dolichospermum* (Adams & Duggan, 1999; Livingstone & Jaworski, 1980). Akinetes are a dormant phase, storing nutrients in cold- and desiccation-resistant conditions (Adams & Duggan, 1999; Paerl, 2017). These akinetes can then germinate into vegetative cells when more favourable conditions return, allowing inoculation of a lake (Reynolds, 2006). These characteristics give cyanobacteria a significant advantage over other phytoplankton, and they can quickly proliferate in ideal conditions (Paerl, 2017).

Cyanobacteria records within Aotearoa New Zealand lakes have historically been limited both in time and scope (Wood, Crowe, Ruck, & Wear, 2005), but some insights are available. Species from a range of families have been identified from Aotearoa New Zealand lakes, with common observations from the *Microcystis*, *Dolichospermum* and *Oscillatoria* genera (Pridmore & Etheredge, 1987; Puddick et al., 2019; Wood et al., 2005). More taxa are generally recorded in North Island lakes (Pridmore & Etheredge, 1987). Community

compositions can change significantly within lakes over time, possibly driven by varying nutrient concentrations, stratification stability, altitude and climate conditions (Pridmore & Etheredge, 1987; Wood, Maier, et al., 2017). Eutrophic lakes tend to have lower cyanobacterial species diversity and more genera capable of toxin production than mesotrophic and oligotrophic lakes (Wood, Maier, et al., 2017).

2.3.1 Cyanobacterial Blooms

Although cyanobacteria are found in lakes across the full trophic spectrum, eutrophied waterways provide highly advantageous growth conditions for cyanobacteria (Conley et al., 2009; Reinl et al., 2021; Wood, Maier, et al., 2017). This relationship is further exemplified by the PhyCol water quality index, which specifies the contribution of cyanobacteria as a key measure (Katsiapi, Moustaka-Gouni, & Sommer, 2016). Genera particularly associated with eutrophic lakes are *Dolichopsermum*, *Microcystis* and *Aphanizomenon* (Cao et al., 2020; Paerl, 2017). Their nutrient harvesting mechanisms can efficiently scavenge nutrients from the water column, with nitrogen-fixing morphologies able to thrive in waterways with a low N:P ratio (Conley et al., 2009; Paerl, 2017). Vertically migratory species such as *Microcystis* can also transport nutrients from the hypolimnion to the epilimnion, further fuelling blooms (Cottingham et al., 2015; Guven & Howard, 2006; Shikata et al., 2015). Warmer waters inhibit competition from diatoms and green algae, while climate change further encourages phosphorous availability with longer stratification (Joehnk et al., 2008; Paerl & Huisman, 2008, 2009). With these eutrophic conditions, cyanobacteria can quickly bloom to very high cell densities, most often seen as a “pea soup” water colour and scums near the lake shore.

The ecosystem effects of cyanobacterial blooms can be catastrophic. Although significant producers of oxygen during photosynthesis, cyanobacteria are equally consumptive of dissolved oxygen during respiration. The most visible result of this is fish kills, often seen towards the end of summer in eutrophic waterways (Paerl, Fulton, Moisander, & Dyble, 2001; Wetzel, 2001). Blooms will increase the lake’s turbidity, preventing deeper light penetration (Paerl & Huisman, 2008). Nitrogen fixed by heterocytes is also released when cells die and lyse, further adding nutrients to the lake system. These factors often mean that cyanobacterial blooms can form a feedback loop that favour their own proliferation and drive lake flipping.

Recreation and food gathering can be affected by dangerous levels of cyanotoxin and unpleasant smells. Cyanotoxins have killed dogs and livestock both within Aotearoa New Zealand and internationally (McAllister, Wood, & Hawes, 2016; Negri, Jones, & Hindmarsh, 1995; Saker, Thomas, & Norton, 1999). Lakes within Aotearoa New Zealand known to contain *Nodularia* blooms have long histories of stock deaths, and saxitoxins were linked to the 1990 AD deaths of 1600 stock on the Murray Darling River in Australia (Bowling & Baker, 1996; Wood, Holland, et al., 2006). Filter feeders such as kākahi (*Echyridella menziesii*) can filter and bioaccumulate cyanotoxins (Clearwater et al., 2014; Wood, Briggs, et al., 2006).

Crassostrea gigas specimens from Hokianga Harbour tested positive for elevated cyanotoxins in 2004, associated with cyanobacterial blooms from Lake Omapere (Wall, Orlovich, Summerfield, Wood, & Rhodes, 2014). These detections resulted in the closure of several aquaculture farms during the season, incurring significant financial costs (Wall et al., 2014). Although a human death from cyanobacteria has not been recorded yet in Aotearoa New Zealand, there have been recorded human harm incidents overseas (Azevedo et al., 2002; Hawkins, Runnegar, Jackson, & Falconer, 1985; Hilborn & Beasley, 2015).

2.3.2 Cyanobacteria Detection

Cyanobacteria monitoring has traditionally been challenging. Visual identification requires a high level of expertise and time (Laroche et al., 2017; Wood, Maier, et al., 2017). Samples may need to be cultivated to aid identification, but this again relies on the time, facilities and expertise available. Blooms can be monitored via satellite imagery targeting both chlorophyll-a and phycocyanin, but this does not allow taxonomic insight. With these challenges, molecular identification is increasingly being utilised via environmental DNA (eDNA). Samples such as water are amplified and sequenced using next-generation sequencing and barcodes designed to target highly-conserved and low-variation sequences within an organism's genome (Taberlet, 2018; Wood, Maier, et al., 2017). The taxonomic composition (metabarcoding) or cell number (quantitative PCR) of the environmental sample can then be described (Taberlet, 2018). It can also allow a higher chance of species detection as litres of water can be concentrated into one eDNA sample (Boivin-Delisle et al., 2021; McColl-Gausden, Weeks, & Tingley, 2020).

Molecular detections do have some limitations. First, taxa detections rely on a well-developed and accurately built library of barcodes for detections (Cristescu & Hebert, 2018; Taberlet, 2018). An inaccurate or out-of-date library will risk missing present taxa and inaccurately assigning taxonomic descriptions to results (McColl-Gausden et al., 2020). Second, the ecology of eDNA is still unclear. Each strand of DNA will be subject to a range of processes including transport and decomposition within an ecosystem, and the extent to which each process has affected detection probability is unknown with each sample (Beng & Corlett, 2020; Cristescu & Hebert, 2018). Thirdly, the high sensitivity of PCR means that any sampling error can quickly be magnified through to results (Taberlet, 2018) . This includes issues like contamination, inappropriate barcode selections and poor study design (Cristescu & Hebert, 2018; McColl-Gausden et al., 2020). While these key limitations require careful method planning and an awareness of the inference precision available from a given set of results, cyanobacteria are more resilient to these limitations than other taxa such as fish. Sampling of cyanobacteria will typically involve capturing of whole cells and their intracellular DNA, conferring more degradation protection than extracellular DNA. Their bloom dynamics also enable easy confirmation of the organism presence within the environment, while their highly conserved genomes means their libraries and barcodes are well-characterised (Nübel, Garcia-Pichel, &

Muyzer, 1997; Shi & Falkowski, 2008). For these reasons, while eDNA continues to develop as a technique, a mix of traditional and molecular methods are used to currently detect cyanobacteria.

2.4 The Role of Paleolimnology

Lake management decisions are often made at the intersection of science and society. While science may inform suitable response options, funding and community preference play a key role in the final management strategies chosen (Gregory, Failing, Harstone, Long, & Ohlson, 2012; Joy & Canning, 2021). For lakes in a precarious or highly eutrophied state, such decisions can be high-stakes. Inappropriate strategies may be expensive and use up community goodwill for little ecological return, and in turn prohibit different actions being taken (Gann et al., 2019; Gregory et al., 2012). A key challenge in making these decisions is the limitations in the scientific data available; monitoring regimes provide decades of information at best, often taken at inconsistent intervals and with changing equipment (Gregory et al., 2012; Hamilton, 2019; Moss, 2018; Smol, 2008). Paleolimnology is a multidisciplinary science that reconstructs previous environmental conditions within lakes by analysing the physical contents of chronologically-laid benthic sediments (Cohen, 2020; Smol, 2008). It can therefore complement monitoring data to provide insight into much longer timeframes (Short et al., 2022; Smol, 2008). The ultimate result of this for lakes is often an insight into a baseline state prior to any human impacts, with proxies allowing exploration of potential drivers and thresholds of environmental change within each lake (Augustinus, Cochran, Kattel, D'Costa, & Shane, 2012; Short et al., 2022).

2.4.1 Reconstructing water quality

Key questions for paleolimnological reconstruction of water quality are frequently about the baseline trophic status of a lake, and the extent to which human actions are responsible (Abell et al., 2019; Kowalewski et al., 2016; Woodward & Shulmeister, 2006). Tracking eutrophication of lakes has traditionally been done via biotic indicators rather than geochemical proxies. Chironomids, diatoms and chrysophyte fossils are frequently used to infer historic lake productivity, due to their contemporary distribution patterns across lakes of different trophic levels (Bennion et al., 1996; Cohen, 2020; Gregersen & Simon, 2022; Kodama, Lyons, Siver, & Lott, 1997; Sandgren, 1991; Smol, 1985; Woodward & Shulmeister, 2006). Macrophyte macrofossils and pollen have also been used to infer trophic status (Kowalewski et al., 2016; Scussolini et al., 2011), while pyrite formation and the Mn/Fe ratio have been interpreted for changing levels of hypolimnetic oxygen (Naeher, Gilli, North, Hamann, & Schubert, 2013; Suits & Wilkin, 1998).

Wolfe et al. used diatoms and isotope analysis to determine that anthropogenic nitrogen inputs to alpine lakes in Rocky Mountain National Park were changing the lakes' algal communities beyond baseline conditions (2001). Diatoms showed that three Welsh lakes enriched by anthropogenic phosphorous inputs since the mid-20th Century were naturally eutrophic prior to modern human impact (Bennion et al., 1996),

while analysis of chironomids produced a clear timeline of eutrophication in a dystrophic Finnish lake linked to industrialisation and catchment ditching (Meriläinen et al., 2000). Valuable insight into eutrophication symptoms are also possible; blooms of *Didymosphenia geminata* during 2006 in two Canadian rivers were assumed to be modern introductions by people, but analysis of two sediment cores from lakes within the river system showed the blooms to be a response to anthropogenic climate change (Lavery et al., 2014).

Paleolimnology studies have also demonstrated that the differentiating factor between natural and cultural eutrophication tends to be the pace of change (Harper, 1992), with diatom stratigraphy in historically oligotrophic English lakes suggesting that eutrophication shifts occurred quicker and at a larger scale with human activity after 1930 AD than with neolithic settlement and deforestation (Haworth, 1985; Pennington, 1981). Wolfe et al. demonstrated that cultural eutrophication was clearly identifiable from natural trophic variability (2001). Some studies have identified both biotic and abiotic early warning indicators for a eutrophic transition (Reavie, 2020), and when important ecological thresholds have been crossed (Smol & Douglas, 2007).

Water quality reconstructions are limited within Aotearoa New Zealand paleolimnology literature (Woodward, 2013). Deforestation during the Māori subsistence era has been linked with increased erosion and minor influxes of nutrients to lakes (McWethy et al., 2010; Woodward, Shulmeister, Zawadzki, & Jacobsen, 2014). Climate has been demonstrated as a key factor in the trophic status of Onepoto maar through diatom analysis (Augustinus et al., 2012), while deforestation and early dairy farming have been linked to increases *Pediastrum* and a *Nodularia* bloom in Lake Forsyth (Woodward & Shulmeister, 2005). Diatoms showed a complete shift from macrophyte dominance to a hypertrophic state during European land-use in the shallow Wainono Lagoon (Schallenberg & Saulnier-Talbot, 2016) and greater nutrient availability in Northland dune lakes (Stephens, Augustinus, Rip, Gadd, & Zawadski, 2018) and Lake Oporoa (Short et al., 2022). Bacterial DNA (discussed further in Section 2.4.3) is increasingly being deployed in Aotearoa New Zealand through the Lakes380 programme (Pearman et al., 2020; Pearman et al., 2022; Picard, Pochon, et al., 2022; Picard, Wood, et al., 2022; Short et al., 2022).

2.4.2 Proxies

While environmental measures are commonly available in contemporary monitoring, paleolimnology relies on indirect measures (Smol, 2008). So-called “paleoenvironmental proxies” are chosen depending on the questions being asked from a sediment core (Smol, 2008). Multiple proxies are then brought together, forming a suite of data that gives insight into the environmental conditions occurring at the time the sediment was deposited (Birks & Birks, 2006; Smol, 2008). Due to the wide range in Aotearoa New Zealand lake types, ecosystem response to stress can vary significantly, and so each paleolimnology study must contextualise its results within the system it is surveying (Abell et al., 2019; Smol, 2008). The full list of

proxies used in this thesis and their interpretation is available in Table 2.1. Full discussion of each proxy is outside the scope of this thesis.

Table 2.1 *List of proxies used in this thesis, and their interpretation.*

Proxy	Interpretation
Pollen and charcoal	Terrestrial vegetation and burning (Faegri & Iversen, 1989; McWethy et al., 2010)
Trace metals	Heavy metal amounts; industrial activity and construction (Pb); aerial topdressing (Cd) (Barnes & Schell, 1973; Bramley, 1990; Cohen, 2020; Goyer, 1990)
Mn/Fe	Time spent in anoxic conditions (Naeher et al., 2013)
XRF scanning (ITRAX)	Elemental composition; erosion (Ti); authigenic carbonate precipitation (Ca/Ti) (Davies, Lamb, & Roberts, 2015)
Hyperspectral scanning ($RABD_{660\text{-}670}$)	Chlorophyll-a amounts (Butz et al., 2015; Butz, Grosjean, Goslar, & Tylmann, 2017)
Digital droplet PCR	Copy number of gene of interest – in this study cyanobacteria specific 16S rRNA (Picard, Pochon, et al., 2022)
Metabarcoding	Community composition – in this study cyanobacteria (Picard, Pochon, et al., 2022)

Pollen

Extensive research on pollen records has established a clear suite of indicator taxa for the different disturbance phases through Aotearoa New Zealand history. *Podocarpus*, *Prumnopitys*, *Dacrydium cupressinum* and other tall native tree pollen are indicative of native forest (McGlone, 1989). Māori arrival in Aotearoa New Zealand is typically inferred from concomitant decline in tall trees and the increase of *Pteridium esculentum*, commonly known as bracken fern, plus other seral species such as tutu (*Coriaria arborea*) (McGlone, 1989; McGlone & Wilmshurst, 1999). Further evidence of Māori settlement is represented by an increase in concentration of larger-size charcoal particles, with the rationale being that larger size particles cannot travel very far and therefore originate from nearby burning (Faegri & Iversen, 1989; McGlone, 1989). Early European arrival is indicated via the appearance of the exotic pollen such as *Rumex* and *Salix* along with renewed burning (Wilmshurst, 1997). *Pinus* pollen and an increase in Poaceae pollen are then associated with the late European conversion of remaining scrubland to pasture (Wilmshurst, 1997).

Cadmium

Cadmium is naturally rare in Aotearoa New Zealand, but high levels detected within our sediment cores are broadly indicative of superphosphate application (Bramley, 1990; Winder, 2009). Large increases are linked with aerial topdressing (Bramley, 1990; Parrish, 2020; Winder, 2009). This link is stronger in Aotearoa New Zealand than many other places in the world due to the country's early reliance on Nauruan guano deposits

for phosphate rock (Bramley, 1990; Gray & Cavanagh, 2022; MacLeod & Moller, 2006). Seabirds nesting within the Nauru area bioaccumulated and deposited high levels of cadmium within their droppings (Gray & Cavanagh, 2022; Morrison & Manner, 2005). Cadmium was then incorporated into superphosphate fertiliser and applied to the land, where it entered the local ecosystem (Bramley, 1990; Gray & Cavanagh, 2022). The depletion of Nauru phosphate rock and increasing awareness of cadmium accumulation motivated a shift to other phosphate sources during the 1990s AD (Gray & Cavanagh, 2022). Cadmium concentrations within Aotearoa New Zealand sediment cores therefore provide a unique insight into agricultural activity during the advent of intensive land-use.

2.4.3 Detection of cyanobacteria in paleolimnology

Characterising cyanobacteria in sediment cores has been historically challenging. As soft-bodied organisms, the cells do not tend to preserve well in sediments (Picard, Wood, et al., 2022). Detection of cyanobacteria has instead usually been via pigments such as canthaxanthin and echinenone (Butz et al., 2017; Gall & Downes, 1997; Picard, Wood, et al., 2022) and akinete germination (Livingstone & Jaworski, 1980).The rationale for this is that algae comprise most of the primary productivity within a lake. Some further resolution may be available in the 615 nm RABD band in hyperspectral scanning, which is theorised to detect phycocyanins (Paul D. Zander, Wienhues, & Grosjean, 2022), although this may instead be detecting chlorophyll-a (Page, 2022). Chlorophyll-a is therefore usually relied upon to interpret changes in algal biomass, as a major component of primary productivity.

Environmental DNA (eDNA) is increasingly being used as a proxy within paleolimnological studies to identify biological diversity, including cyanobacteria. Quantitative PCR techniques such as droplet digital PCR (ddPCR), and high-throughput sequencing techniques such as metabarcoding can be applied to lake core sediments (Picard, Pochon, et al., 2022), but the novelty of eDNA in paleolimnology studies means there are few examples of its use in cyanobacteria detection. Genetic detection of cyanobacteria in two perialpine Swiss lake cores has been confirmed to align with historic reports of cyanobacterial blooms, with toxin-producing genes detected in more recent decades (Monchamp, Pomati, Spaak, & Walser, 2016). Studies in Aotearoa New Zealand and internationally have linked land-use intensification and human activity within lake catchments to increases in cyanobacterial DNA copy numbers in sediment cores, as well as the expansion of potentially toxic cyanobacteria genera within a lake's community (Cao et al., 2020; Hobbs et al., 2021; Picard, Pochon, et al., 2022; Yan et al., 2019). Cyanobacteria have also been utilised as part of wider 16S rRNA bacterial datasets to successfully identify lakes with elevated trophic levels (Pearman et al., 2022). Some studies have suggested a link between introductions of exotic fish both in Aotearoa New Zealand and internationally and changing DNA copy numbers, and established possible baseline community composition (Hobbs et al., 2021; Picard, Pochon, et al., 2022). Changes in

cyanobacterial community composition have also been detected during establishment of a water reservoir (Li, Zhang, Xie, & Wang, 2019; Tse et al., 2018) and are linked to climate change (Monchamp et al., 2018).

As with any novel technique, key limitations remain for eDNA interpretation from sediment cores. The first limitation comes from unknown degradation dynamics (Cristescu & Hebert, 2018; Gilbert, Bandelt, Hofreiter, & Barnes, 2005). Detection of DNA within the sediment core requires several coalescing processes: the release of DNA from the target organism, the sinking of the target organism to the benthos, and the long-term preservation of DNA within the sediment (Cristescu & Hebert, 2018; Gilbert et al., 2005; Monchamp et al., 2021; Nwosu et al., 2021). Similar to surface water samples, there are unknown effects of organism ecology, degradation and oxidation upon the DNA. Quantitative interpretation of cyanobacterial DNA can also be complicated by the presence of more than one copy of the target gene in some cyanobacteria genera. For example, some *Cyanobium* have two copies of the 16S rRNA gene targeted by ddPCR in this study, and other genera such as *Microcystis* can have up to four copies (Picard, Wood, et al., 2022; Rinta-Kanto et al., 2005; Schirrmeister, Dalquen, Anisimova, & Bagheri, 2012). For these reasons, inference from sediment core eDNA must be made with a combination of proxies.

3 Chapter 3 – Site Description

3.1 Geography

The Manawatū-Whanganui region is situated within the central North Island of Aotearoa New Zealand, bordered by the Tasman Sea to the west (Figure 3.1). The area is culturally significant with extensive Māori habitation before European arrival. After European arrival, the catchments become largely agricultural, supporting primarily dairy, sheep and beef. There is also some production forestry involving exotic species including *Pinus radiata* (Palmer et al., 2010). The larger urban settlements within the Manawatū-Whanganui area are Whanganui, Palmerston North and Bulls, with many other small towns dotted throughout the landscape.

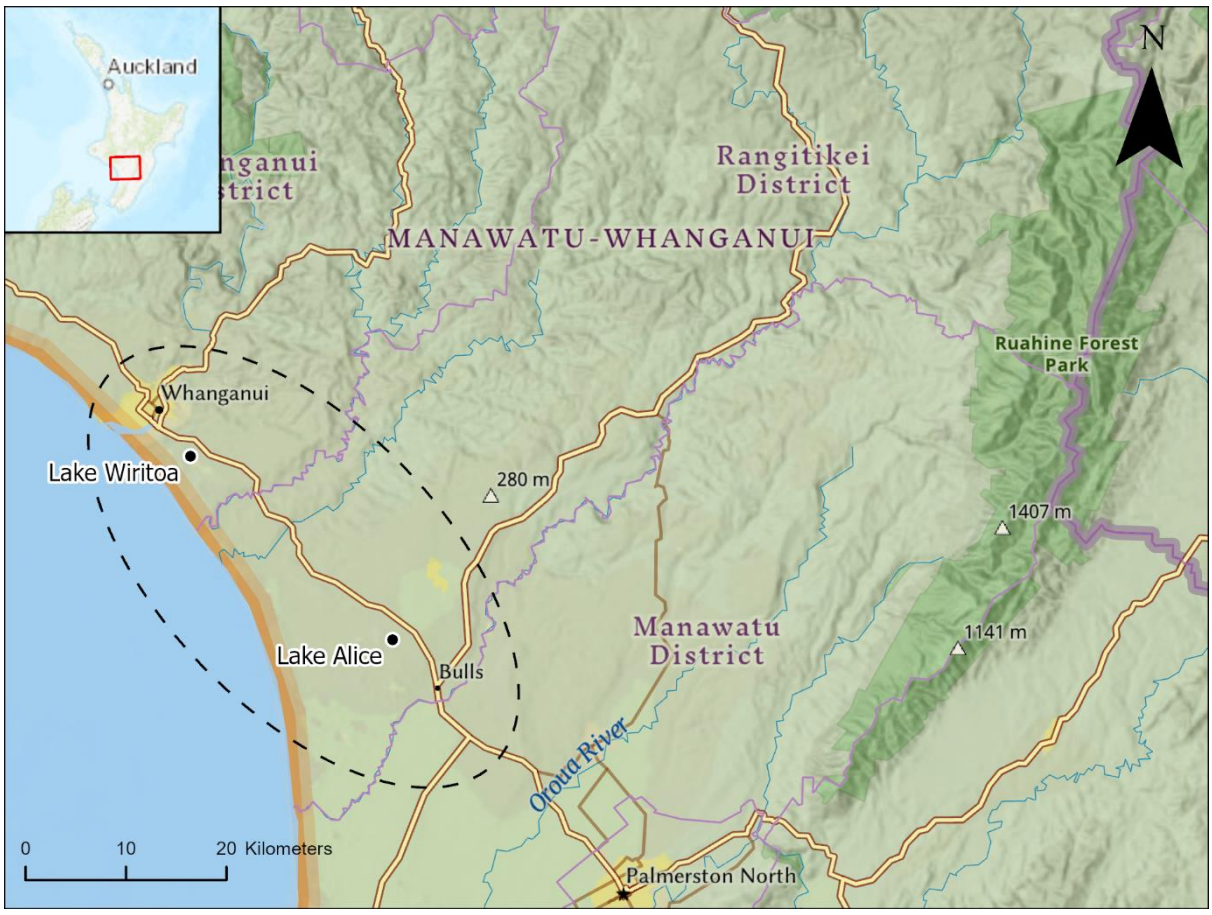

Figure 3.1 *Map of the Manawatū-Whanganui coastal plain, showing the locations of Lake Alice and Lake Wiritoa within the study area (dashed oval), and the Ruahine Ranges (Ruahine Forest Park).*

The Whanganui Basin extends from the west coast towards the Ruahine Ranges (Anderton, 1981; Rees, Palmer, & Palmer, 2019). It is geologically young, comprising late Quaternary sediments (Carter & Naish, 1998; Pillans, 2017). Massive sandstone dominates the inland areas, before transitioning to loess and then windblown sands closer to the coast. The coastal plain sits on top of the basin, extending approximately 13 km inland (Cowie & Campbell, 1965), formed through tectonic uplift in late Pleistocene time <1 Ma

(Trewick & Bland, 2012). Groundwater is deep and confined near the ranges (Hocking, 1964; Pattle Delamore Partners, 2019), and becomes shallower towards the coast, where it is often only inches below the surface (Hocking, 1964; Pattle Delamore Partners, 2019). In terms of pH, most of the coastal plain's groundwater is reducing, with a small oxic area to the west of Lake Alice (Horizons Regional Council, 2019). The Manawatū-Whanganui area generally experiences mild winters and warm summers (Hocking, 1964), with mean air temperatures in summer and winter of approximately 22°C and 5°C respectively (Chappell, 2015). The predominant winds are westerlies and north-westerlies with strong winds common throughout the year (Chappell, 2015; Hocking, 1964). Total rainfall in the lowland coastal plain is among the lowest in the North Island due to high country in the north and east, averaging less than 900 mm/year (Chappell, 2015).

The Manawatū-Whanganui coastal dunes cover approximately 109,265 hectares, and stretch east in consistency of the westerly prevailing winds (Hocking, 1964). The Whanganui, Whangaehu, Turakina, Rangitīkei and Manawatū rivers have then dissected the dunes while depositing sediment at the coast (Cowie & Campbell, 1965; Hocking, 1964). These dunes have been built over time in phases (Muckersie & Shepherd, 1995; Cowie, 1963; Hocking, 1964). The Foxton phase possibly started accumulating around 6,500 years before present (BP) (Muckersie & Shepherd, 1995). The dunes migrated inland until around 1,500 years BP, although this movement was likely intermittent and potentially influenced by climate variations associated El Niño/Southern Oscillation events (Muckersie & Shepherd, 1995). Older dunes have then likely been remobilised with Māori and European colonisation to create the Motuiti and Waitārere phases (Muckersie & Shepherd, 1995; Cowie, 1963). These reactivations over time due to the loss of vegetation cover have resulted in more complex and undifferentiated formations than the basic dune pattern (Hocking, 1964; Muckersie & Shepherd, 1995). The soils of the Whanganui coastal plain are mainly inorganic in their composition, reflecting the catchment geology of greywacke, mudstone, sandstone and volcanic rock (Hocking, 1964). These soils are broadly classified as naturally unsuitable for agriculture due to their sensitivity to disturbance, especially in the most active dune areas (Cowie & Campbell, 1965; Fletcher, 1987; McKelvey, 1999).

3.2 Dune Lake Ecosystems

The dune lake system along the Manawatū-Whanganui West Coast is of a globally rare type and so of high ecologically importance. Dune lakes (or aeolian lakes) are formed by wind movement of sand on a coast, and can be formed in three main ways. Dune barrage lakes can form behind shifting dunes as hollows, streams and depressions are dammed by advancing sand (Löffler, 2004). These lakes are typically very transitory unless deflation continues to scour the basin out (Wetzel, 2001), and ephemeral with increasing salinity due to evaporation (Tundisi & Tundisi, 2012). Deflation basins form as sand is picked up and moved by wind, scouring out a basin (Wetzel, 2001). These can also be highly transitory unless the basin becomes

deeper than the groundwater; these lakes are therefore often considered as exposures of shallow water tables instead of retained surface water (Löffler, 2004; Wetzel, 2001). While barrage lakes are usually triangular with the deepest point closest to the dune (Wetzel, 2001), deflation lakes are typically irregular oval in shape with concave shorelines downwind of the prevailing wind direction (Löffler, 2004). The rarest lake type is the perched dune lake, which can only form in old dune systems that have been stabilised by vegetation (Löffler, 2004). Their formation requires podsolization between organic matter and siliceous sand to form impermeable hardpans (Löffler, 2004); their retention requires either additional dune barrage or deflation processes (Wetzel, 2001).

The Whanganui West Coast dune lake system is comprised of both barrage and deflation formations within 10 km of the Tasman Sea (Cunningham, 1957; Fowles, 1984). Their shorelines are frequently concave on their southeast margins, matching their likely formation by westerly to north-westerly winds. The shallow and unconfined groundwater in the area is the primary water source for the lakes, supplemented by with rainfall and some minor surface flows (Cunningham, 1957; Hocking, 1964). Most of the lakes are exposed to the prevailing westerly winds, which assists water turnover throughout the year (Cunningham, 1957). Most have small outlets that drain to the Tasman Sea (Cunningham, 1957).

Very little historic information on the natural state of the dune lakes and wetlands exists. The earliest available report is from 1957 AD, in which some lakes are described as having a range of margins from drifting sand to dense vegetation (Cunningham). Noted plant species include *Typha*, *Eleocharis* and *Cladium* present to varying extents (Cunningham, 1957; Esler, 1978). Wading birds including *Phalacrocorax* frequently fed and nested around the lake margins (Cunningham, 1957). Phytoplankton communities within Aotearoa New Zealand dune lakes have been described as low abundance and taxonomically consistent, comprising mainly of *Volvocales*, diatoms and Peridiniidae (Cunningham, 1957). Both long-finned and short-finned *Anguilla* populations were present, some individuals reaching 9 kg in size (Cunningham, 1957). Freshwater invertebrates included freshwater mussels (*Echyridella*), kōura (*Paranephrops*), and crabs (*Amarinus lacustris*) in variable abundances (Cunningham, 1957). *Galaxias*, *Retropinna* and *Gobiomorphus* fish species were present at low numbers in dune lakes nationally (Cunningham, 1957).

3.3 Ecosystem pressures

The West Coast dune lakes face a number of pressures that are broadly resulting in eutrophication and poor water quality. The lakes are recognised as highly degraded and in need of management intervention (Drake et al., 2009; Gibbs & Champion, 2013; Horizons Regional Council, 2019; Waters, Kelly, Doehring, & Floerl, 2018). The low relief of the coastal plain and relatively high proportion of versatile soils has resulted in extensive modification including agriculture and forestry (Figure 3.2) (Booth, 1965; Fletcher, 1987). The

natural vegetation of the area was predominantly kahikatea (*Dacrycarpus dacrydioides*) forests, with areas of mataī (*Prumnopitys taxifolia*) forest inland (Esler, 1978; Maseyk, 2007). Dunelands were likely relatively consistent along the coast, sometimes reaching several kilometres inland (Hocking, 1964). Areas of historic duneland are now largely covered with exotic pine forestry used for timber production and to stabilise sand in the absence of native vegetation, and make the land more amenable to agriculture (Hocking, 1964; Wilson, 1959). Urban land-use along the coast is limited and concentrated into three main areas, of which the biggest is Whanganui. Applications of fertiliser, other soil amendments and drainage installation have expanded the area suited for agriculture, enabling pasture production and dairy farming almost to the coast despite the less-suitable soils (Booth, 1965).

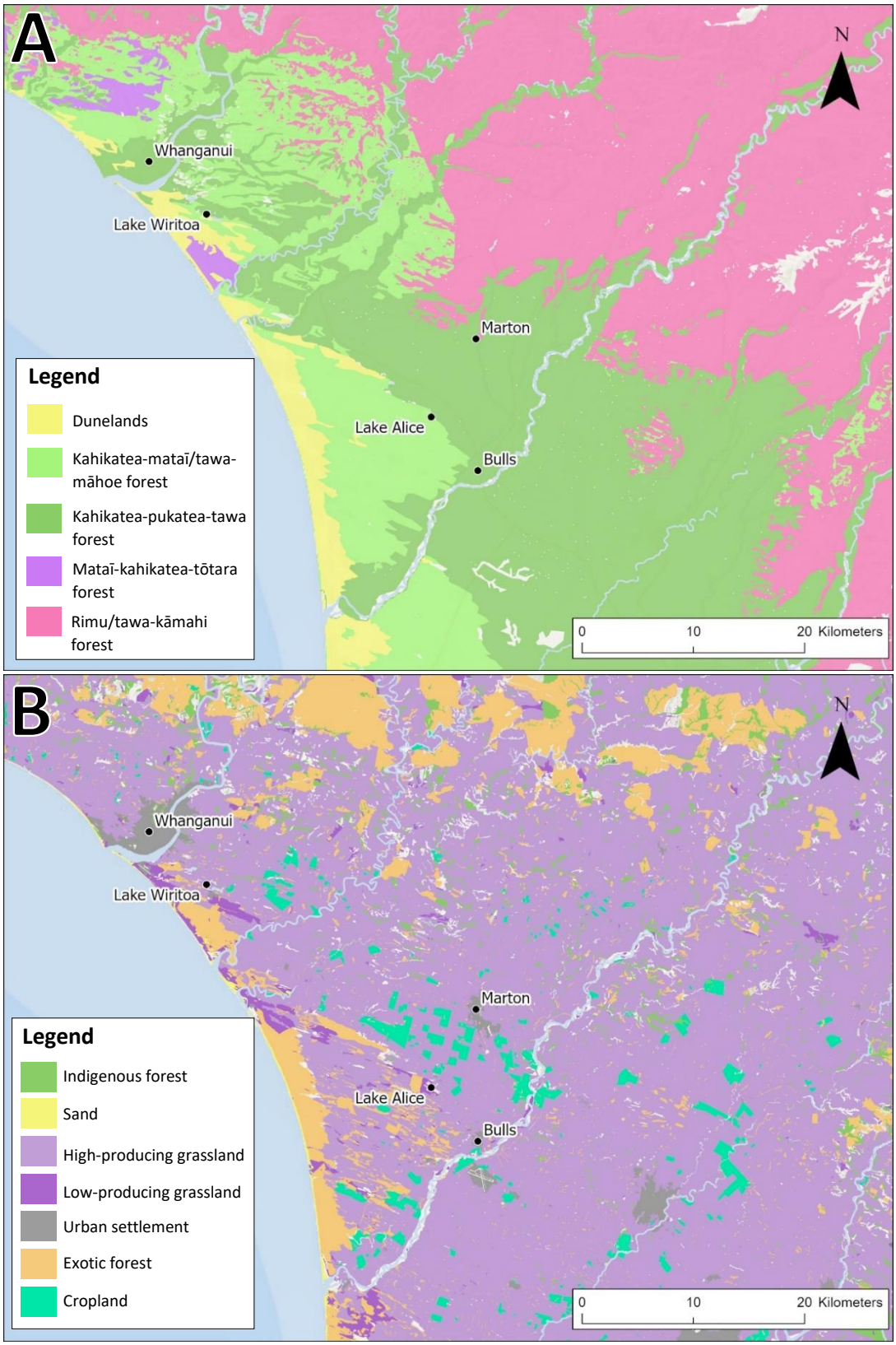

Figure 3.2 *The Whanganui West Coast, showing the potential vegetation (A) and 2018 land-use (B). Agriculture and exotic forestry have largely replaced the predicted kahikatea forests of the coastal plain. The location of urban centres and the two lakes studied are indicated. Data reproduced from the Potential Vegetation Layer (Leathwick, McGlone, & Walker, 2012) and the Land Cover Database v5.0 with permission from Manaaki Whenua Landcare Research New Zealand.*

Contaminants associated with agriculture such as phosphorus and nitrogen can enter the lakes via their small lotic inflows, overland flow after rain and groundwater seepage. While not completely endorheic, their small outflows limit the lakes' flushing capacity (Cunningham, 1957; Wetzel, 2001). Removal of terrestrial vegetation is likely to have warmed the lakes' waters, increased the amount of light available for photosynthesis, reduced shelter from winds and increased and accelerated overland water flow (Baillie & Neary, 2015; Fernandez, 2017; France, 1997; McCable, 1985; McGrane, 2016; Shatwell, Thiery, & Kirillin, 2019; White, Xenopoulos, Hogsden, Metcalfe, & Dillon, 2008; Wilmshurst, 1997). While current consented groundwater abstraction for irrigation and urban settlements is identified has having minimal pressure on levels (Pattle Delamore Partners, 2019), the additional presence of pine plantations could reduce the available lake recharge water (Fahey, 1994). Many lakes also have grazed margins, reducing the riparian area available for denitrification and contaminant sequestration outside the water (Clarkson et al., 2013; Gibbs & Champion, 2013). Through a combination of these factors, many lakes within this dune system are now classified as supertrophic with TLI scores above 5 with higher turbidity (Cunningham, 1957; Horizons Regional Council, 2019; Stats NZ, 2022; Waters et al., 2018).

Further pressuring the dune lakes is the presence of exotic flora and fauna. Exotic introductions tend to quickly follow migrations of people, both through intentional releases and accidental transfer (Burton, 2021; Pears, 1982). With many of the Whanganui lakes now used for recreational boating and fishing facilities, exotic aquatic plants can easily be transferred between lakes through contaminated equipment. Key aquatic weeds in these lakes include *Elodea canadensis*, hornwort (*Ceratophyllum demersum*), and oxygen weed (*Lagarosiphon major*) (Clayton, 1996). The Lake Submerged Plant Index (LakeSPI) scores of lakes within the area vary between minor (e.g., Lake Herbert) to severe (e.g. Lake Dudding) impact of exotic plant species (Burton, 2021). Some, including Lake Westmere are non-vegetated (Burton, 2021). Historic surveys support this current mix of scores, with Cunningham (1957) recording a mix of *Elodea*, *Ottelia*, *Potamageton ochreatus* and *Chara* species. Fauna introductions dominated by coarse fish such as perch (*Perca fluviatilis*), carp (Cyprinidae) and Gambusia (*Gambusia affinis*) have compromised the native ecology (Horizons Regional Council, 2019). Rainbow and brown trout (*Oncorhynchus mykiss* and *Salmo trutta*) have been successfully established in the dune lakes (Cunningham, Moar, Torrie & Parr, 1953).

3.4 Lake Alice

Lake Alice (40° 8'0.42"S, 175°19'54.75"E Figure 3.3) is located around 7.7 km from Bulls township, on private land. It has a maximum depth of 3.2 m, with surface area of around 12 ha (Land Air Water Aotearoa, 2023a). It has a polymictic mixing pattern without seasonal stratification (Land Air Water Aotearoa, 2023a). While some restoration planting has been completed around the lake perimeter, its 238 ha catchment is still dominated by agriculture.

Figure 3.3 *Lake Alice in the Manawatū-Whanganui coastal region, and associated streams. The star icon shows the sediment coring site.*

Lake Alice attracts significant bird life, including introduced Canada geese (*Branta canadensis maxima*), grey x mallard hybrid ducks (*Anas superciliosa × platyrhynchos*) and paradise ducks (*Tadorna variegata*), and game bird shooting is popular at the lake. The New Zealand Freshwater Fish Database (2002 and 2014) recorded native eels (*Anguilla* spp.), common bullies (*Gobiomorphus cotidianus*) and brown mudfish (*Neochanna apoda*), and introduced perch and goldfish (*Carassius auratus*) in the lake (Stoffels, 2022). The lake is described as being in moderate condition by LakeSPI due to the presence of the introduced plants *Potamogeton crispus*, *Egeria* and *Elodea* (Burton, 2021).

Lake Alice sits within the Southern Whanganui Lakes water management zone under Horizons Regional Council, which has been identified as having aesthetic, recreation, mauri, irrigation and biodiversity values to the local community within the One Plan, the regional resource management document (Horizons Regional Council, 2014). This zone has also been identified as a priority area for nutrient management (Land Air Water Aotearoa, 2023a). The lake is monitored for water quality quarterly via helicopter. Within the National Objectives Framework (NOF), Lake Alice sits in band B for median phytoplankton and band D for maximum phytoplankton and total lake nitrogen (Horizons Regional Council, 2019). The lake also fails to reach the One Plan targets for average and maximum chlorophyll-a, total nitrogen and total phosphorus

(Horizons Regional Council, 2019). It does reach the One Plan targets for ammoniacal nitrogen and *E. coli* (Horizons Regional Council, 2019). Lake Alice's TLI score is a supertrophic 5.9, and has been generally increasing from 4.8 in 2014 (Land Air Water Aotearoa, 2023a).

3.5 Lake Wiritoa

Lake Wiritoa (-39° 58' 28.70", 175° 5' 23.62"; Figure 3.4) is located about 7.7 km from Whanganui city, approximately 37 km north of Lake Alice. Lake Wiritoa is monomictic, and mixes in autumn (Land Air Water Aotearoa, 2023b). It has a maximum depth of 19.5 m, with a lake area of 22 ha (Land Air Water Aotearoa, 2023b). The lake has a mixture of private and public ownership in its 171 ha catchment, and is widely used for recreation (Gibbs & Champion, 2013; Land Air Water Aotearoa, 2023b). Farming dominates the lake's southern banks, the west is occupied by a holiday park, and its northern bank hosts a water-skiing club. There are extensive in-lake cables and structures built to accommodate water-skiing, including a boat ramp. It is hydrologically connected to Lake Pauri via a small stream that usually feeds from Pauri to Wiritoa; this can occasionally reverse (Gibbs & Champion, 2013). Due to its heavy recreational use, Wiritoa attracts less bird life than Lake Alice but there are some native and exotic species. It is classified as being in poor condition by LakeSPI due to impacts from *Egeria, Vallisneria*, *Potamageton crispus* and *Ceratophyllum* (Burton, 2021). The New Zealand Freshwater Fish Database records native eels and exotic perch, rainbow trout (*Oncorhynchus mykiss*) and goldfish (*Carassius auratus*) within the lake between 1979 and 1985 AD (Stoffels, 2022).

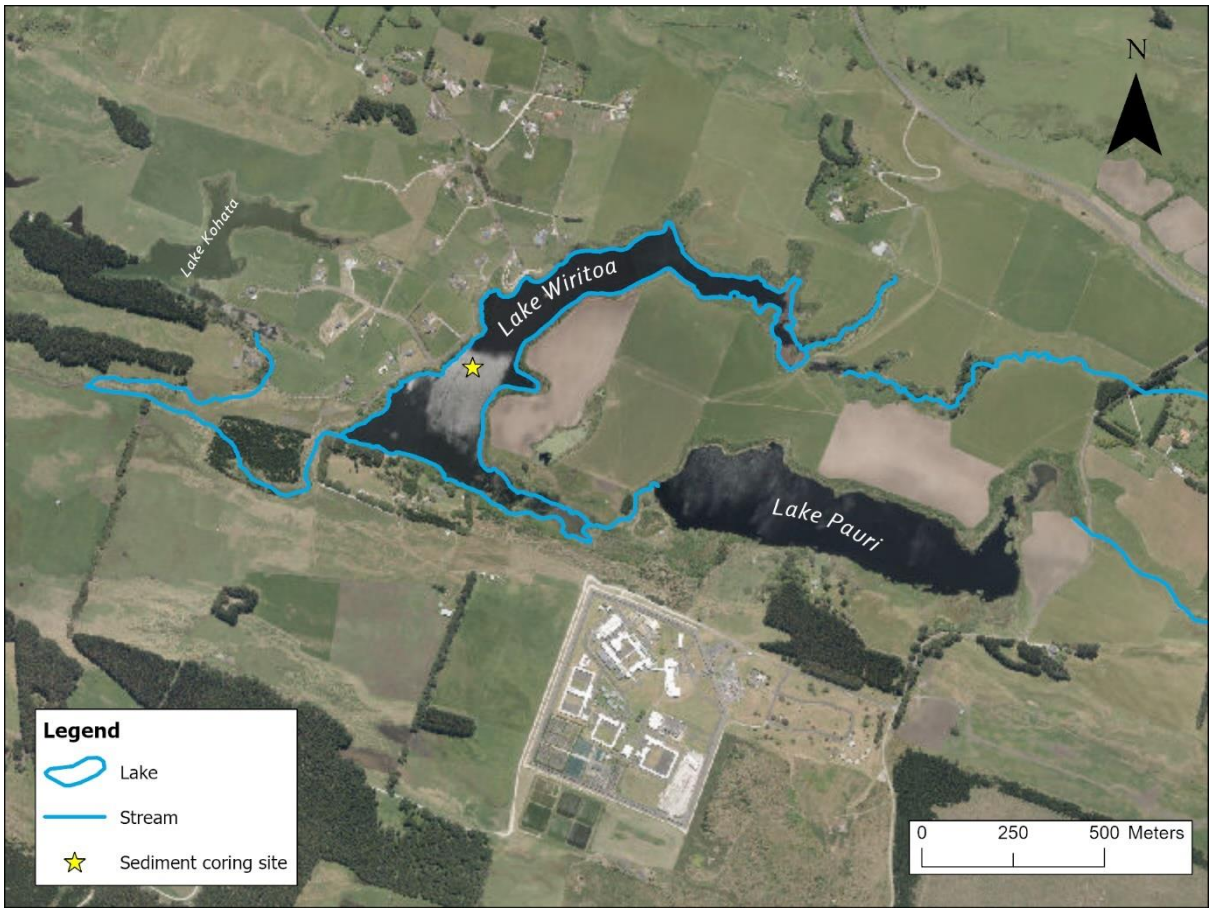

Figure 3.4 *Lake Wiritoa in the Manawatū-Whanganui coastal region, and associated streams. The star icon shows the sediment coring site.*

Lake Wiritoa is in the Kaitoke water management zone under Horizons Regional Council, an area that has been identified as a priority area for nutrient management (Horizons Regional Council, 2014; Land Air Water Aotearoa, 2023a). It has been recognised as having mauri, recreational, stock water, trout fishing and aesthetic values to the local community by the Council (Horizons Regional Council, 2014). Water quality sampling is conducted quarterly via boat, with additional bacterial and algal bloom sampling between November and May as part of contact recreation monitoring. Wiritoa is in band D for median phytoplankton, maximum phytoplankton and total lake nitrogen under the NOF; it fails to reach One Plan targets for average and maximum chlorophyll-a, total phosphorus and total nitrogen (Horizons Regional Council, 2019). As with Lake Alice, levels of ammoniacal nitrogen and *E. coli* in Lake Wiritoa are within One Plan targets. Wiritoa is, however, considered eutrophic with a TLI score of 4.4 and this has been trending down from 5.8 in 2014 (Horizons Regional Council, 2019; Land Air Water Aotearoa, 2023b).

4 Chapter 4 – Methods

A combination of contemporary field sampling and paleolimnological analyses were used to address the objectives in Section 1.1. These methods are outlined below. DNA analysis was conducted on both contemporary and sediment core samples (Table 4.1), with the workflow for both shown in Figure 4.1.

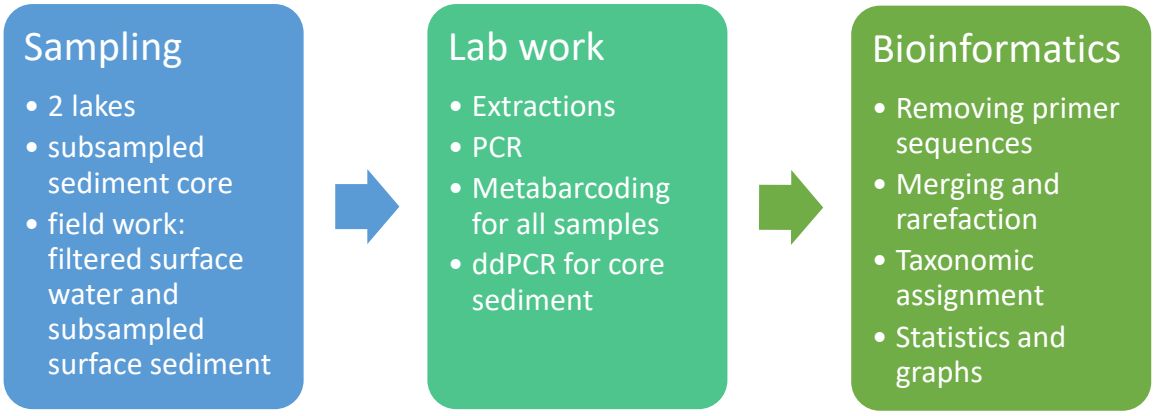

Figure 4.1 *Workflow for all DNA analysis used in this research.*

Table 4.1 *Summary of the sample types, mediums and respective DNA techniques used in both Lakes Alice and Wiritoa for this research.*

Sample collection	**Sample sourced from**	**Sample medium**	**DNA techniques used**	**Purpose**
Field work	Surface Sediment	Sub-sampled surface sediment from field work core	Metabarcoding	Validating sedimentary representativeness of sediment core DNA
	Surface water	1.2 µm and 0.22 µm Filters		
Lake coring	Lake sediment core	Sub-sampled core sediment	Metabarcoding & ddPCR	Identifying historic cyanobacteria communities

4.1 Historical Research

Historical research was conducted by the author to assemble a social history of the lakes, and provide a comparison to results from the proxies. Historic imagery was exported from Retrolens and Google Earth. Images were georeferenced, and key features annotated in ArcGIS Pro 2.8.2. Social history reconstructed from newspapers (PapersPast) and literature searches.

4.2 Surface Water (Contemporary Sampling)

4.2.1 Sample collection and processing

Field work for water and surface sediment samples was conducted at both Lake Alice and Lake Wiritoa over six months from November 2021 to April 2022 AD by the author. Sampling at both lakes each month was conducted on the same day via boat. Weather conditions, site shading, surface choppiness, water colour and type of visible cyanobacteria (suspended, scums, mats) were recorded at each visit. A 200 mm diameter black-and-white Secchi disk was used to determine clarity/turbidity of the lakes. Water temperature measurements were taken using a YSI Incorporated 30M Handheld Salinity, Conductivity, & Temperature System (Ohio, USA), off the same side as the Secchi disk. As the conductivity sensor was malfunctioning, these measurements were not recorded. Temperature readings were taken at 0.5 m intervals for 2 m to match the integrated sample depth, and then taken at 1 m intervals down the water column for the thermocline in Lake Wiritoa. Water samples were then taken with a 1.5 m long integrated sampler, constructed using 32 mm diameter pipe and bung. Water samples were always taken on the opposite side of the boat from the temperature and Secchi disk readings to minimise the risk of sediment contamination. After mixing to evenly distribute the cyanobacteria throughout the sample, the water was funnelled into a clean 1 L Schott bottle wrapped in tinfoil to minimise the degradation of cyanotoxins. Three replicates were taken each site visit. Water samples were immediately placed into a large Ziploc bag and then placed onto ice upon arrival at shore.

Lake sediment samples were taken in April 2022 AD using a Pylonex HTH gravity corer (Umeå, Sweden), at the end of the summer sampling period. Sediment sampling was conducted after water collection to minimise cross-contamination from disturbed sediment, and were taken in the location was the water samples. The top 5 mm of each sediment sample was scraped off and kept in a sterile Ziploc bag. Sediment samples were then double-bagged for protection, and placed immediately on ice.

All equipment was washed after sampling using a 20% solution of domestic bleach (0.2% sodium hypochlorite before dilution) to minimise cross-contamination between the lakes. All possible surfaces including the Secchi disk, raft and sediment corer were scrubbed with bleach, while the integrated sampler tube was soaked in bleach. Bleached equipment was left for 20 minutes before being rinsed with tap water. PPE was used during sampling and gloves were changed between lakes. Some equipment could not be

effectively bleached, and may be a source of contamination. This includes the water quality meter and ropes. Therefore, the DNA samples were obtained in minimised-contamination environments rather than sterile environments.

All field samples were kept on ice until processing in the laboratory within 24 hours of collection. The samples from Lake Wiritoa and Lake Alice were processed separately from each other to minimise cross-contamination, and were always processed in the order they were obtained (first Alice, then Wiritoa). Laboratory equipment and benchtop were cleaned with 20% bleach solution for 20 minutes before first processing. Gloves were changed between each sample. Each replicate was inverted to mix and processed as follows:

1) 50 mL of water frozen at -4°C for toxin analysis
2) 100 mL preserved with Lugols iodine (prepared according to Wood, Hamilton, Paul & Williamson (2009)) for visual identification
3) ~1 L water filtered through 47 mm 1.2 µm filter (LabServ; Massachusetts, United States of America) paper, filtered volume recorded
4) The water from (3) passed through a 47 mm 0.22 µm filter (Membrane Solutions; Shanghai, China)

Each filter membrane was cut in half using sterilised scissors, and each half stored in a labelled Eppendorf tube. The filters were then placed in new, labelled Ziploc bags and frozen at -80°C until extraction.

Each sediment sample was subdivided into three sterile 50 ml falcon tubes to provide technical replicates, and frozen at -80°C in labelled Ziploc bags. All laboratory equipment and benchtop were cleaned between filtering samples from different lakes with a 20% bleach solution before being rinsed with tap water.

Filtration controls to detect contamination were conducted on the fourth field sampling visit (February). This date was chosen as both lakes were sampled in this date, and land access was guaranteed with enough time for laboratory preparations. Tap water was filtered through the above protocol after the filtration of Lake Alice and the subsequent bleaching, and before the filtration of Lake Wiritoa samples. These control samples were stored in the same way as the other samples.

4.2.2 Contemporary Sample Metabarcoding

Metabarcoding was conducted on surface water and sediment samples to identify the contemporary cyanobacteria community composition (Pawlowski et al., 2022). The full workflow of sampling, extracting and bioinformatics is shown in Figure 4.1. Samples were extracted at Cawthron Institute in Nelson by the author after transport on ice. Polymerase chain reaction (PCR) was conducted by Cawthron Institute PCR was conducted at Cawthron Institute. Each step of the molecular process was conducted in dedicated and

partitioned sterile laboratories, with sequential workflow to minimise the risk of cross-contamination. Laboratories dedicated to DNA extraction, PCR set-up and template addition were equipped with UV sterilisation, which was switched on at least 15 minutes before and after each use. PCR set-up and template addition was always performed in laminar flow cabinets equipped with HEPA filtration, and aerosol barrier tips (Axygen; California, USA) were used throughout the process. All extractions were performed with the DNeasy Power- Soil DNA Isolation Kit (Qiagen; Hilden, Germany).

Using both the 1.2 µm and 0.22 µm filters, two filter halves from each surface water sample and control type (avoiding samples that had issues such as contamination) were transferred to the first tube of a DNeasy PowerSoil Pro Kit (Qiagen; Hilden, Germany) using tweezers wiped with ethanol between each transfer. Sediment samples from the final visit in April 2022 AD were thawed in a refrigerator over 24 hours, and 500 µl from each sample was placed within the Powerbead tube. DNA was then extracted from each sample type following the manufacturer instructions in batches of six to twelve samples. Due to difficulty sufficiently breaking down the 0.22 µm filters, these were manually broken down with a new pipette tip to aid smashing. A negative control containing all reagents but no sample was included once with the field samples. A spectrophotometer (Eppendorf AG; Hamburg, Germany) was used to measure DNA concentrations and quality with 2 µl of final elution. Any errors or observations made during the extraction process were recorded against the relevant sample ID.

PCR was conducted using the cyanobacteria-specific 16S rDNA primers CYB359-F (5'-GGGGAATYTTCCGCAATGGG-3') and CYB784-R (5'-ACTACWGGGGTATCTAATCCC-3') (Nübel et al., 1997). These primers amplify a fragment of approximately 400 base-pairs in length, in the V3 and V4 regions of the 16S rRNA gene. 10 µl MyFi DNA Polymerase (Bioline; Ohio, USA), 4 µl ddH_20 (Life Technologies; California, USA), 2 µl Primer F at 10 µm (Life Technologies; California, USA), 2 µl Primer R at 10 µm (Life Technologies; California, USA) and 2–5 µl template DNA were added to each PCR tube, with the goal was a 1:10 dilution of DNA to primer. The volume of DNA added varied depending on the concentration measured earlier: 2 µl of target DNA was added when concentrations were greater than 7 ng, 3 µl when concentrations were between 2–7 ng/µl, and 5 µl when concentrations were below 2 ng/µl.

PCR was conducted in a Mastercycler Nexus Gradient (Eppendorf; Hamburg, Germany). Denaturation was performed at 94°C for one minute. Thirty cycles were then conducted of 95°C for 15 seconds, annealing at 52°C for 15 seconds, extension at 72°C for 15 seconds, and final extension at 72°C for 7 minutes. PCR products were visualised using 1.5% agarose gel electrophoresis stained with RedSafe DNA Loading Dye (iNtRON Biotechnology Inc; Gyeonggi-do, Korea). PCR products were purified (Agencourt AMPure XP Kit, Beckman Coulter; California, USA), quantified (Qubit 2.0 Fluorometer, Invitrogen; USA), diluted to 5 ng μl^{-1}. The cleaned samples were sent to Auckland Genomics Facility (New Zealand) for paired-end (2 x 250 base

pairs (bp)) sequencing on an Illumina MiseqTM platform. Sequence libraries were prepared as detailed in the Illumina 16S metagenomics library prep manual. The protocol only deviated after the indexing PCR, where 5 ml of each sample was pooled and clean-up was undertaken on the pooled library.

4.2.3 Bioinformatic pipeline

All bioinformatic and statistical analyses were conducted using R (v4.0.2; R Core Team 2020) implemented in RStudio (RStudio Team, 2020) unless otherwise stated. The bioinformatic pipeline used is as described by Pearman et al. (2020) for Lakes380, and was done by Dr. John Pearman (Cawthron Institute) due to time constraints. Cutadapt58 (Anaconda environment adapted in R) was used to remove primer sequences with a 1 basepair mismatch allowed (Martin, 2011). General sequence quality assessment, quality profile plots, and the full amplicon workflow of quality filtering, merging paired-end reads, dereplication, chimera identification, sample inference and taxonomy assignment were performed in DADA2. Forward reads were truncated at 225 basepairs while reverse reads were truncated at 215 basepairs. The maximum number of expected errors (maxEE) per read was set at two and four for forward and reverse reads respectively, with other parameters set to default. A parametric error matrix was calculated for forward and reverse reads using the first 108 basepairs of the sequences, which were checked for convergence. Sequences were dereplicated, and pseudo-pooling was used to infer the sequence variants based on their respective error matrix. Singletons were discarded. The remaining paired-end reads were then merged allowing a 1 basepair maximum mismatch and requiring a minimum overlap of 10 basepairs. This produced a sequence table, prepared in the phyloseq package. Samples from all sequencing runs were merged into one sequence table, with amplicon lengths filtered to retain only those ranging from 379 to 403 basepairs. These were then checked for chimeras via the consensus method. Taxonomic assignment was completed for each resulting Amplicon Sequence Variant (ASV) from Kingdom to Genus using a training set from the SILVA database r138. The taxonomy for each rank was assigned to the ASV if the prediction of the SILVA classifier was estimated to be correct at 85% or more (min bootstrap).

Phyloseq was further used to undertake merging, rarefaction and richness measures . All non-bacterial reads were removed from the dataset. The vegan package was used to plot rarefaction curves, visualising sampling depth for each sample. Rarefaction of the entire dataset was undertaken in phyloseq at 10,400 reads per sample on the remaining bacterial reads through random sub-sampling with no replacement. Some samples appeared to have no cyanobacteria ASVs following rarefaction as their very low numbers of cyanobacteria reads were removed during the rarefaction process. Only ASVs assigned for photosynthetic cyanobacteria were selected for further univariate and multivariate analysis.

4.3 Sediment Core (Environmental Reconstruction)

4.3.1 Lake Coring

Both Lakes Alice and Wiritoa were cored by the Lakes380 team on 29th July 2020, with an UWITEC (Mondsee, Austria) hammer gravity corer cleaned with bleach (2% sodium hypochlorite) before coring. Cores were taken from the lake depocenters. Florist foam was packed into the top of the cores to prevent sediment movement. Cores were cut into lengths of one metre for refrigerated transport after settling. Cores were then stored in complete darkness at 4°C until subsampling.

4.3.2 Sub-sampling

Sediment cores were systematically sub-sampled by the Lakes380 team for chronology, pollen counting, trace metal analysis, ddPCR and metabarcoding. Cores were halved using a manual saw and guillotine in a room isolated from all DNA work. The sediment colour, type and presence of organic material were all described, and the cores were photographed. Half of each core was used for non-destructive analyses via a hyperspectral imaging scanner (HSI) and an ITRAX X-Ray Fluorescence scanner (XRF). Destructive analyses were conducted on the other core halves. A DNA-free spatula was used to remove the top 2–3 mm of the half-core to prevent cross-contamination during splitting. Sub-samples of approximately 0.5 g were taken from the centre of the core-half, every 1–2 cm in newer sediments and every 4–5 cm in older sediments. This resulted in 164 sediment subsamples for Lake Wiritoa and 61 for Lake Alice. Sub-samples used for DNA analysis were frozen at -20°C and kept in the dark until extraction.

4.3.3 Pollen analysis

Pollen and charcoal processing and counting was conducted at GNS Science by Dr. Xun Li. Pollen was extracted from 0.25cm^3 of sediment following the standard laboratory technique described in Faegri & Iversen (1989), with 10% hot hydrochloric acid, acetolysis and 6-micron sieving. Samples were taken at variable intervals depending on depth down the core: every 1–2 cm and 3–4 cm in the upper 65 cm of core, and every 10 cm for lower sections. Calculation of pollen concentrations was achieved by adding exotic *Lycopodium* tablets (Batch# 140119320). Pollen and spores were observed on a light microscope at 400x and 1000x magnification. Both standard texts and reference collections of Aotearoa New Zealand pollen were used to make spore and pollen identifications. Charcoal was counted as a number of fragments and presented as a concentration per cm^3.

Pollen diagrams were prepared by the author, and presented as relative frequencies of minimum 150-grain sums, inclusive of all dryland plants (trees, shrubs and herbaceous plants, exotic taxa and the bracken fern *Pteridium esculentum*). Other plant groups including wetland and aquatic taxa, ferns, tree ferns and non-palynomorphs were instead presented as percentages of the dryland pollen in addition to the respective group. *Pteridium esculentum* was included within the dryland sums due to its functional morphology being

more similar to a shrub than a fern within disturbed landscapes (McGlone et al., 2005). Pollen data was then used to identify undisturbed pre-human, Māori subsistence and European intensifying agriculture occupation periods within the catchments of both Lake Alice and Lake Wiritoa.

4.3.4 Trace Metals

Trace metal analysis was conducted by Analytica laboratories (Hamilton, Aotearoa New Zealand) for cadmium (Cd), iron (Fe), manganese (Mn), and lead (Pb). Sediment was dried and then analysed according to the United States Environmental Protection Agency's method 200.8, utilising acid digestion and Inductively Coupled Plasma-Mass Spectrometry (ICP-MS). The Mn/Fe ratio was then calculated from the returned values. Reporting limits are described in Table 4.2.

Table 4.2 *Reporting limits of the trace analysis for each element tested within the sediment cores for Lake Alice and Lake Wiritoa.*

Metal	**Reporting limit (mg kg^{-1})**
Cadmium (Cd)	2.5
Iron (Fe)	0.05
Manganese (Mn)	0.075
Lead (Pb)	0.005

4.3.5 Itrax Scanning

Itrax scanning was conducted by the University of Otago Repository for Core Analysis using a Cox Analytics Itrax µ-XRF Core Scanner. Potential contaminants were removed by scraping away 1–2 mm of the surface sediment. A chromium and molybdenum x-ray tube configured at 30 kv, 55 ma and 10 s integration time was then used to obtain relative downcore abundance data of major and trace elements at a 1 mm resolution. While a range of elements were analysed, only concentrations of titanium normalised to incoherent scattering and normalised concentrations of calcium to titanium (Ca/Ti) were included (Davies et al., 2015; Hinojosa, Moy, Vandergoes, Feakins, & Sessions, 2019).

4.3.6 Hyperspectral Image Scanning

Hyperspectral imaging was undertaken by GNS Science. Only the relative absorption band depth 660–670 index ($RABD_{660–670}$) was scanned. The results are then interpreted as indicative of chlorophyll-a and therefore algal abundance (Butz et al., 2017; Schneider, Rimer, Butz, & Grosjean, 2018; P. D. Zander, Żarczyński, Tylmann, Rainford, & Grosjean, 2021). A Specim sCMOS-CL-50-V10E-SCB camera was used to scan the cores, following methods outlined by Butz et al. (2015). The spatial resolution of the captured measurements was 41 µm, while the spectral resolution was 1.3 nm. After analysis with the $RABD_{660–670}$ index, results were then converted to a spectral index (Butz et al., 2015). Values ranged between 1–2, with higher values indicating higher amounts of chlorophyll-a and its degradation compounds.

4.3.7 Sediment core DNA samples

The 0.25 g sediment core sub-samples taken during the step at Section 4.3.2 were used for both ddPCR and metabarcoding. All sediment core DNA extractions and processing were conducted by Cawthron Institute staff. Extraction, amplification and bioinformatics methods followed were the same as described in Section 4.2.2 with aerosol barrier tips (Axygen; California, USA for PCR or epT.I.P.S., Eppendorf; Hamburg, Germany for ddPCR), except where described below.

4.3.7.1 Sediment core ddPCR

Digital droplet polymerase chain reaction (ddPCR) was used to quantify the amount of total cyanobacteria from core sedimentary samples. All samples were diluted for the ddPCR process, ranging from 1/10 to 1/1000 depending on sample depth. ddPCR was completed using the BioRad QX200 system (California, USA), along with the CYAN 108F (5'-ACGGGTGAGTAACRCGTRA- 3') (Urbach, Chisholm, & Robertson, 1992) and CYAN 377R (5'- CCATGGCGGAAAATTCCCC-GACTACTGGGGTATCTAATCCCATT-3') (Nübel et al., 1997) primers. These target a ~270 basepair region of the 16S rRNA gene . All plates contained at least one negative control with no template DNA, and one positive control (cultured cyanobacteria DNA). Each 22 µl reaction was loaded onto a semi-skirted 96-well plate with 0.2 µl of each primer at 10 µm, 4 µl of diluted template DNA, 2×BioRad QX200 ddPCR EvaGreen Supermix (California, USA) and 7.6 µl of DNA/RNA-free water (Life Technologies; California, USA). Nanodroplets were generated for each reaction containing 20 µl of the mixture and 70 µl of Evagreen droplet oil by the BioRad QX200 system. The resultant 40 µl nanodroplets were then transferred to another semi-skirted 96-well plate for amplification. The thermo-cycling conditions were denaturation at 95°C for 5 minutes, 50 cycles at 95°C for 30 seconds, annealing at 56°C for 1 minute, extension at 4°C for 5 minutes and final extension at 90°C for 5 minutes. The plate was then analysed on the QX200 droplet reader. Droplet counts were fitted to a Poisson distribution using the QuantaSoft Analysis software (BioRad; California, USA), giving a target DNA concentration expressed as number of gene copies μl^{-1}. Gene copies were then standardised to total DNA concentration using the equation below:

Equation 4.1 *Calculation of target DNA concentration (ng μl^{-1}) by normalising to total DNA.*

$$\text{Target DNA concentration (ng } \mu l^{-1}) = \frac{\left(\frac{\text{nb copies}}{\mu l} * \frac{\text{total Mastermix volume (22µl)}}{\text{template DNA volume (4µl)}} * \text{dilution factor (10-1000)} * \text{DNA extraction volume (100µl)}\right)}{\text{total DNA concentration in sample}}$$

4.3.7.2 Sediment core metabarcoding

Metabarcoding in the core was used to reconstruct the historic cyanobacteria communities within the lakes. PCR was conducted using the cyanobacteria-specific 16S rDNA primers CYB359-F (5'-GGGGAATYTTCCGCAATGGG-3') and CYB784-R (5'-ACTACWGGGGTATCTAATCCC-3') (Nübel et al., 1997). Thermocycling conditions were denaturation at 95°C for 1 minute, 35 cycles at 95°C for 30 seconds, annealing at 52°C for 15 seconds, extension at 72°C for 15 seconds, and final extension at 72°C for 7 minutes. Sedimentary PCRs were amplified in batches of 20 samples with a negative and positive control, containing AmpliTaq Gold 360 Master Mix (Life Technologies; California, USA), 360 GC enhancer (Life Technologies; California, USA), Bovine Serum Albumin (Sigma-Aldrich; Massachusetts, USA), primers at 10 µm, DNA/RNA free water (Life Technologies; California, USA) for a total volume of 48 µl each. PCRs were conducted using the same primers as in Section 4.2.2. A 1.5% agarose gel electrophoresis gel stained with RedSafe DNA Loading Dye (iNtRON Biotechnology Inc; Gyeonggi-do, Korea) was used to visualise all amplicon products, with UV illumination to check for amplication of a single 400 basepair product. PCR products were diluted to 5ng μl^{-1} and sent to sequencing at Auckland Geomics (University of Auckland) after purification (Agencourt AMPure XP Kit; Beckman Coulter, USA) and quantification (Qubit 2.0 Fluorometer, Invitrogen; Massachusetts, USA). The Nextera™ Index kit (Illumina; California, USA) was used to add sequencing adapters and sample-specific indices to each amplicon via a second short round of PCR. Amplicons were pooled into a single library and paired-end sequences (2 x 250 bp) were generated on a MiSeq™ instrument using the TruSeq™ SBS kit (Illumina; California, USA). Sequence data were demultiplexed using MiSeq Reporter (v2), with forward and reverse reads then assigned to samples.

4.4 Statistical analysis

All downstream analysis was conducted by the author in RStudio version 4.0.2 (RStudio Team, 2020). Packages used were vegan (Oksanen et al., 2020), tidypaleo (Dunnington, Libera, Kurek, Spooner, & Gagnon, 2022), phyloseq (McMurdie & Holmes, 2013), ggplot2 (Wickham, 2016), tidyverse (Wickham et al., 2019) and rioja (Juggins, 2020). Pollen diagrams were created in TILIA 3.0.1 (Grimm, 2019) and rioja (Juggins, 2020). Species occurrence patterns from all metabarcoding datasets were summarised using non-metric multi-dimensional scaling (NMDS) with a Bray-Curtis distance (Legendre & Legendre, 2012). Zones within the sediment core were delineated using paleolimnological proxies. Statistical significance in the cyanobacterial community composition between these zones was then tested for using the adonis function from the vegan package (Oksanen et al., 2020). Statistical significance of drivers was tested for using a distance-based redundancy analysis with a Bray-Curtis distance and depth as a condition. Constrained hierarchical clustering (CONISS) analysis was used to identify zones of similarity within the cyanobacterial communities of each lake in rioja (Juggins, 2020). This was performed using Bray-Curtis distance matrices at the genus level, with sample order as the constraining factor.

5 Chapter 5 – Results

5.1 Historical Research

Archaeological evidence of extensive Māori settlement has been found along the Whanganui coastal area, including shellfish pits, settlement sites and middens (Marr, 2003). An 1851 AD account of the Whanganui coastal dune area by early settler George Rees describes the forests as having been cleared by Māori for hundreds of years before European arrival, with vegetation instead comprising of indigenous scrub, grasses, rushes and flax (Hocking, 1964; Marr, 2003). Semi-nomadic groups have been dated in the area to the 1400s AD, prior to bigger tribal settlements (Marr, 2003). The Whanganui coastal inland waterways were highly valued by Māori, and populations often increased in summer during seasonal fishing (Waitangi Tribunal, 2015). The exact date of European arrival in the Whanganui area is unknown, though most likely occurred during the 1830s AD (Marr, 2003). Alteration of the lakes and their surrounding landscapes occurred quickly after European arrival, with both catchments becoming largely agricultural. Aerial topdressing in the Kaitoke Lakes area first occurred in May 1950 AD ("Wanganui Farmer Uses Own Plane to Put Manure on his Farm," 1950). While Lake Alice sits outside of the Kaitoke Lakes catchment, its proximity suggests that timelines for aerial superphosphate dressing of Alice were similar to that of Wiritoa.

5.1.1 Lake Alice

The earliest account of Lake Alice in written history is in 1858 AD, where the land is described as sheep farmland planted in English grass ("Valuable Freehold Land, Sheep and Sheep Run,"). Advertisements in 1862 AD repeat this description with the additional information of 30 acres being covered in manuka ("Town and Country Lands,"). Gorse was removed around the lake in 1934 AD ("Engineer's Report,"). Dairy farming was first recorded around Alice in 1913 AD ("Clearing Sale of High Class Dairy Stock,"), after the construction of Lake Alice Road around 1907 AD ("Rangitikei County Council").

Lake Alice Hospital was the most significant urban development, situated approximately 1 km north of the lake. The hospital was proposed as a villa-style treatment centre for the mentally ill in 1938 AD ("New Mental Hospital,"), with work beginning in 1945 AD ("New Institution,"). The hospital was self-sufficient, including plans for a herd of 100 dairy cows ("First Part of £2,000,000 Mental Home Completed," 1950; "New Mental Home," 1945). Water was temporarily drawn from the lake for the facility in 1948 AD when the water tower commenced operation ("Lake Alice Water Tower," 1948). The hospital opened with 50 patients in October 1950 AD ("First Part of £2,000,000 Mental Home Completed," 1950). Hundreds of patients were housed before the facility closed in 1999 AD (Stowell, 2010). Following closure, the hospital site remained in a dilapidated state until being sold with the aim to return the area to dairy pasture ("New vision for Lake Alice," 2009).

As a key indicator of European presence, establishing when *Pinus* species arrived within the Whanganui region is important. The Forest Branch of the New Zealand Lands Department was founded in 1897 AD with the goal of establishing forestry nationally (McKelvey, 1999). The encroachment of sand dunes onto pasture along the highly mobile west coast was identified as a key concern for settlers. The passage of the 1903 Sand-Drift Act directly addressed this, legislating for schemes to control the movement of sand by both the government and affected landowners (McKelvey, 1999). Experimental government planting of pine to achieve this goal in the Whanganui-Rangitīkei coastal area started in 1916 AD, with *Pinus radiata* becoming the preferred species (McKelvey, 1999). Exact dates of planting around Lake Alice are unavailable, although the largest forest in close proximity to the lake today is Santoft Forest. Santoft was reported as being in its second rotation by 1988 AD (Ellegard, 2019; McKelvey, 1999), indicating that the forest was likely originally planted between 1950 and 1965 AD.

Lake Alice was described as a favourite of New Zealand Governor Sir George Grey during his 1862 AD visit to Whanganui with the goal of introducing exotic fish, birds and other animals ("Fish Lakes," 1862). Exact introductions to Alice are not mentioned, but it is likely the lake is grouped into the wider group of Whanganui Lakes by the Whanganui Acclimatisation Society (founded in 1863 AD and later Fish & Game). Therefore, fish introductions to Lake Alice mirror those described for Lake Wiritoa in Section 5.1.2. Game bird hunting is prevalent both historically and today at Lake Alice. Reports of significant numbers of duck start in 1924 AD ("Good Duck Shooting"), with frequent reports of kill numbers throughout historic newspapers. The lake was fenced off from cattle with significant riparian planting taking place by 2009 AD ("New vision for Lake Alice"). It is unknown if this has positively influenced the ecological status of the lake as of 2022 AD.

5.1.2 Lake Wiritoa

The social history of Lake Wiritoa is much more comprehensively documented than that of Lake Alice. The Campbell family started dairy farming adjacent to Lake Wiritoa in 1841 AD (as cited in McPhail, 2015). Jessie Campbell's journals and letters describe the land as being easily cleared, with a dairy herd of cattle by 1843 AD (as cited in McPhail, 2015). Further land clearance occurred in 1845 AD. Ownership of the lakebed was transferred to the Crown with the Whanganui Purchase in 1848 AD; the Crown then sold part of the lakebed to private owners while retaining the rest as public land (Waitangi Tribunal, 2015). All tuna (eel) and īnanga cuts (man-made drains from lakes or swamps that facilitate fishing) within the lake were reserved for Māori as part of the purchase (Waitangi Tribunal, 2015; Marr, 2003). The completion of the transfer resulted in more land surrounding the lake being granted to European settlers (Waitangi Tribunal, 2015). By 1858 AD, the area between Lake Wiritoa and the Whanganui River was described as being partly in pasture, part horticulture and part bush and fern ("Newton Lees"). By 1870 AD, a flax mill was present on the banks of Lake Wiritoa ("£10 Reward"), although further details are unknown.

Lake Wiritoa was a primary location for the introduction of exotic species by the Whanganui Acclimatisation Society. Black swans (*Cygnus atratus*) were released into the lake in 1866 AD, and formed a breeding population ("Black Swans"). Carp (*Cyprinidae*) were introduced in January 1868 AD, while perch (*Perca fluviatilis*) and trout (*Salmonidae*) were imported in October of the same year ("Acclimatization" 1868; "Wanganui Acclimatisation Society," 1868). Tench (*Tinca tinca*) and more perch were ordered from Melbourne in November 1870 AD for release in Whanganui ("Acclimatisation Society," 1870). By 1875 AD, the introduction of perch to the area was declared a tentative success, while efforts to introduce carp continued with a further release in 1872 AD ("Untitled," 1875; "Wanganui Acclimatisation Society," 1872). The detection of these species in the lake during the 1970s AD to today indicates the introduction efforts were successful.

As part of the same dune lake system as Lake Alice, Lake Wiritoa was also affected by the 1903 Sand-Drift Act. Harakeke Forest (also known as Lismore Sand Forest) is the pine plantation closest to Wiritoa, approximately 1.5 km west of the lake. Its plantation date is unknown, but may be similar to that of Santoft. Development around Lake Wiritoa increased after the 1940s AD. Scouts New Zealand leased land from the Government on the lake's west bank in 1951 AD for construction of Scoutlands camp (Flahive, 2018). This camping facility continues to operate today in private ownership as Lakelands Holiday Park (Dudman, 2018). Management of the lake water was transferred from the Crown to Wanganui County Council in 1971 AD, with recreational areas to be developed (Fowles, 1984; Waitangi Tribunal, 2015). Water skiing facilities were constructed in the lake, with tournaments being reported during the 1970s AD ("Canterbury skier leads," 1971). Kaitoke Prison (also known as Whanganui Prison) was constructed in 1978 AD on the south bank of the hydrologically-connected Lake Pauri (Department of Corrections, 2010; Gibbs & Champion, 2013). By 2005 AD, the prison had opened more units to house a total of 252 inmates (Department of Corrections, 2010). While the prison's sewage treatment plant discharged treated effluent to land at the south of the facility, stormwater is discharged directly into Lake Pauri near its ephemeral connection to Lake Wiritoa (Gibbs & Champion, 2013). Given the proximity of the prison to the lake, there are still some unresolved questions about whether the discharged effluent is infiltrating the lakes through surface or sub-surface flow (Gibbs & Champion, 2013).

5.2 Cyanobacterial blooms and water clarity

Lake Alice and Lake Wiritoa both had visible algal blooms during field sampling (Figure 5.1). Wiritoa experienced blooms large enough to form scums in November. Lake Alice had significant algal blooms throughout the season, but especially in March and April. The water colour at both lakes was always

greenish brown, except for January at Wiritoa, where the water was brownish yellow. Due to resource constraints, preserved samples could not be visually counted to support the molecular results.

Figure 5.1 *Cyanobacterial blooms during March 2022 AD in Lake Alice (A) and November 2021 AD in Lake Wiritoa (B).*

5.2.1 Environmental Parameters

Water temperature

The water temperatures peaked in March at approximately 23°C in both lakes before cooling in April to approximately 17°C (Figure 5.2).

Thermal stratification was measured in Lake Wiritoa across the season. Lake Wiritoa's thermocline weakened as the season progressed, although it remained at a 10 m depth throughout the study period. The thermal stratification in Lake Wiritoa was weakened in April, suggesting it was beginning to turn over. There was weak stratification in Lake Alice in March despite its shallow depth. This coincided with a period of fine, calm weather. Temperature measurements were limited to 2.5 m depth in Lake Wiritoa during April due to sudden raft deflation.

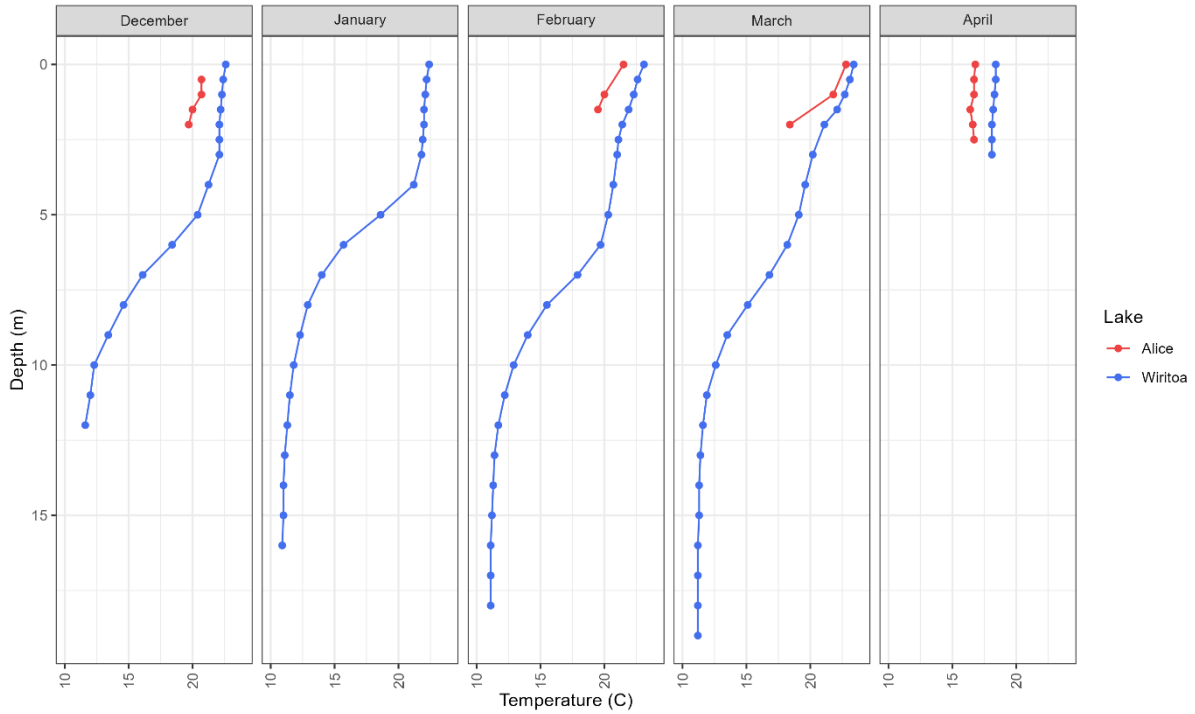

Figure 5.2 *Water temperature in lakes Alice and Wiritoa, 2021-2022 AD. Measurements are missing for both lakes in November due to equipment unavailability, and for Lake Alice in January due to no site access.*

Secchi Disk Depth

Lake Wiritoa experienced its lowest Secchi Disk depths in December 2021 AD, and highest in March 2022 AD, while Lake Alice had consistently poor Secchi Disk depth (always <1 m) (Figure 5.3).

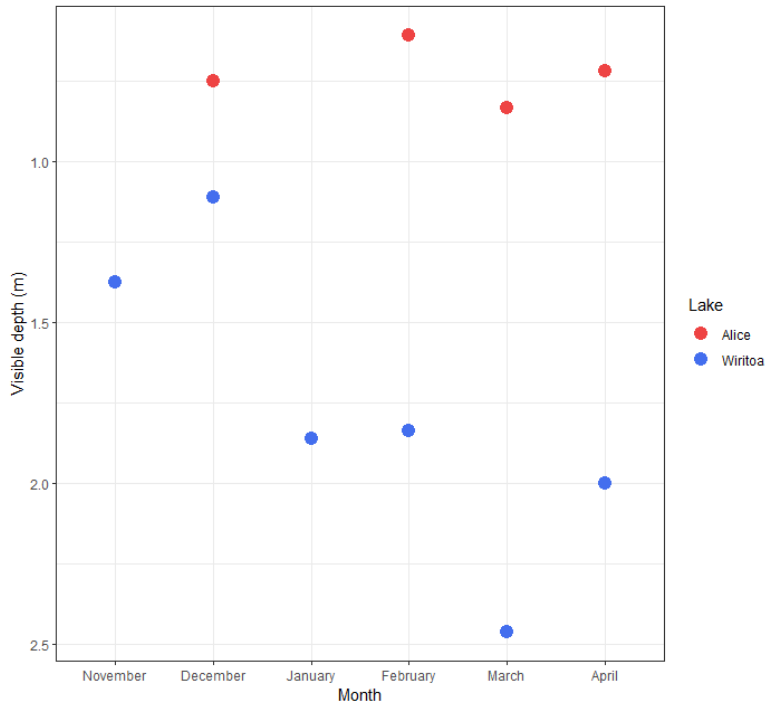

Figure 5.3 *Secchi Disk depths in lakes Alice and Wiritoa (summer 2021 and 2022 AD). Measurements are missing for Lake Alice in November and January due to no site access.*

5.2.2 Surface Water Metabarcoding

Rarefaction of the metabarcoding sequence data resulted in the removal of three water filters from the Lake Alice dataset, and five water filters and one sediment sample from the Lake Wiritoa dataset. Up to 725 photosynthetic cyanobacteria ASVs were detected throughout the sampling period in both lakes.

A total of 120,977 ASV reads from 502 ASVs were detected in the surface water and sediment samples of Lake Alice after rarefaction, while 224,249 ASV reads from 261 ASVs were detected in Lake Wiritoa after rarefaction. Lake Wiritoa had around 3000 more ASV reads per water filter than Lake Alice, but Lake Alice had twice as many ASV reads per sediment sample. In both lakes, water samples had significantly more relative ASV reads per sample than sediment samples. The majority of the ASVs were classified as non-photosynthetic bacteria. Species accumulation curves indicated that the sampling was insufficient to capture the full cyanobacterial diversity in these lakes as the curve never reaches the asymptote (Figure 5.4).

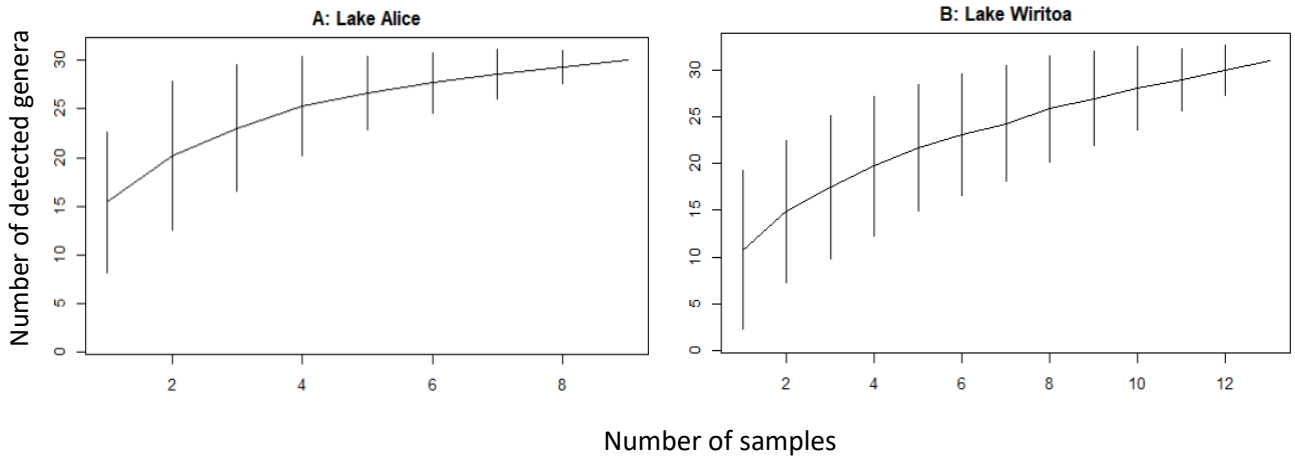

Figure 5.4 *Species accumulation curves of photosynthetic cyanobacteria in the summer sampling programme for Lakes Alice and Wiritoa.*

Thirty cyanobacteria ASVs were identified in Lake Alice across four months and while 31 were detected in Lake Wiritoa across six months. The vast majority of ASV in both lakes could be classified to genera level (98.9% in Lake Alice and 95.7% in Lake Wiritoa). The ASV detected in the surface sediment samples were similar to those in the water samples, albeit with slightly different proportions (Figure 5.5).

Lake Alice had a high relative portion of *Microcystis*, and consistent low abundance of *Cuspidothrix* (Figure 5.5a). *Cyanobium* dominated the Lake Alice ASVs in December, with a transition to *Dolichospermum* and then *Microcystis* dominance as the summer progressed. Unclassified ASVs from the typically benthic Phormidiaceae family were detected in April. The number of low abundance (<1% of the sampling visit) cyanobacteria taxa increased in April. Most of the taxa detected in the water were detected in the April

sediment samples, although Phormidiaceae ASVs was not. *Sphaerospermopsis* was only detected in the sediment.

Lake Wiritoa had increasing abundance of *Snowella* over the study period, with consistent low amounts of *Microcystis* (Figure 5.5b). There were small amounts of unclassified ASVs between Wiritoa 3 (January) and Wiritoa 5 (March). The "Wiritoa 3" sample taken in January 2022 AD had much lower read numbers than other months, with only one filter remaining after rarefaction. The community composition of this month is also remarkably different than other months with over 75% being *Cyanobium* and higher amounts of ASV reads unclassified to genus level. It is unknown if this sample reflects a genuine community shift, or if the results were influenced by other factors. If this samples is an outlier, then the Lake Wiritoa cyanobacterial community transitioned from *Dolichospermum* dominance to *Snowella* with increasing *Planktothrix* across the sampling period. *Cyanobium* was not detected in the surface sediment, but the other main taxa of *Dolichospermum*, *Microcystis*, *Pseudoanabaena* and *Snowella* were.

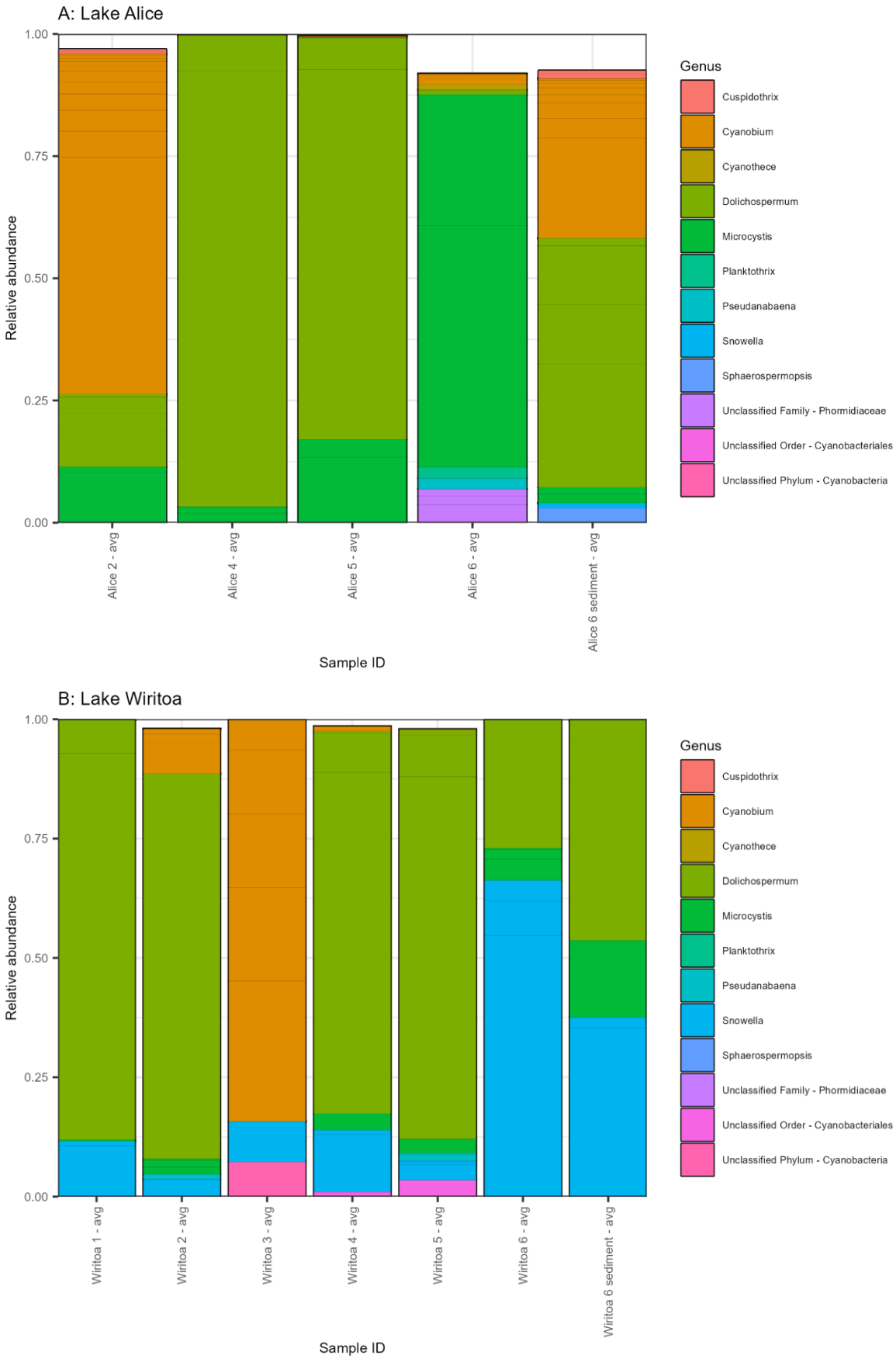

Figure 5.5 *Cyanobacteria community composition in Lakes Alice (A) and Wiritoa (B) from November 2021 (1) and April 2022 (6) AD.*

Observed species richness in the pelagic samples ranged from 5 to 22 in Lake Alice, and 3 to 10 in Lake Wiritoa (Table 5.1). The sediment sample observed richness in both lakes was at the upper end of their respective pelagic ranges (16 in Lake Alice, 7 in Lake Wiritoa). The Chao1 estimator was identical to observed richness in the pelagic samples, and slightly higher in the sediment samples for both lakes. The lowest observed richness in Lake Alice occurred in February in Lake Alice (Alice 2 – avg), and January in Lake Wiritoa (Wiritoa 3 – avg). Shannon diversity varies in Lake Alice between 0.3 and 1, while it remained above 0.5 in Lake Wiritoa except for November (Wiritoa 1 – avg). The Simpson diversity was relatively stable in both lakes, but is slightly higher in Lake Alice. Shannon diversity and Simpson diversity were slightly higher in the sediment samples than the pelagic samples in both lakes.

Table 5.1 *Alpha diversity measures in Lake Alice and Lake Wiritoa (summer 2021/22 AD), averaged for each month/visit. "Sediment" refers to surface sediment samples taken in April.*

Sample ID	Observed richness	Chao1	Chao1 SE	Shannon	Simpson
Alice 2 – avg *(December)*	15	15.00	0.242	0.926	0.460
Alice 4 – avg *(February)*	5	5.00	0.447	0.154	0.066
Alice 5 – avg *(March)*	12	15.00	4.133	0.498	0.292
Alice 6 – avg *(April)*	22	22.00	0.244	1.070	0.400
Alice 6 sediment – avg *(April)*	16	16.33	0.920	1.257	0.616
Wiritoa - 1 avg *(November)*	6	7.0	2.220	0.382	0.211
Wiritoa - 2 avg *(December)*	10	10.0	0.474	0.710	0.325
Wiritoa - 3 avg *(January)*	3	3.0	0	0.544	0.278
Wiritoa - 4 avg *(February)*	6	6.0	0	0.707	0.340
Wiritoa 5 – avg *(March)*	9	9.0	0	0.643	0.258
Wiritoa 6 – avg *(April)*	5	5.0	0.447	0.814	0.484
Wiritoa 6 sediment – avg *(April)*	7	7.5	1.270	1.027	0.619

5.2.3 Comparing surface water and surface sediment

Multidimensional analysis shows that while there is some overlap, the cyanobacteria communities in lakes Alice and Wiritoa were significantly different (Figure 5.6; PERMANOVA $f = 5.9572$, $p < 0.01$). The community composition of different sample types differed between the lakes. Sediment samples in Lake Alice were

more similar to the water samples, particularly in December (visit 2). Sediment samples are outside the confidence ellipse in Lake Wiritoa and are similar to the third visit (Wiritoa 3), of which only one filter remains. Therefore, it is difficult to determine whether this water sample is an outlier or truly reflective of the cyanobacterial community in January 2022 AD.

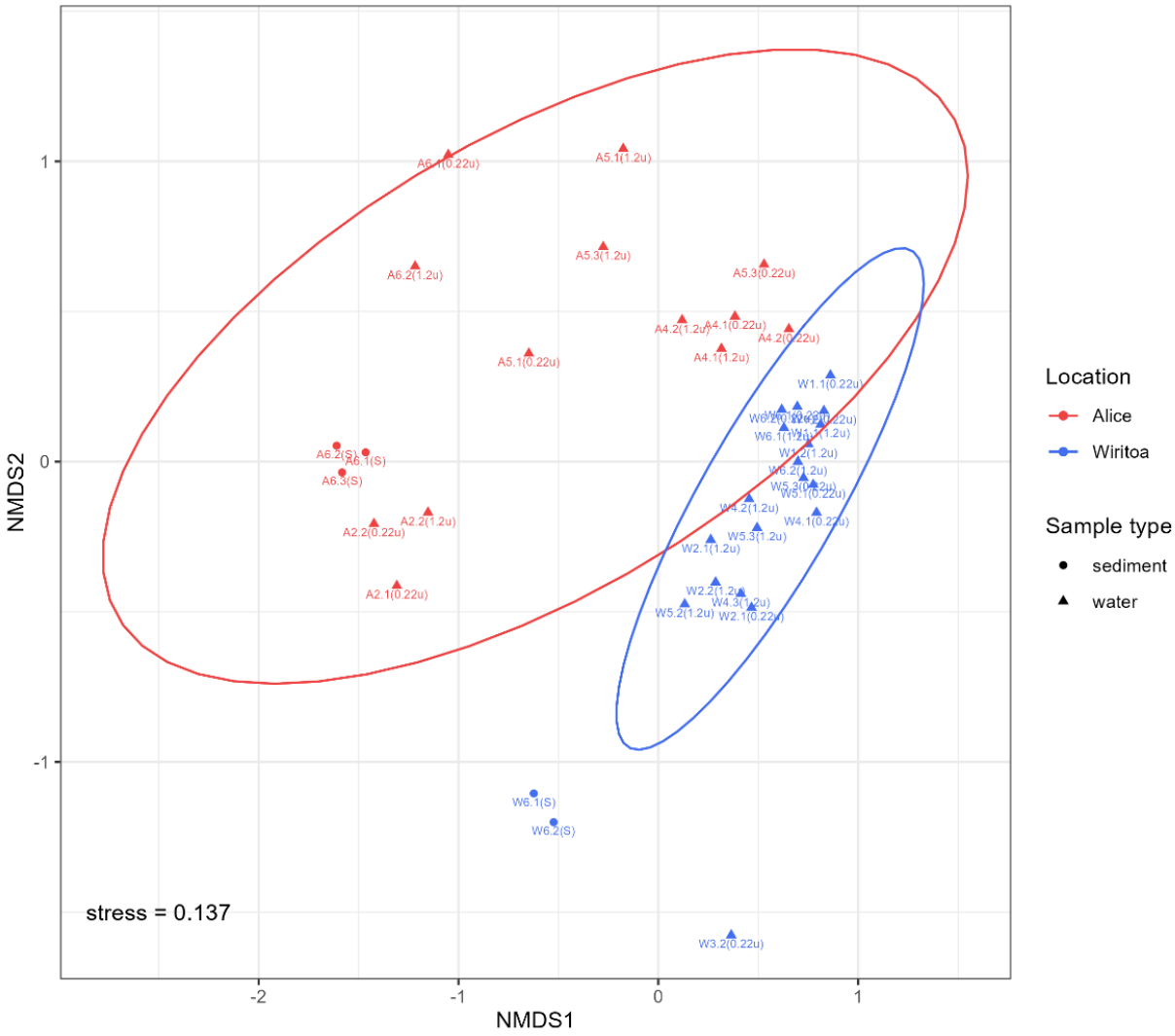

Figure 5.6 *Two-dimensional NMDS of surface water samples by lake (colour) and sample type (shape) with 95% confidence ellipses.*

5.3 Sediment Cores

5.3.1 Palynology

Lake Alice Zone 1 – Māori occupation/Subsistence Living

This zone encompasses 130 cm depth to 60 cm depth in the sediment core (Figures 5.7a & 5.8). The spectra in this zone are dominated by *Pteridium esculentum*, which peaks at 60% in the bottom of the core. *Typha* declines quickly to around 20% presence throughout most of the zone. *Coriaria arborea* steadily increases from 10% to 20% at 70 cm depth, before quickly declining. Low amounts of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Fuscospora* remain present

throughout this zone. Charcoal peaks at around 120 cm depth. The sharp rise in charcoal at 130 cm may suggest that the core was close to capturing the transition from the pre-human era.

Lake Alice Zone 2 – European occupation/Intensifying agriculture

Zone 2 starts at 60 cm depth, and spans to the top of the core (Figures 5.7a & 5.8). It is characterised by the appearance of *Pinus,* Poaceae and *Plantago* pollen. Other exotic taxa including *Rumex* and *Betula* appear and maintain at low percentages. *Coriaria arborea* and *Typha* remain present but decline. Most tall trees decline to zero in the upper 30 cm. Wetland taxa remain present in low percentages, while *P. esculentum* notably declines to around 5%. Charcoal concentration also declines.

Lake Wiritoa Zone 1 – Pre-human era/Undisturbed era

Zone 1 in Lake Wiritoa extends from 110–170 cm depth (Figures 5.7b & 5.9). Tall trees including *D. cupressinum*, *P. taxifolia, Nestegis, D. dacrydioides, P. ferruginea* and *Podocarpus* dominate the pollen sum. Shrubs including *Dodonaea viscosa* and *Myrsine* are present in low percentages, along with *Cyathea* spores.

Lake Wiritoa Zone 2 – Māori occupation/Subsistence living

Zone 2 encompasses 60 cm to 110 cm depth (Figures 5.7b & 5.9). Levels of *P. esculentum* and charcoal concentrations quickly increase, while tall tree pollen and tree fern spores decline markedly. Poaceae pollen appears, remaining at low percentages. *Coriaria* also appears and quickly peaks at 80 cm depth.

Lake Wiritoa Zone 3 – European occupation/Intensifying agriculture

Zone 3 in the Lake Wiritoa core covers from 60 cm to 0 cm (Figures 5.7b & 5.9). Exotics including *Rumex acetocella* and *Pinus* appear, the latter quickly rising to 60% of the pollen sum at 20 cm depth. Poaceae also increases to between 25% and 40% of the pollen sum at various depths. Tall trees and shrubs continue to decline. *P. esculentum* quickly drops to near zero presence at the top of the core. Charcoal declines to near zero above 30 cm.

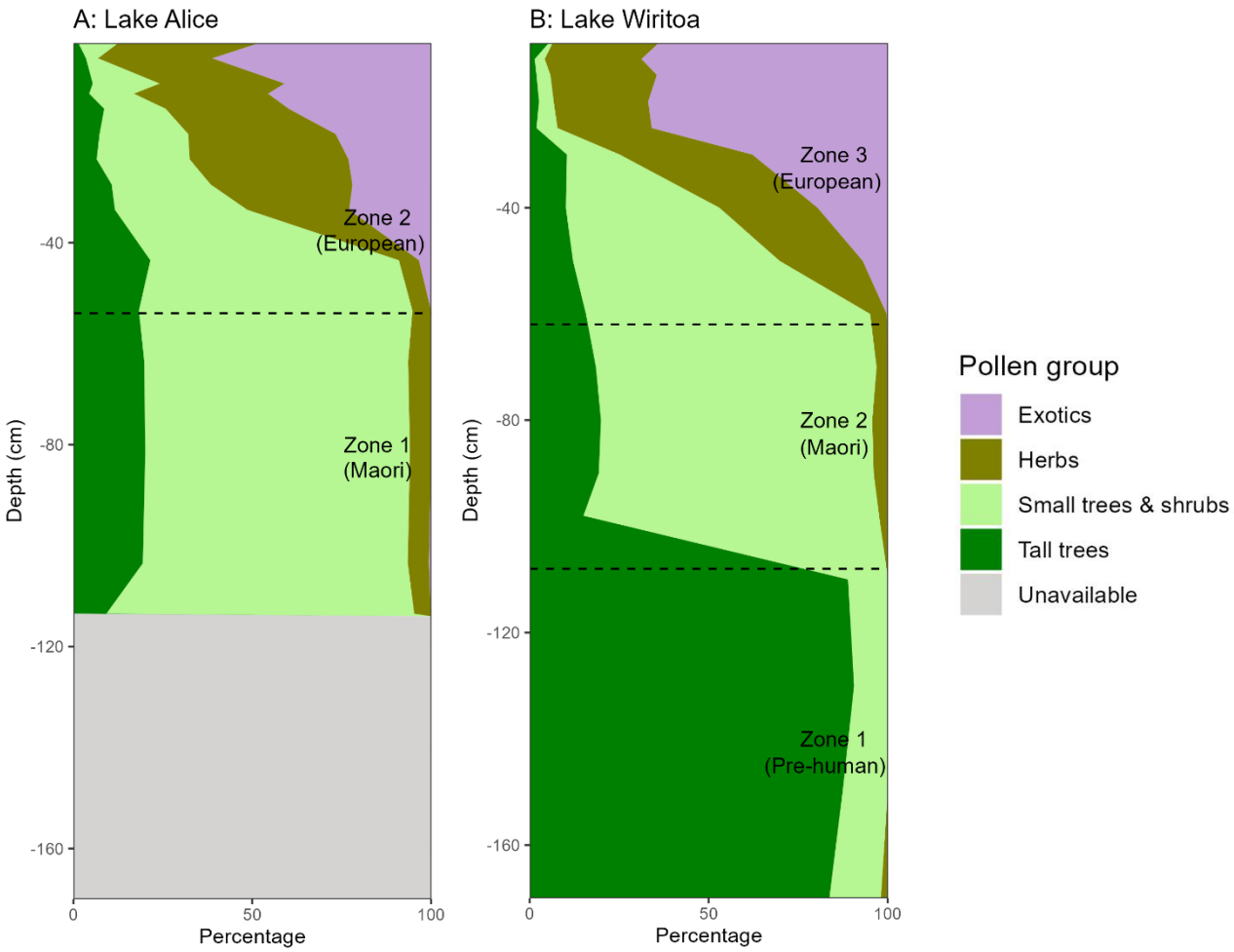

Figure 5.7 *Summary pollen diagrams for Lake Alice (A) and Lake Wiritoa (B), showing the declines in tall tree forest over time, and the emergence of exotic taxa. The dashed lines indicate the depth boundaries between the labelled zones. The "unavailable" pollen group denotes the bottom of the Lake Alice sediment core.*

Lake Alice

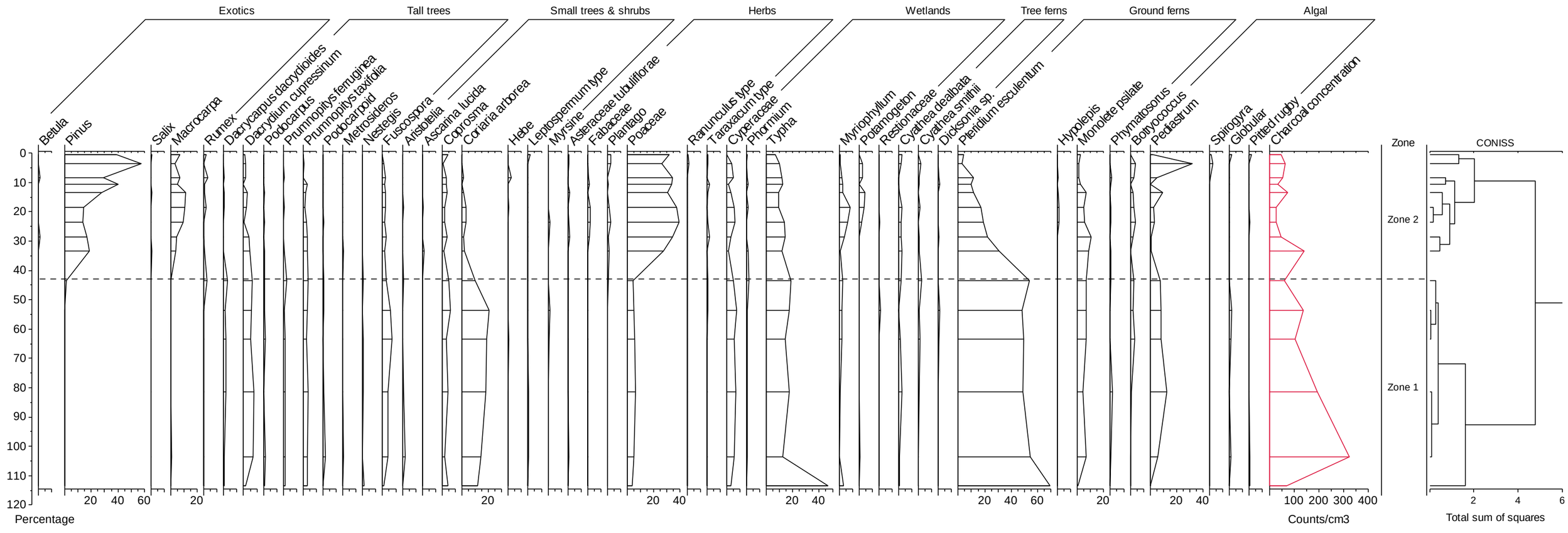

Figure 5.8 *Pollen diagram for Lake Alice, showing the percentage of pollen taxa and concentration of charcoal. Peaks of charcoal and Pteridium esculentum indicate Māori settlement, while European settlement is indicated by an increase of exotic taxa. The absence of high proportions of tall tree taxa indicate the pre-human stratigraphy was not captured in this sediment core.*

Lake Wiritoa

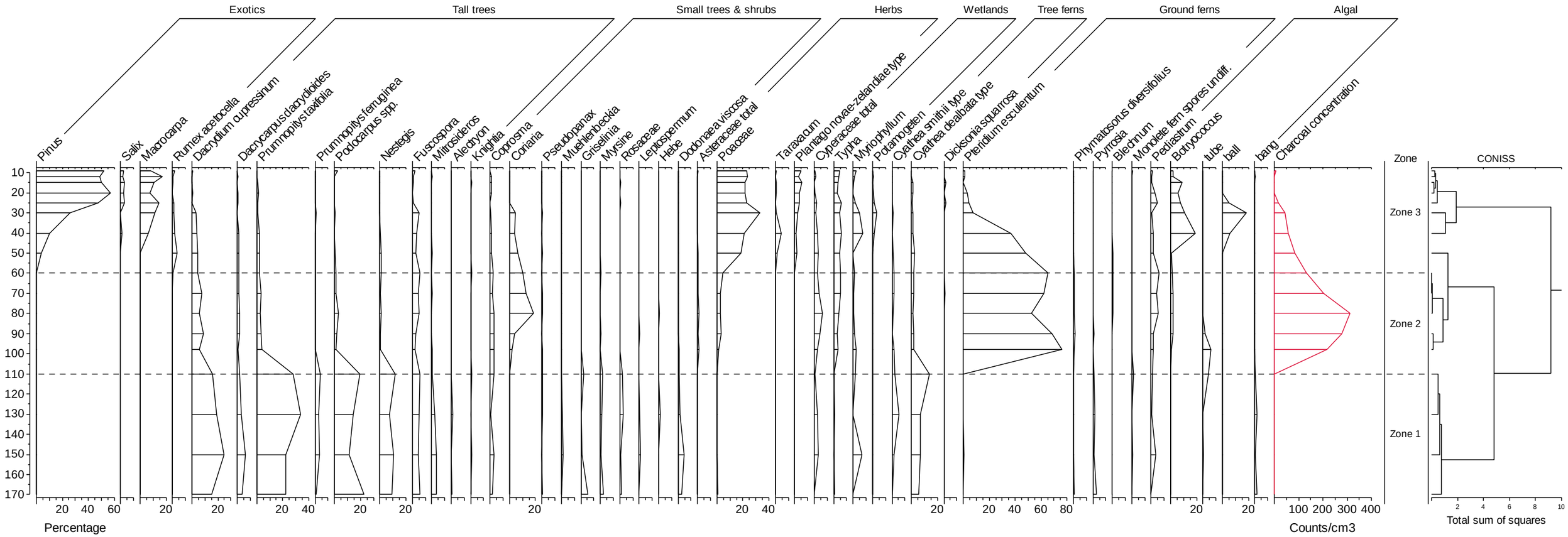

Figure 5.9 *Pollen diagram for Lake Wiritoa, showing the percentage of pollen taxa and concentration of charcoal. Pre-human stratigraphy is indicated by high proportions of tall tree taxa. Peaks of charcoal and Pteridium esculentum indicate Māori settlement, while European settlement is indicated by an increase of exotic taxa.*

5.3.2 Trace Metals

Cadmium

Cadmium (Cd) in Lake Alice remains at approximately 0.1 mg kg^{-1} dry weight from the bottom of the core to around 60 cm depth (Figure 5.10a). Above 60 cm, cadmium concentrations climb rapidly around 0.26 mg kg^{-1} dry weight above 25 cm. Cd levels then seem to stabilise around 0.25 mg kg^{-1} dry weight above 25 cm. Cd amounts in Wiritoa vary between 0.2 mg and 0.25 mg kg^{-1} dry weight below 110 cm depth (Figure 5.10b). Levels then steadily decline to 0.09 mg kg^{-1} dry weight from 110 cm to 40 cm depth, before a rapid increase to between 0.27 and 0.35 mg kg^{-1} dry weight above 40 cm.

As cadmium is a proxy for superphosphate aerial topdressing, a further "Intensive agriculture" zone was identified at 24 cm in Lake Alice, and 26 cm in Lake Wiritoa.

Lead

Lead (Pb) concentrations in the Lake Alice core remain around 3 mg kg^{-1} dry weight from the lower core to 50 cm depth (Figure 5.10a). Above 50 cm, Pb levels rise to 20.7 mg kg^{-1} dry weight at 6 cm depth. The largest increase is from 29 to 23cm, with Pb levels almost doubling. Pb levels in Lake Wiritoa broadly follow the pattern seen in Lake Alice (Figure 5.10b). Amounts during the pre-human, subsistence and intensifying agriculture eras are generally stable around 10 mg kg^{-1} dry weight. Lead then increases quickly at 26 cm to 62.7 mg kg^{-1} dry weight, before declining and stabilising around 30 mg kg^{-1} dry weight.

Manganese/Iron ratio

Lower values of the Manganese/Iron (Mn/Fe) ratio indicate relatively more time in anoxic conditions. The Mn/Fe ratio for Lake Alice varies slightly from the surface until 35 cm depth (Figure 5.10a). The ratio then dips to 0.01 at 23 cm, before climbing to 0.02 at 3 cm depth. The Mn/Fe ratio for Lake Wiritoa is generally lower than that for Lake Alice, which concurs with its deeper and monomictic characteristics (Figure 5.10b). The deepest measurement at 160 cm is 0.01, before the ratio climbs at 115 cm. The ratio then decreases at the onset of Māori occupation. Variability then increases in the mid-European era, before an increase to around 0.015 in the upper centimetres of the core. Due to the easy mobility of Fe and Mn under anoxic conditions, the upper centimetres of the cores may not provide representative ratios of their chronology.

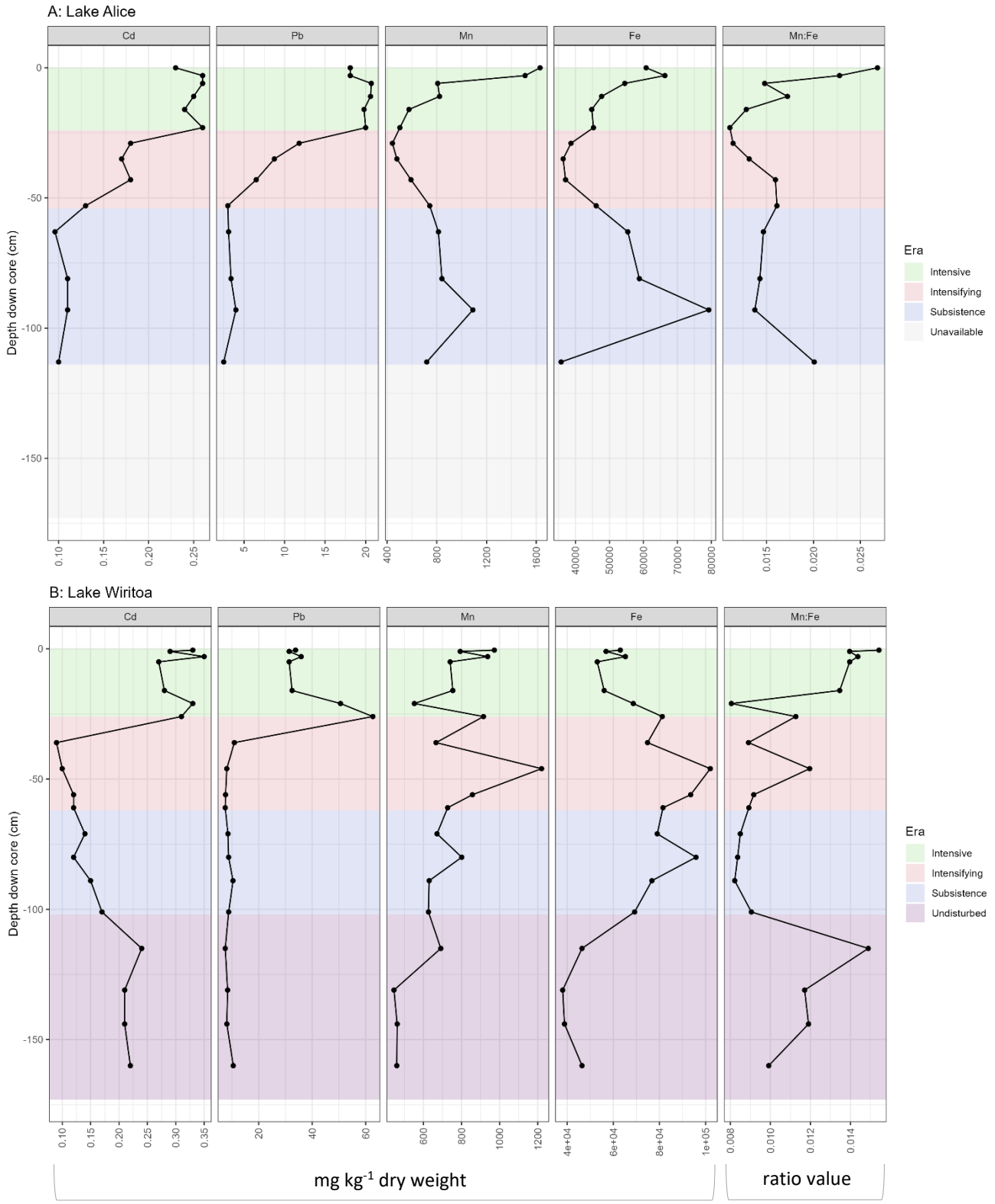

Figure 5.10 *Trace metal results for Lake Alice (A) and Lake Wiritoa (B), as milligrams per kilogram of dry weight or the Manganese/Iron ratio value. X-axis values are different between the two lakes.*

5.3.3 Itrax Scanning

Titanium/Incoherent scattering

The ratio of titanium to incoherent scattering is a proxy for erosion and allochthonous sediment input. Ti/Inc in Lake Alice is stable and relatively low in the Māori to early European eras of the core (Figure 5.11a). Above 50 cm depth, it begins to increase before peaking before briefly declining at above 10 cm. Ti/Inc values in Lake Wiritoa are generally higher than those in Alice, and more variable (Figure 5.11b). Ratio values start at around 0.06, and decline until a brief increase at the Māori arrival horizon. Values then decline again, jumping sharply at around 50 cm depth before continuing to decline in the upper sediments.

Calcium/Titanium

The ratio of calcium to titanium is a proxy for authigenic carbonate precipitation within a lake, associated with phytoplankton photosynthesis. Ca/Ti in Lake Alice starts at a relatively high value of around 1.5, before steadily declining throughout the core until the surface sediment (Figure 5.11a). Lake Wiritoa starts at a lower ratio value than in Lake Alice, and steadily increases up the sediment core (Figure 5.11b). It peaks at around 50 cm depth, and briefly declines until around 25 cm depth. It then becomes more variable in the upper 25 cm of core.

5.3.4 Hyperspectral Imaging

Individual peaks and troughs in $RABD_{660–670}$ were not interpreted as meaningful results; instead, trends were interpreted when large shifts occurred. In Lake Alice the $RABD_{660–670}$ remains stable around 1.1 until 110 cm in depth, before it declines (Figure 5.11a). Its lowest values occur between 80 and 40 cm depth. Above 40 cm, it quickly increases. It exceeds the earlier peak within 10 cm and continues to increase until the top of the core. The brief drop in chlorophyll-a at around 2.5 cm depth coincides with a spot of light-coloured sediment in the core photograph; this drop may therefore be an artefact of scanner placement rather than a true decline in $RABD_{660–670}$. The hyperspectral scanning in Lake Wiritoa shows a similar pattern to Lake Alice, with stable values around 1.1 from 170 cm to approximately 90 cm depth (Figure 5.11b). Values then decline to around 1.0 until 35 cm depth, before increasing throughout the upper core.

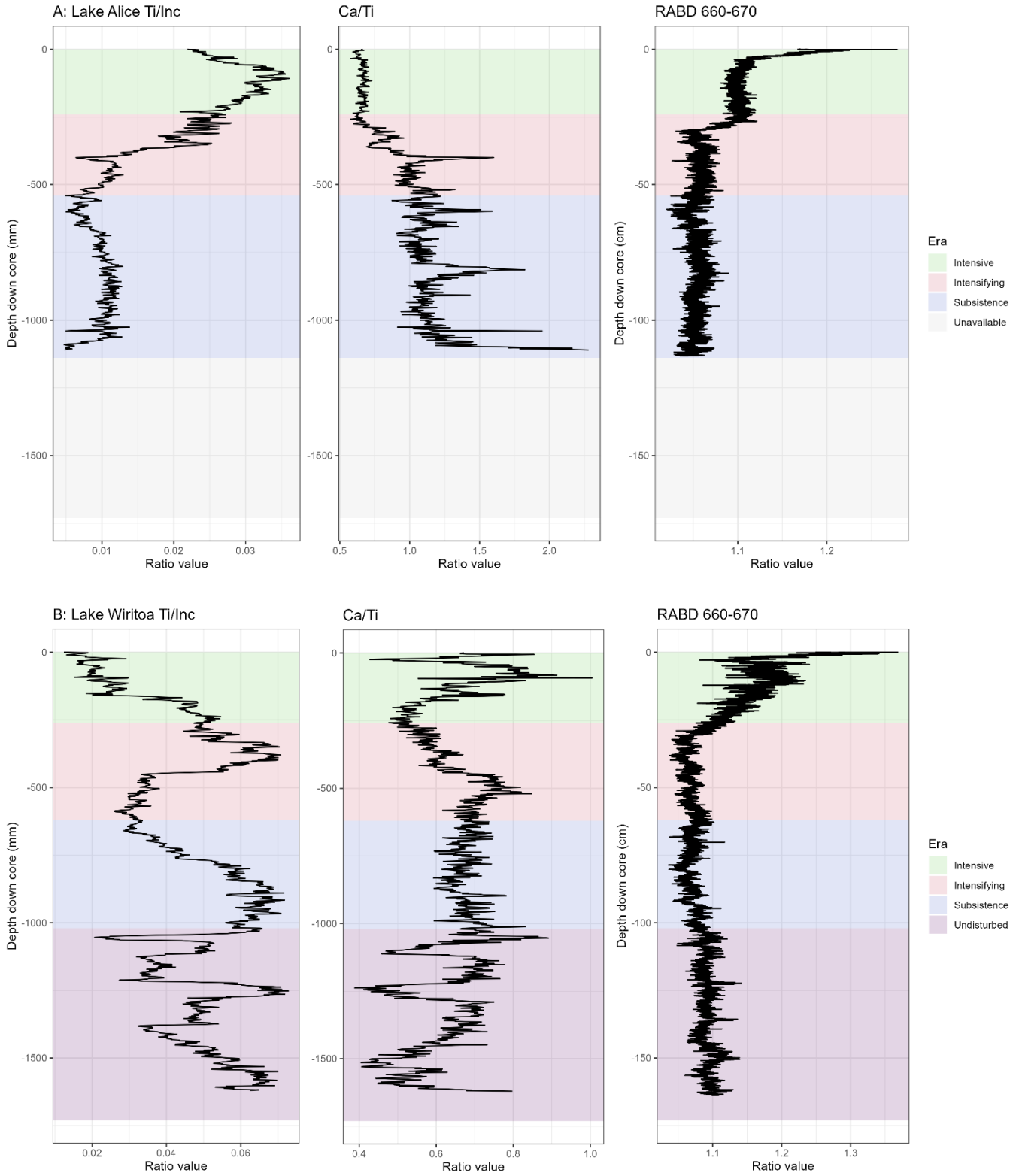

Figure 5.11 *XRF scanning results and $RABD_{660–670}$ index from hyperspectral scanning for Lake Alice (A) and Lake Wiritoa (B). Coloured areas denote land-use areas.*

5.3.5 Droplet digital PCR

Droplet digital PCR shows similar patterns in copy numbers between both lakes (Figure 5.12). DNA copies are stable in both lakes in the lower sediments. Increases in Lake Alice start at 50 cm in the European era, while small increases start in the Māori subsistence era in Lake Wiritoa. Larger increases then quickly occur in Lake Wiritoa above 50 cm. One outlier in Lake Wiritoa was removed at 0 cm, with a DNA copy number of 10,376,289.

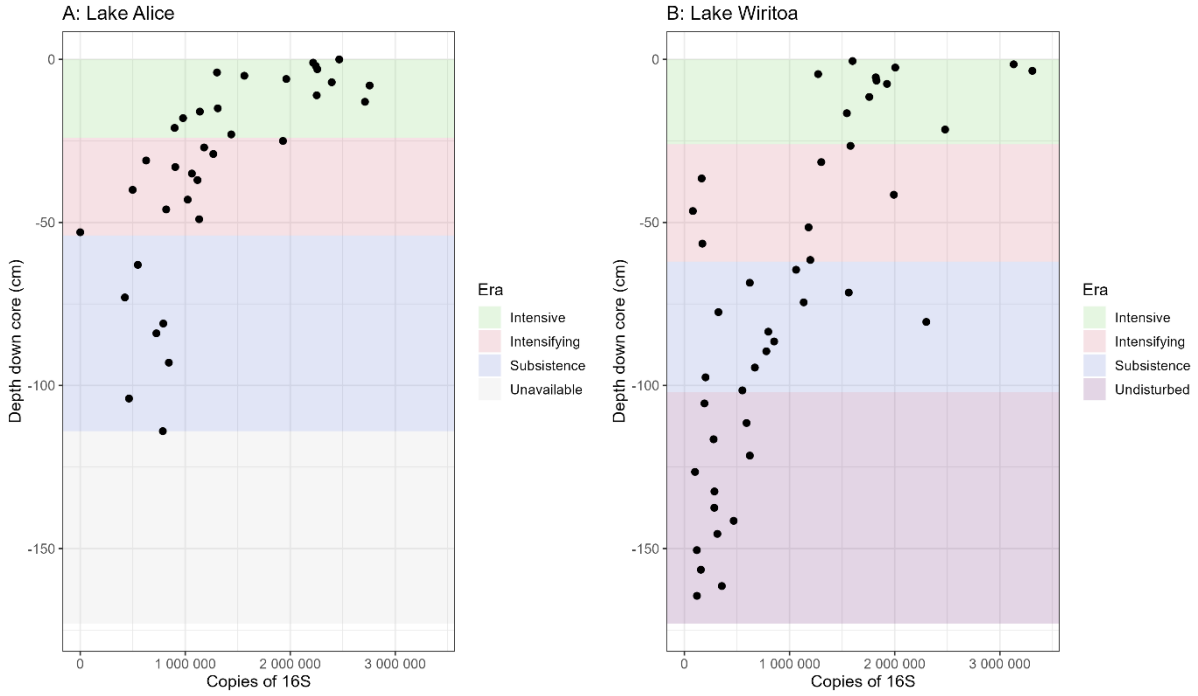

Figure 5.12 *Results from the droplet digital PCR of the cyanobacterial 16S rRNA gene in Lake Alice (A), and Lake Wiritoa (B)*

5.3.6 Core Metabarcoding

A total of 22,974 ASV reads were detected in the sediment core samples of Lake Alice after rarefaction, and 12,221 in Lake Wiritoa. Up to 334 ASVs were detected across nearly 40 cyanobacterial genera. Several samples did not contain any ASVs after rarefaction – one from Lake Alice and nine Lake Wiritoa (Tables 9.1 & 9.2 – Appendix). Most of these zero-read samples were located at the bottom of the sediment cores. The upper few centimetres of each core had slightly lower ASV read numbers than the surface sediment from the field sampling, and ASV totals generally declined with depth (Figure 9.1 - Appendix). Up to 166 ASV reads in Lake Alice (1%) and 744 ASV reads in Lake Wiritoa (6%) could not be classified to genus level.

Cyanobacteria community composition in the sediment cores shifted over time (Figures 5.13 & 5.14). *Cyanobium* or unclassified cyanobacteria ASVs are the only taxa detected below 60 cm in Lake Alice (Māori era), and below 70 cm in Lake Wiritoa's core (Pre-human to mid-Māori zones). The one exception to this is around 90 cm depth in Lake Alice, with ~10% presence of *Dolichospermum* detected. During the late Māori

through European era in Lake Alice *Dolichospermum* ASVs increased, and *Microcystis*, *Nostoc* and *Synechocystis* were present. *Cuspidothrix* was detected in low abundance (<1%) in the upper few centimetres of core. Lake Wiritoa also diversifies in cyanobacteria detections in the late Māori subsistence era, but with different taxa. Unclassified ASVs assigned to the Leptolyngbyaceae and Synechococcaeceae families appear at 64 cm depth. Within the European era, taxa including *Dolichospermum*, *Synechococcus* and *Aphanizomenon* increased in abundance. Above 20 cm depth, *Microcystis* dominates, with small proportions of *Dolichospermum* and *Aphanizomenon*.

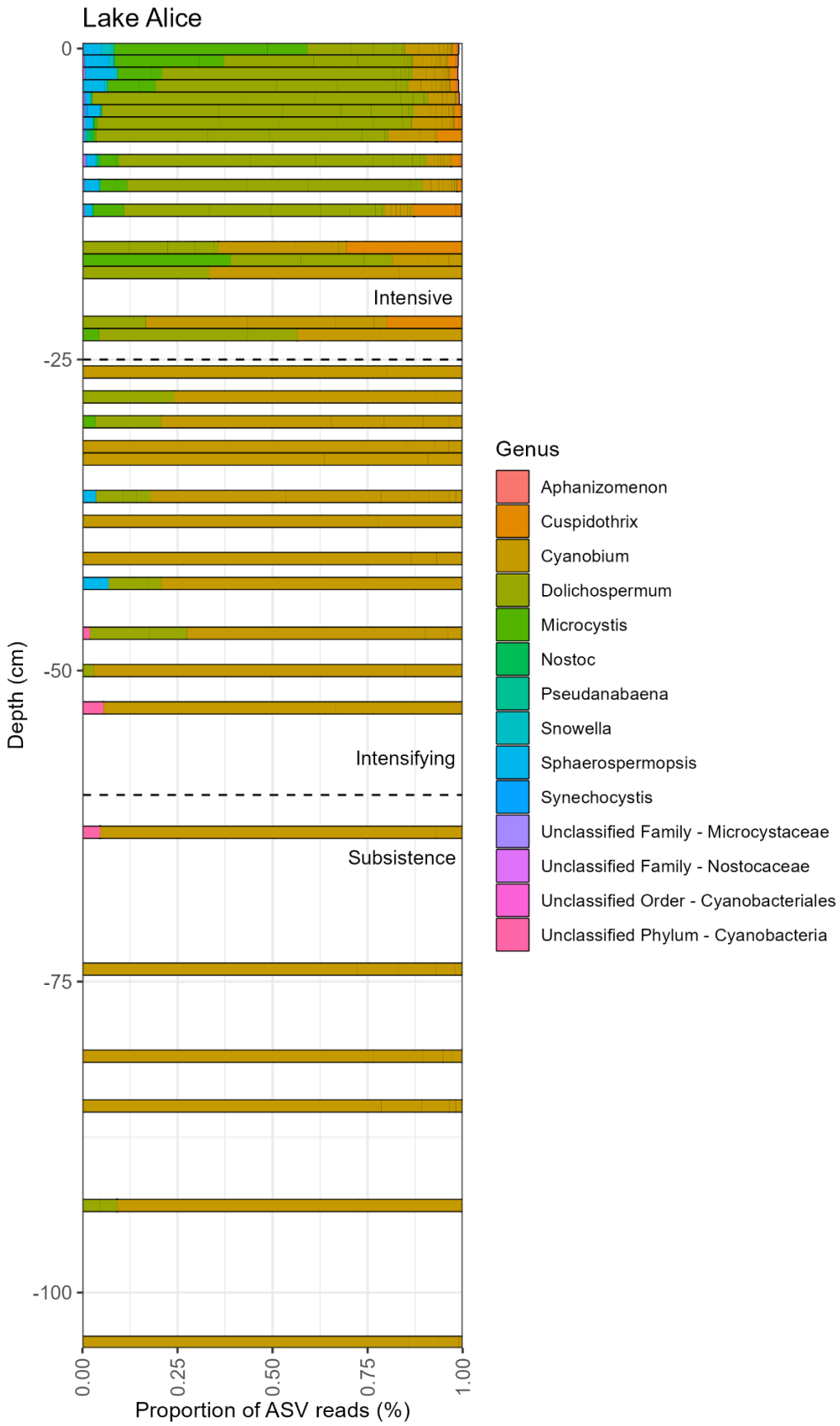

Figure 5.13 *Taxonomic composition of cyanobacteria amplicon sequence variants (ASVs) in sediment core metabarcoding samples from Lake Alice. Dashed lines denotes era zone boundaries.*

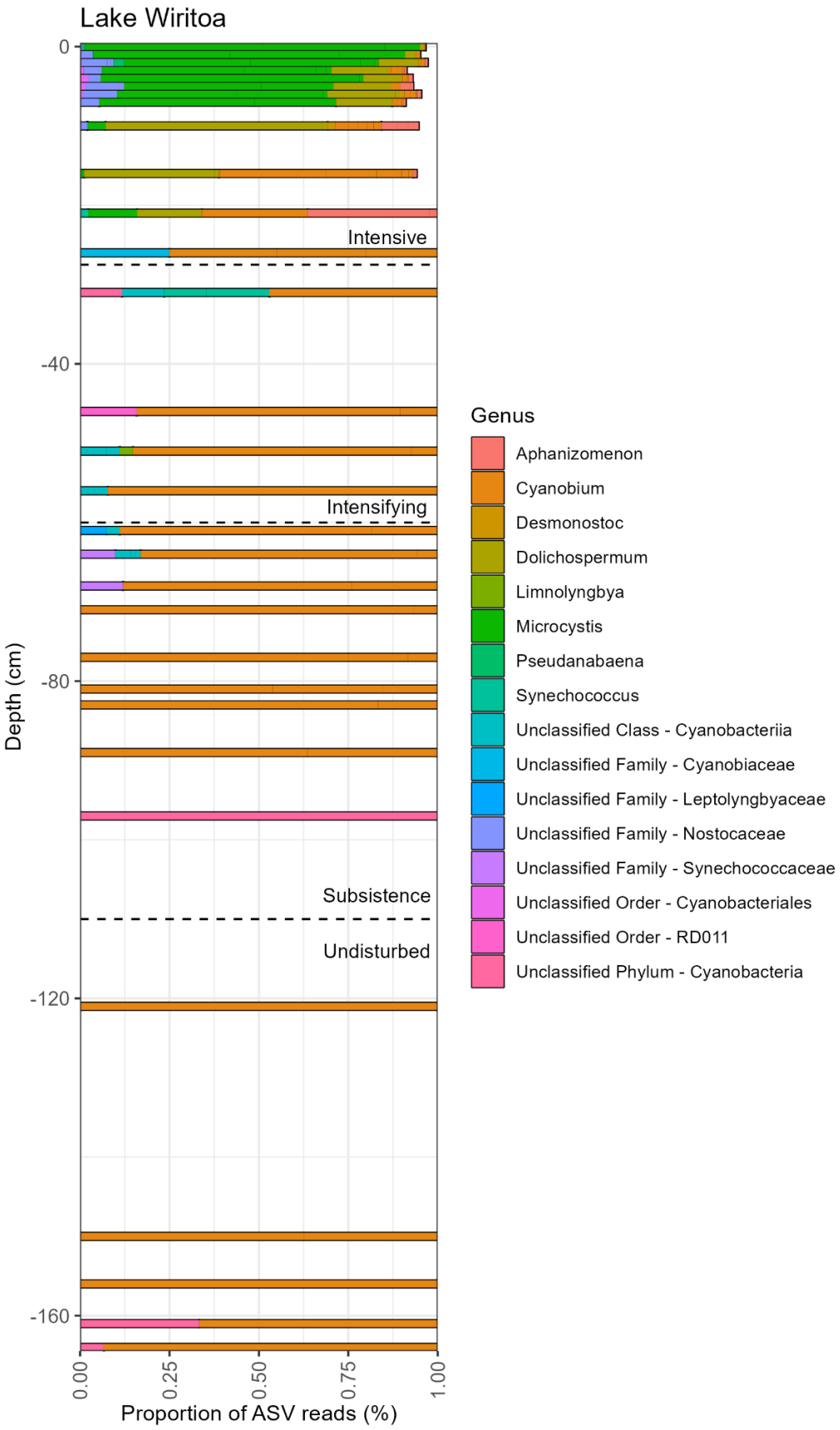

Figure 5.14 *Taxonomic composition of cyanobacteria amplicon sequence variants (ASVs) in sediment core metabarcoding samples from Lake Wiritoa. Dashed lines denotes era zone boundaries.*

Two-dimensional NMDS plots of the samples from the sediments shows a general taxa divergence in upper sediments, before a homogenising of taxa in the uppermost centimetres (Figure 5.15). PERMANOVA confirms that the cyanobacterial communities in two sediment cores are different from each other (f = 4.723, $p < 0.001$.

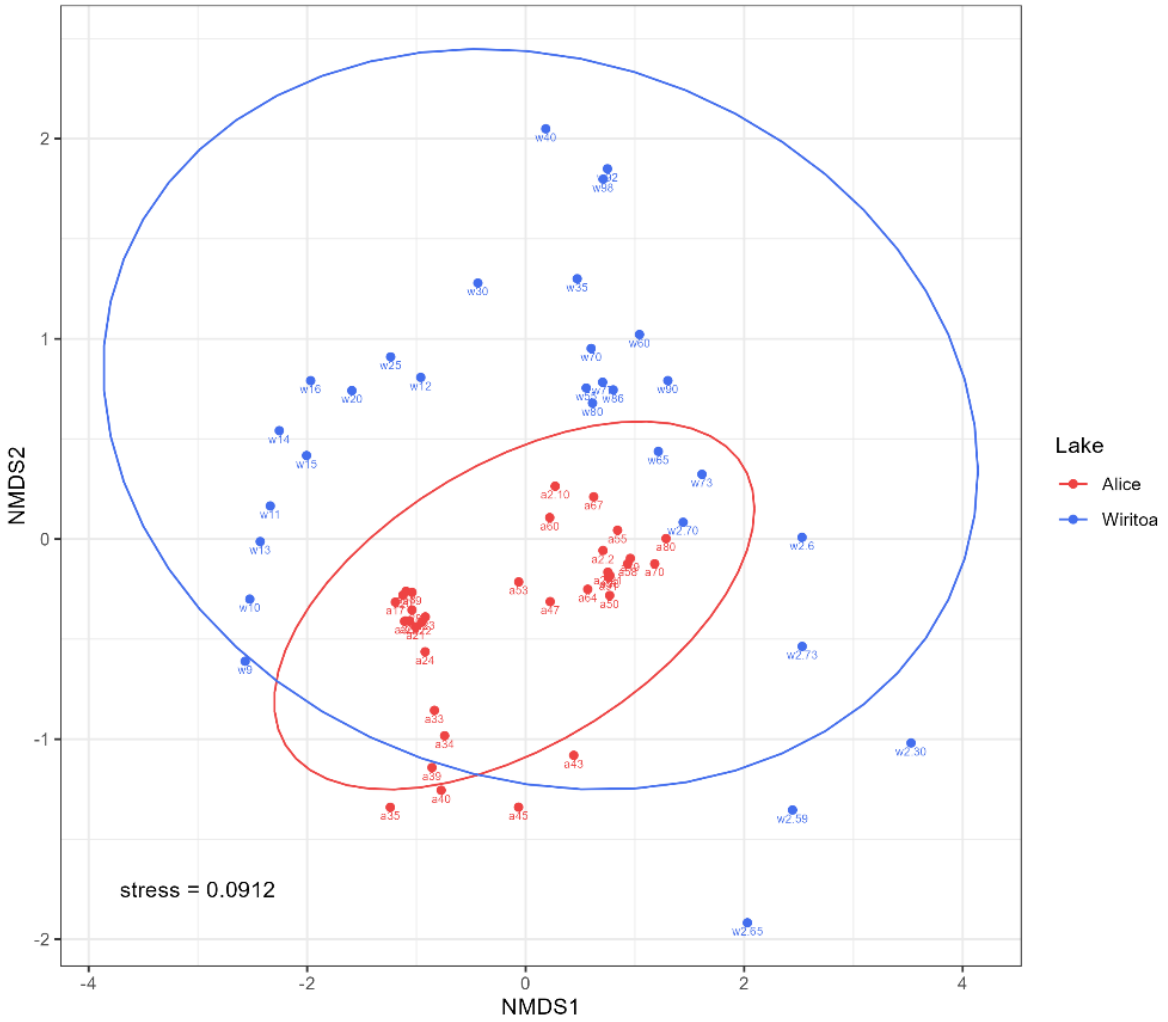

Figure 5.15 *Two-dimensional NMDS of the photosynthetic cyanobacteria communities in Lakes Alice and Wiritoa sediment cores with 95% confidence ellipses.*

Two-dimensional NMDS of the detected DNA communities demonstrated both lakes experienced progressive change. PERMANOVA found statistically significant change in the cyanobacterial communities in Lake Alice (r^2 = 0.167, f = 3.114, $p < 0.01$) and Lake Wiritoa (r^2 = 0.394, f = 5.6412, $p < 0.001$).

Statistical testing of Lake Alice is limited due to the small number of available metabarcoding samples for the intensifying era and the absence of a pre-human phase (Figure 5.16a). The cyanobacteria community is similar in the subsistence and intensifying era. The intensive agriculture era remains similar to the previous eras, but becomes more variable with points distancing on both axes. The subsistence, intenfying and intensive eras overlap in Lake Alice, but variation increases in the intensive era. Statistical analysis of the

different zones suggests similar levels of effect on the cyanobacterial community between pollen (PERMANOVA $r^2 = 0.119$, $f = 4.340$, $p < 0.001$; dbRDA $f = 3.330$, $p < 0.01$ (depth as a condition)) and cadmium (PERMANOVA $r^2 = 0.097$, $f = 3.429$, $p < 0.01$; dbRDA $f = 3.758$, $p < 0.001$ (depth as a condition)).

The change in the Lake Wiritoa cyanobacterial community is more pronounced (Figure 5.16b). The undisturbed, subsistence living and intensifying agriculture eras retain some overlap, but show a clear progression of gradual change in community composition. PERMANOVA between the indentified land-use phases identified statistically significant differences between the Subsistence vs Undisturbed zones ($r^2 = 0.232$, $f = 3.93$, $p < 0.001$) and the Intensive vs Intensifying zones ($r^2 = 0.326$, $f = 6.0$, $p < 0.001$), but not between the Intensifying and Subsistence zones ($r^2 = 0.105$, $f = 1.64$, no significance). Cadmium had a higher explanatory power in detected community shifts (PERMANOVA $r^2 = 0.352$, $f = 7.332$, $p < 0.001$; dbRDA $f = 3.302$, $p < 0.001$ (depth as a condition)) than pollen (PERMANOVA $r^2 = 0.257$, $f = 4.669$, $p < 0.001$; dbRDA $f = 2.632$, $p < 0.001$ (depth as a condition)).

Constrained hierarchical clustering (CONISS) analysis was used to identify zones of similarity within the cyanobacterial communities of each lake. The three most significant divisions in the Lake Alice sediment core occurred at -3 cm, -13 cm, and -23 cm (Figure 5.17). Within Lake Wiritoa, the three most significant divisions were at -7 cm, -21 cm and -89 cm (Figure 5.18).

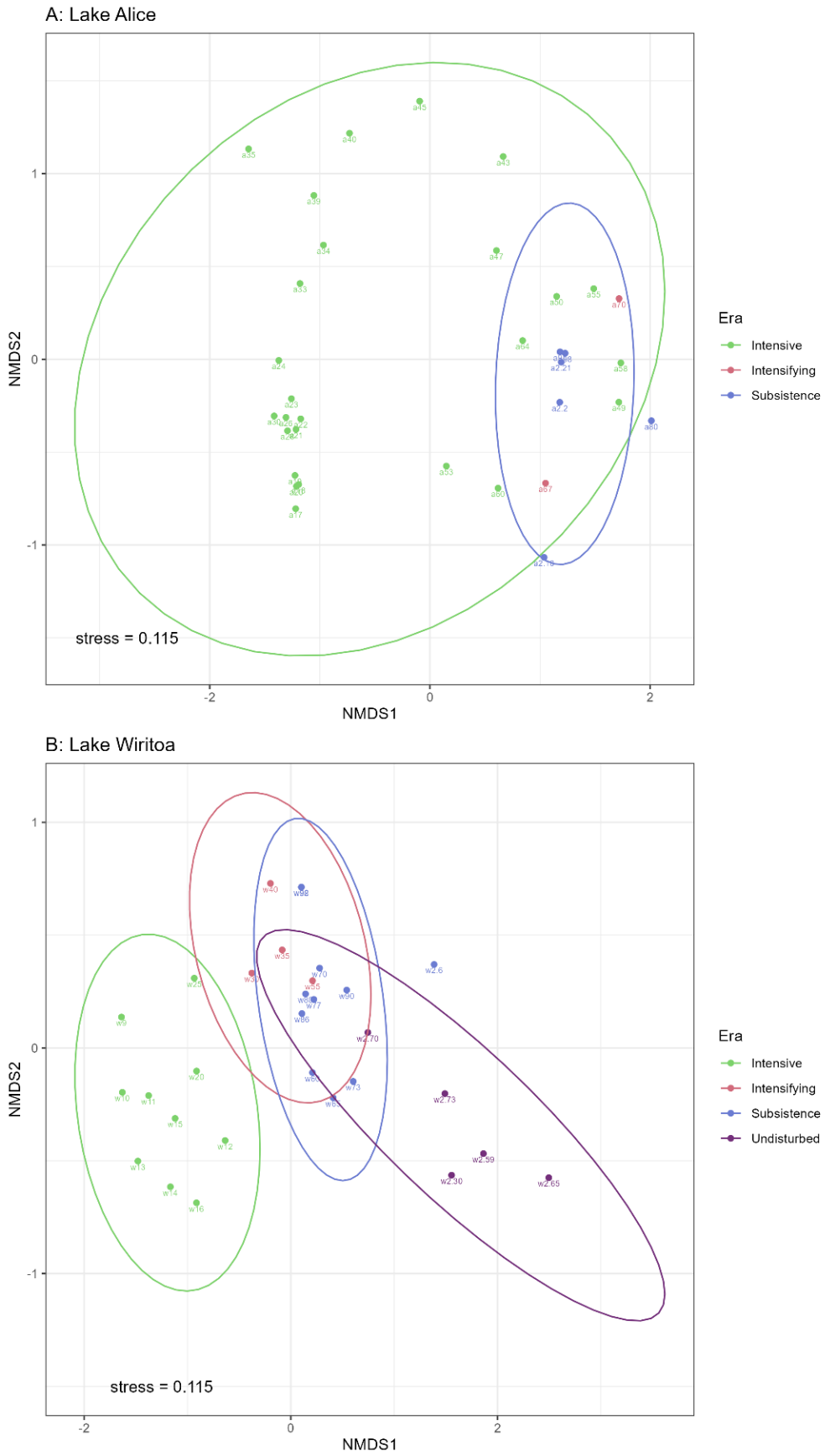

Figure 5.16 *Two-dimensional NMDS of the photosynthetic cyanobacteria communities in Lake Alice (A) and Lake Wiritoa (B) sediment cores with 95% confidence ellipses, according to land-use phase.*

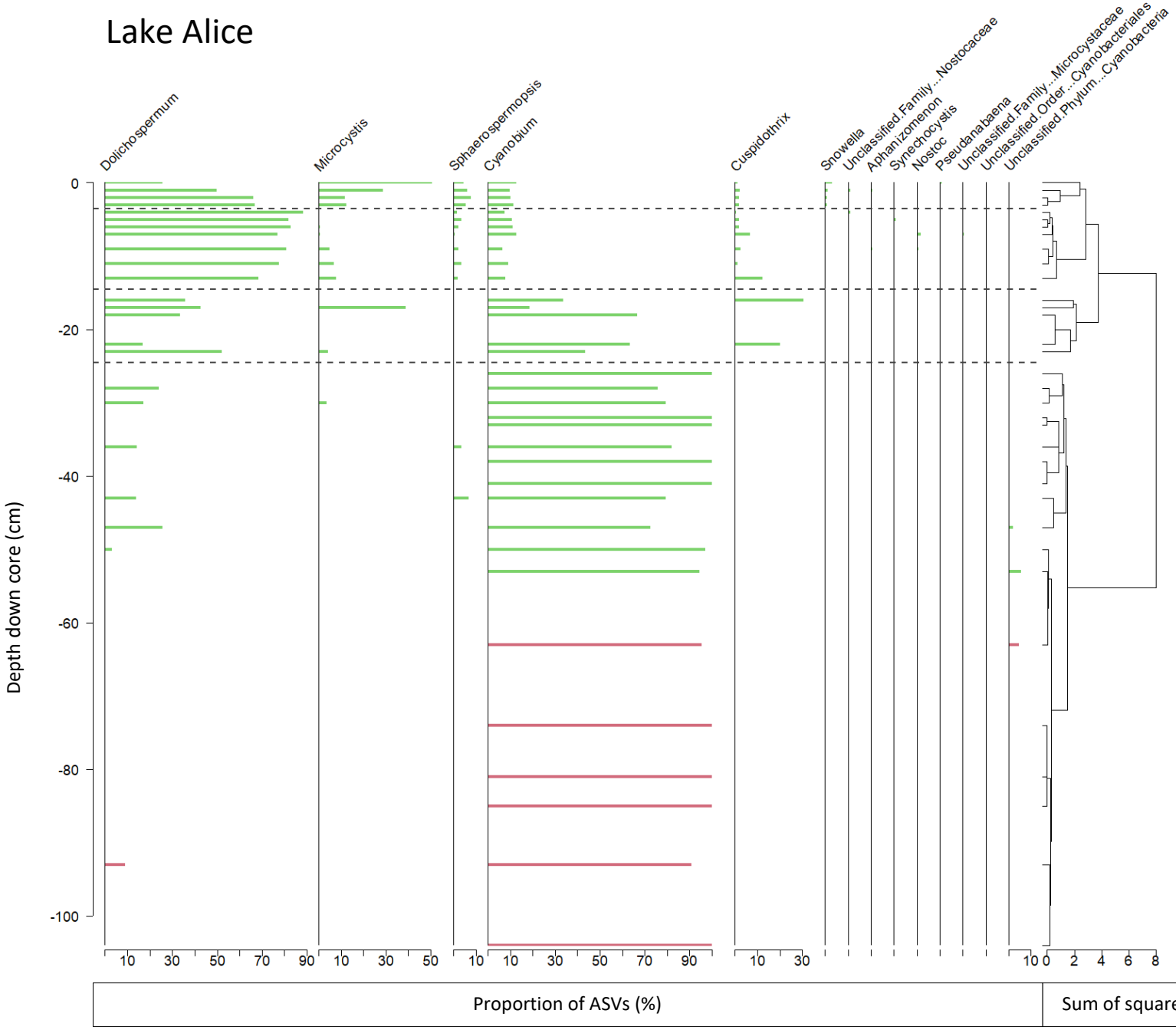

Figure 5.17 *CONISS analysis of photosynthetic cyanobacterial sediment core DNA in Lake Alice performed in rioja (Juggins 2020), showing four primary identified zones (dashed lines). Colour denotes pollen-identified occupation periods (pink = Māori, green = European).*

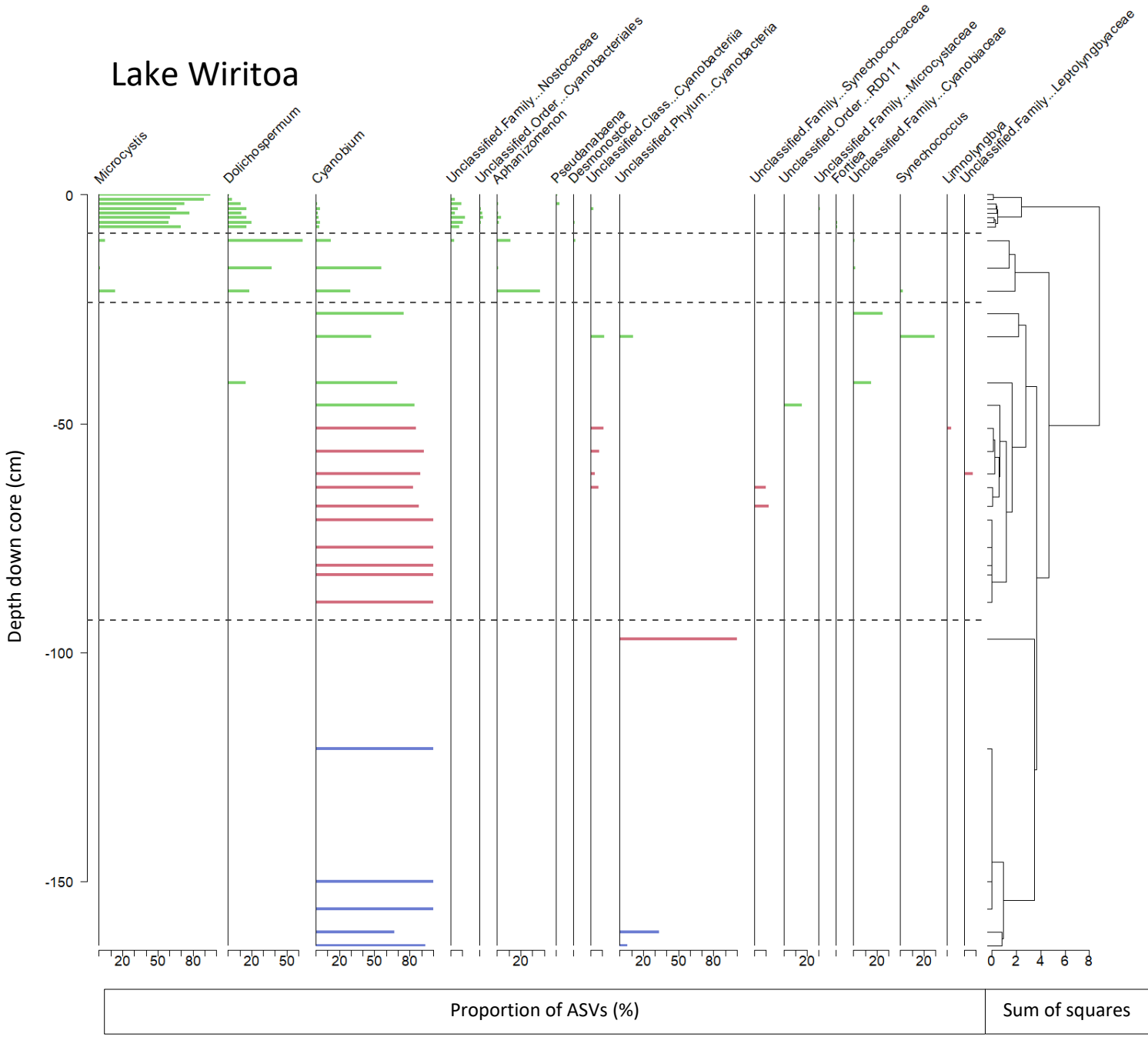

Figure 5.18 *CONISS analysis of the photosynthetic cyanobacterial sediment core DNA in Lake Wiritoa performed in rioja (Juggins 2020), showing four primary identified zones (dashed line). Colour denotes pollen-identified occupation periods (blue = pre-human, pink = Māori, green = European).*

6 Chapter 6 – Discussion

This research has utilised environmental DNA to analyse both contemporary and historic cyanobacterial communities in two Manawatū-Whanganui dune lakes. The summer sampling programme showed the lakes have dynamic cyanobacterial communities, and found some differences in the community composition between the water column and surface sediment as detected in the metabarcoding data. The environmental reconstructions of both Lake Alice and Lake Wiritoa demonstrated a similar change in the cyanobacterial communities of both lakes, with bloom-forming taxa becoming more abundant in recent sediments. Similar proxy records of environmental change were also detected within the lakes, particularly for pollen and cadmium. This allows exploration of the potential drivers of contemporary cyanobacterial blooms, and how eutrophication dynamics differ between a shallow and a deep lake in a globally rare and heavily impacted ecosystem.

6.1 Summer cyanobacterial communities

The two lakes have quite different cyanobacteria communities when averaged over the summer, as determined from metabarcoding data (Figure 5.5a & b). Both have high amounts of *Dolichospermum*, particularly around February and March. This coincides with the highest water temperatures in both lakes (Figure 5.2). *Cyanobium* and *Microcystis* are the next most abundant genera throughout the season in Lake Alice, while in Lake Wiritoa it was *Cyanobium* and *Snowella*. This differs from another shallow lake within the Manawatū-Whanganui dune system, which is often dominated by *Microcystis* during seasonal blooms (Gibbs et al., 2022). Studies over a longer period would be required to confirm these observations. The detection of the typically benthic Phormidiaceae with a marked decrease in *Dolichospermum* may suggest greater light penetration in Lake Alice in April (Komárek, 2016), despite the shallow Secchi disk reading on the day (Figure 5.3). *Planktothrix* detections towards from the beginning of Autumn in both lakes may indicate decreasing light availability, while earlier *Planktothrix* in Lake Wiritoa may represent metalimnetic populations (Nwosu et al., 2021; Reynolds, 2006). High amounts of *Dolichospermum* and *Microcystis* are consistent with other blooms reported in Aotearoa New Zealand (Gibbs et al., 2022; Puddick et al., 2022). The majority of ASV reads detected were also from potentially toxigenic genera, including those that produce anatoxins and saxitoxins. Although toxin testing on the water samples was not performed, the high proportions of potentially toxic taxa and consistently visible scums suggest that the lakes posed a health risk to human and animals (Hobbs et al., 2021; Wood et al., 2009).

While the cyanobacteria community of Lake Wiritoa was relatively even throughout the season, the community in Lake Alice seems more prone to blooms and swings in abundance, supported by the multidimensional analysis showing less cyanobacterial community variability in Lake Wiritoa over the season than Lake Alice (Figure 5.6). Blooms in both lakes were already occurring at the onset of sampling,

and so it is difficult to tell whether akinete formation facilitated the quick expansion of *Dolichospermum* (Reynolds, 2006). Species accumulation curves (Figure 5.4) further confirm that community turnover throughout the season, as neither lake reached a steady state (Reynolds, 2006). To confirm these observations more sampling with a higher frequency, i.e., at least weekly, would be required.

6.1.1 Comparing pelagic and sediment DNA

The pelagic and sedimentary communities of both lakes were broadly similar, indicating sedimentary DNA likely provides a good record of water column cyanobacterial communities (Figure 5.6). This is consistent with findings from Monchamp et al. (2016), who found that sedimentary community composition was reflective of pelagic sample microscopy over a period of 50 years. Alpha diversity metrics in Lakes Alice and Wiritoa were also similar between sediment and pelagic samples (Table 5.1), mirroring results from Nwosu et al. (2021). Proportions of *Dolichospermum* and *Snowella* were relatively similar between the sediment and pelagic samples (Figure 5.5); *Dolichospermum* akinetes may explain its relative ease of sedimentary detection in both lakes (Salmaso et al., 2015). The slight differences in the sedimentary proportions of genera compared to the water samples, such as lower sedimentary proportions of *Planktothrix*, may be explained by accumulated settling. Taking sediment samples from a core rather than suspended sediment traps means that multiple years of blooms were likely captured within each sample (Milan et al., 2022).

The sediment cyanobacteria community of Lake Alice was more representative of the pelagic community than in Lake Wiritoa, as demonstrated by multidimensional analysis (Figure 5.6). *Cyanobium* was over-represented in the sediment samples for Lake Alice and under-represented in Lake Wiritoa, while *Microcystis* was under-represented in Lake Alice and over-represented in Lake Wiritoa (Figure 5.5). The greater dissimilarity between the sediment and water column communities in Lake Wiritoa than Lake Alice may be explained by a combination of genera ecology and lake depth. Colonial cyanobacteria forms have been shown to settle preferentially (Nwosu et al., 2021; Visser et al., 2016), while the thermocline density gradient likely entrains lighter forms; this both prevents them from sinking to the sediment, and extends their exposure to heterotrophic decomposition (Nwosu et al., 2021). The unicellular *Cyanobium* and metalimnetic *Planktothrix* may therefore be slowed in their settling by Lake Wiritoa's stratification.

6.2 Environmental reconstruction

6.2.1 Undisturbed era

The pre-human, undisturbed era is only available for Lake Wiritoa. The catchment was dominated by podocarp forest (*Dacrydium cupressinum*, *Prumnopitys taxifolia* and *Podocarpus* species). There was a sub-canopy containing *Cyathea* tree ferns, *Coprosma* and *Griselinia*, with akeake (*Dodonaea viscosa*) likely occurring on the drier, younger dunes. *Cyathea* is consistent with a warm, humid climate (Bussell, 1990), while akeake is found in coastal forests and dunefields (Allan, 1982). This forest stand is consistent with the

potential vegetation for the Manawatū-Whanganui coast described in Figure 3.2a (Leathwick et al., 2012), Maysek (2007), Esler (1978) and McGlone (1989). Small amounts of the seral tree *Myrsine* may suggest small clearings (Wilmshurst, McGlone, & Partridge, 1997). Minimal charcoal indicates this forest cover was well-established with few natural fires. Just prior to Māori occupation, *Cyathea dealbata* type spores peak, accompanied by small decreases in tall native tree taxa and a slight increase in *Coprosma*. This could be indicative of small-scale forest clearing by Māori similar to those described by Wilmshurst et al. (2004) of early Māori settlement, but the absence of charcoal suggests a natural event. Stable levels of Cd, Pb and Ti/Inc suggest minimal delivery of terrestrial/clastic sediment (i.e. from erosion) into the lake, consistent with mature forest cover in the catchment. With little external/allochthonous input, the ecosystem was likely characterised by internal nutrient cycling rather than external nutrient inputs (Capblancq, 1990; Li, Liu, Zhao, Hastings, & Guo, 2015).

Low amounts of chlorophyll-a are indicated by the $RABD_{660–670}$ and Ca/Ti indicate Lake Wiritoa was a stable and low-productivity system (Figure 5.11a). This is supported by the low cyanobacterial cell numbers detected through ddPCR, as well as Mn/Fe ratios showing no signs of anoxic shifts (Figures 5.11b & 5.12). Core metabarcoding suggests the cyanobacterial community during this time was dominated by *Cyanobium*, with a small proportion of ASV reads unable to be classified beyond phylum level (Figure 5.14). Studies suggest picocyanobacterial *Cyanobium* abundance tends to decline with increasing nutrients (Schallenberg & Burns, 2001). Lake Wiritoa was therefore likely in oligotrophic to mesotrophic condition with minimal toxicity and stable ecosystem functioning. *Cyanobium* also have low concentrations of toxin production (Bláha & Maršálek, 1999). This ecosystem stability prior to human arrival is seen in other lake cores as well (Cooper & Brush, 1993; Schallenberg & Saulnier-Talbot, 2016; Short et al., 2022).

There is a slight increase in cyanobacteria 16S rRNA copies within the upper 20 cm centimetres of the undisturbed era that is unaccompanied by an increase in the $RABD_{660–670}$ ratio (Figures 5.11a & 5.12). While the pollen record for this pre-human zone shows an abrupt transition to Māori land clearance (Figure 5.9), this may not be entirely accurate. Newnham et al. have outlined how low resolution of pollen sampling may obscure a two-step pattern of Māori land clearance, with smaller land clearances followed by larger clearances (2018). Removing terrestrial vegetation could have improved light availability or slightly increased nutrient availability via erosion. As *Cyanobium* can have two gene copies per cell (Picard, Wood, et al., 2022), even a small increase in cell numbers could be readily detected by ddPCR. Quantitative eDNA techniques may therefore be able to detect small changes in lake productivity undetectable by hyperspectral scanning.

6.2.2 Subsistence era

The subsistence era is captured in both Lake Alice and Lake Wiritoa. Tall forest-indicative taxa are already at relatively low levels at the bottom of the Lake Alice core while charcoal is continuing to climb; this indicates the core likely starts part way through the Māori subsistence era (Figures 5.7a & 5.8).

Both lakes show signs of rapid deforestation by fire and a transition to scrubland (Figures 5.8 & 5.9). This is consistent with the landscape described by early European settlers to the Whanganui region, and evidence from many other Aotearoa New Zealand pollen records (Bevins, 2019; Bussell, 1988; McWethy et al., 2010; Wilmshurst, 1997; Wilmshurst et al., 1997). The increase in seral taxa such as *Coriaria, Pteridium esculentum* and Poaceae provides further indications of disturbance (Esler, 1978; McGlone & Wilmshurst, 1999; Wilmshurst et al., 2004). More wetland taxa were found in Lake Alice than Lake Wiritoa, which may reflect its relatively greater littoral area (Scheffer, 2001; Wetzel, 2001). Cyperaceae and *Typha* appear in similar percentages in Lake Alice to those in Lake Wiritoa. The increase in *Typha* from pre-human times in Lake Wiritoa could reflect either increased light availability after forest clearance, or possibly deliberate cultivation by Māori (Lyver et al., 2015; Marr, 2003; McCallum & Carr, 2012). Lake margins may also be shallowing due to erosion, however this is not supported by Ti data (Figure 5.11b). Lead levels remain stable and low in both lakes (Figure 5.10). Cd and Ti/Inc in Lake Alice indicate a slight increase in erosion after the onset of deforestation, although this is not observed in Lake Wiritoa (Figures 5.10 & 5.11). While the declining Cd is suggestive of increased erosion due to the low organic content in Whanganui coastal soils, declining Ti/Inc over the same timeframe is suggestive of less erosion.

There is no clear reason for this difference, as the similar charcoal peaks suggest relatively synchronous deforestation around both lakes (Figures 5.8 & 5.9) while the iron sands along the Whanganui coastline would be readily reflected with increased aeolian mobilisation (Brathwaite, Gazley, & Christie, 2017; Davies et al., 2015). These results are highly unusual within the XRF and paleolimnology literature, which broadly identifies Ti as a reliable terrigenous sediment inflow indicator and valuable for normalisation of other elements (Davies et al., 2015; Evans et al., 2021; Metcalfe, Jones, Davies, Noren, & MacKenzie, 2010).

The $RABD_{660–670}$ index does not detect any change in primary productivity in either lake during the subsistence era, consistent with Ca/Ti results for Lake Wiritoa as a proxy for authigenic carbonate precipitation (Figure 5.11). Ca/Ti results in Lake Alice trend slightly towards lower productivity (Figure 5.11a). The lack of pre-human stratigraphy for Lake Alice makes its Mn/Fe difficult to interpret, but a shift towards more anoxic conditions in Lake Wiritoa may suggest increased biological demand for oxygen (Figure 5.10b). ddPCR results are similar between the two lakes, with the 16S rRNA copy numbers increasing throughout the subsistence zone in Lake Wiritoa (Figure 5.12). Again, ddPCR is potentially detecting an in-lake response to changing catchment conditions prior to the hyperspectral scanning.

Cyanobium is still the dominant cyanobacterial genus within both lakes, however both lakes show early signs of elevated productivity during this phase (Figures 5.13 & 5.14). The detection of two *Dolichospermum* ASV reads in Lake Alice at just above 100 cm coincides with a higher value in the ddPCR and a spike of Ca/Ti (Figures 5.11a & 5.12a), and small numbers of Synechococcaceae and Leptolyngbyaceae ASV reads are detected in Lake Wiritoa (Figure 5.14). These changing conditions suggest a slight increase in trophic status after early human activities, similar to results seen in lakes both nationally (Picard, Pochon, et al., 2022; Short et al., 2022; Woodward et al., 2014) and globally (Haworth, 1985; Smol, 2008).

6.2.3 Intensifying agriculture

European settlement in the Whanganui region occurred around 1840 AD (Marr, 2003), and is signalled through the appearance of pollen of *Pinus*, *Salix* and *Rumex* within both cores (Figures 5.7, 5.9 & 5.9). Removal of the podocarp forest continued, and *Pteridium* declines. Transition to pasture is indicated by a synchronous jump in Poaeceae and herb pollen, confirming colonial descriptions in the mid-1800s of pasture around both lakes. The two-step model of European settlement described by Wilmshurst (1997) is not shown within either core, despite being identified in Lake Horowhenua within the same dune system (Bevins, 2019). Wetland taxa remain more prevalent in Lake Alice, but proportional increases in both lakes could reflect greater light availability with ongoing forest clearance.

Increased erosion in the catchments is indicated by the increase in XRF Ti relative to the previous zone in both lakes, while stable Pb levels imply minimal industrial activity (Figures 5.10 & 5.11). Cadmium supports increased delivery of sediment generated by erosion in Lake Wiritoa, however sediment resuspension in Lake Alice's shallow basin may explain its Cd increase throughout this zone (Figure 5.10). With much of the protective forest canopy cleared by this time, the shallower basin was likely more exposed to sediment resuspension by wind (Wetzel, 2001). Furthermore, boat access to the lake and the probable release of exotic fish in the early 1900s AD likely led to increased benthic sediment disturbance (de Winton et al., 2001; Nedohin & Elefsiniotis, 1997). As both Cd and Pb jump to high concentrations with the advent of intensive agriculture (discussed in Section 6.2.4), it is possible that sediment core layers were mixed in Lake Alice after human settlement, effectively averaging its contents across multiple sampling depths.

Both lakes show a general trend of increasing lake productivity, as indicated by $RABD_{660–670}$ when compared to the subsistence zone, although a simultaneous decrease in Ca/Ti suggests lower authigenic carbonate precipitation (Figure 5.11). Lake Wiritoa shows little signs of change in its redox trends, although more variability trending towards anoxia is present in Lake Alice (Figure 5.10).

The cyanobacterial community across both lakes remains highly responsive to land-use change, although it is difficult to know the timescales this response occurred on without age control. Cyanobacteria cell

numbers increase slightly in Lake Alice, with *Dolichospermum* recorded in half of all samples analysed across this zone (Figure 5.13). *Cyanobium* remains the dominant genus in each sampled depth, however two eutrophic-indicative taxa are also detected (*Sphaerospermopsis* and *Microcystis*) (Figures 5.13 & 5.14). Cell numbers are much more variable in Lake Wiritoa, recording values both similar to and 3–4 times those of the undisturbed era (Figure 5.12b). While *Cyanobium* is still the majority of ASV reads detected, there is increasing diversity in the community (Figure 5.14). This overall similarity in nutrient status between early European and subsistence Māori phases is also seen in *Pediastrum* records of a lake in the same dune system (Bevins, 2019), molecular records (Picard, Pochon, et al., 2022; Short, Tibby, Vandergoes, Wood, Lomax, Puddick, Pearman, Howarth, Moy, & Šunde, 2022), and diatom records (Schallenberg & Saulnier-Talbot, 2016). As wetland taxa remain prominent in this zone (Figures 5.8 & 5.9), wetlands were likely attenuating early nutrient applications and additional erosive inputs (Schallenberg & Saulnier-Talbot, 2016).

The first indications of trophic shift occur approximately midway through the intensifying agriculture zone with the detection of *Dolichospermum* (Salmaso et al., 2015) (Figures 5.13 & 5.14). Both lakes show a trend towards potentially toxic and bloom-forming species, although at lower ASV read numbers than detected in the contemporary sampling (Figure 9.1 - Appendix). Newspaper adverts during the in the early 1900s AD indicate some low-intensity fertiliser application was occurring in the area ("Kempthorne, Prosser and Co.'s Westfield Manure Price List," 1900). The lake ecosystems are thus likely becoming characterised by external nutrient inputs rather than internal nutrient cycling (Capblancq, 1990; Conley et al., 2009; Y. Li et al., 2015). *Dolichospermum* seems particularly responsive to this (Figures 5.13 & 5.14), and may be a sentinel taxa for accelerating eutrophication.

6.2.4 Intensive agricultural phase

The advent of intensive agriculture is marked by Cd peaking in both lakes, indicating the start of superphosphate aerial topdressing (Figure 5.10). This is supported by the simultaneous spike of Pb as a proxy of industrial activity and construction (Figure 5.10). Although age control is unavailable, newspaper reports benchmark this zone as starting around 1950 AD. Terrestrial vegetation in this zone is very similar to that of the previous (intensifying agriculture) zone (Figures 5.7, 5.8 & 5.9). Pine pollen quickly reaches nearly 60% of the pollen sum in both lakes, likely reflecting *Pinus radiata* planting for both forestry and dune stabilisation (Figures 5.8 & 5.9). Charcoal continues to decline in both lakes, and the indicators of podocarp forest is almost entirely absent from the pollen records. Pasture as the dominant land-use in the catchments is demonstrated by the high amounts of grass and herb pollen (Figure 5.7). Wetland taxa increase slightly in Lake Alice but decline in Lake Wiritoa, potentially reflecting the restoration planting around Lake Alice in recent years (Figures 5.8 & 5.9). Catchment erosion peaks in Lake Alice and continues to decline in Lake Wiritoa, although this latter interpretation may be flawed (Figure 5.11).

$RABD_{660–670}$ shows large increases in primary productivity in both lakes, contrasting with Ca/Ti (Figure 5.11). *Pediastrum* increases relative to the intensifying agriculture zone, jumping to particularly high levels in Lake Alice (Figure 5.8). As there is minimal forest removal in this phase, this likely reflects an increase in the lakes' nutrient levels. Mn/Fe suggests more anoxia in both lakes, consistent with a higher biological oxygen demand with more eutrophic conditions (Figure 5.10). However, inference from this is limited in the upper few centimetres of both cores due to the ease of Fe and Mn mobilisation with changing redox conditions (Makri et al., 2021; Naeher et al., 2013). Cyanobacteria cell numbers increase reaching five times the 16S rRNA copies recorded in Lake Wiritoa's undisturbed era (Figure 5.12).

The most statistically significant shift in the cyanobacteria community for both lakes occurs as *Cyanobium* decrease while bloom-forming and potentially toxigenic taxa proliferate (Figures 5.13 and 5.14). The lakes also diverge in their community compositions at this point, closely resembling the average cyanobacterial communities detected in the contemporary sampling (Section 6.1; Figures 5.5, 5.6 & 5.15). There is a rapid shift to *Dolichospermum* dominance in Lake Alice, with rising proportions of *Microcystis* reads in the upper few centimetres of the sediment core (Figure 5.13). *Cuspidothrix*, *Sphaerospermopsis* and *Aphanizomenon* are also newly detected in this uppermost zone. The cyanobacteria community also changes quickly within Lake Wiritoa, first to *Dolichospermum* and then *Microcystis* dominance (Figure 5.14). *Aphanizomenon* and unclassified Nostocaceae are emergent throughout the zone. These cyanobacterial assemblages are seen in eutrophic lake systems both in Aotearoa New Zealand and internationally (Conley et al., 2009; Paerl et al., 2001; Wood, Maier, et al., 2017); they are also associated with dangers to livestock and recreation due to cyanotoxin production (Hilborn & Beasley, 2015; Wood et al., 2009).

6.3 Patterns and Drivers of Cyanobacterial Community Change

While there is some disagreement between proxies, collectively they represent a destabilisation of the aquatic ecosystems in both lakes as land-use changed. Metabarcoding and ddPCR demonstrate a transition in both lakes from low trophic status, low toxicity systems to eutrophic systems that are potentially toxic. Bloom-forming cyanobacteria were not detected in the pre-human phases of Lake Wiritoa, unlike some other Aotearoa New Zealand lakes (Picard, Pochon, et al., 2022). The oldest sediments in both cores were almost entirely comprised of *Cyanobium* and ASV reads that could not be classified to genus level (Figures 5.13 & 5.14). While it is possible that these unclassified reads were degraded specimens of different genera or novel taxa not yet described, it is equally likely that they are just degraded *Cyanobium* reads. Contemporary sampling indicated that *Cyanobium* is not over-represented in lake sediments, and the absence of preferentially-settled taxa such as *Dolichospermum* gives further confidence in the sedimentary molecular record (Figure 5.5).

Both the multidimensional and CONISS analyses showed a clear shift in the cyanobacterial communities with changing land-use, although to different extents in each lake (Figures 5.16, 5.17 & 5.18). Other studies have found a homogenisation of cyanobacterial communities with eutrophication (Monchamp et al., 2018), however this was not seen within Lake Alice and Lake Wiritoa. It is difficult to know if the wider range of genera detected with cultural eutrophication is matched by an expansion of species present, as ASV distribution among the detected genera is uneven and the extent to which each ASV represents a different species is unknown (Callahan, McMurdie, & Holmes, 2017; Schloss, 2021). Future research would be valuable to determine if this is a unique characteristic of Manawatū-Whanganui dune lakes, or an artifact of sedimentary DNA preservation.

6.3.1 Potential drivers of change

The similar community composition trend between both lakes as well as the relative temporal and taxonomic cohesion in the deforestation of both catchments provides an opportunity to explore potential drivers of cyanobacterial community change in two dune lakes that differ primarily in depth. Without pre-human stratigraphy, it is impossible to judge the impact of deforestation on the cyanobacterial community in Lake Alice. Within Lake Wiritoa, PERMANOVA showed a statistically significant change in the cyanobacterial community between the undisturbed and subsistence zones. However, these communities overlapped significantly within multidimensional analysis and the CONISS clustering (Figures 5.16b & 5.18). Furthermore, with no ASV detections of taxa associated with cyanobacterial blooms during the subsistence era (Figure 5.18), it is likely that deforestation had a minimal effect on lake productivity. Therefore light availability is not the key driver of the blooms and ecosystem destabilisation seen today.

In both lake cores, the major decline in podocarp forest pollen occurs during the subsistence area, and so the transition to intensifying agriculture is unlikely to have greatly increased light availability (Figures 5.8 & 5.9). This is supported in Lake Wiritoa by the similarity of the cyanobacterial communities between these two zones (Figure 5.16b). Determining the magnitude of any shift in Lake Alice is difficult with only two data points for the intensifying agriculture era. However, the two data points sitting comfortably within the subsistence era confidence ellipse suggests minimal change in the cyanobacterial community with the onset of early European settlement (Figure 5.16a). Despite these similar patterns, the greater effect of the pollen proxy in Lake Alice than Lake Wiritoa within the dbRDA suggests community composition in shallow lakes is more vulnerable to changes in light availability or shallowing (Wetzel, 2001) or erosion influxes (Scheffer et al., 1993) than deep lakes.

The biggest change in the cyanobacteria communities in both lakes coincides with the onset of aerial superphosphate topdressing, although to different extents. While the intensive agriculture cyanobacterial community retains significant overlap with the previous zones, additional nutrient availability in Lake Alice

saw increased variability (Figure 5.16a). In contrast, Lake Wiritoa's cyanobacterial community during the intensive agriculture phase is entirely separated from the previous three zones, supported by the highest *f* statistics in the PERMANOVA and dbRDA (Figure 5.16b). This is consistent with much of the paleolimnological and limnological literature, which link nutrient additions – particularly of phosphorous – to both cyanobacterial blooms and a shift towards more toxigenic taxa (Cao et al., 2020; Hobbs et al., 2021; Monchamp et al., 2018; Monchamp et al., 2016; Picard, Pochon, et al., 2022; Woodward, 2013; Yan et al., 2019).

There are several possibilities for why Lake Alice shows less cyanobacteria response with nutrient enrichment. Historical research identified the first aerial topdressing in Whanganui as likely occurring around Fordell, close to Lake Wiritoa's catchment of Kaitoke ("Wanganui Farmer Uses Own Plane to Put Manure on his Farm," 1950), and potentially reflected in the sudden Cd jump in the Wiritoa sediment core (Figure 5.10b). Without age control, it is difficult to identify whether the gradual increase of cadmium in the Lake Alice core is due sediment disturbance mixing the sediments or less enthusiastic adoption of aerial topdressing (Figure 5.10a). Furthermore, the Cd increase in Lake Wiritoa is to a higher concentration (around 0.3 mg kg^{-1} dry weight) than Lake Alice (around 0.25 mg kg^{-1} dry weight). While this may indicate that Lake Wiritoa reached a "critical level" of phosphorus input that Lake Alice has not reached yet, it could also be explained by the natural variation of cadmium concentrations within Nauru phosphate rock (Reiser et al., 2014).

6.3.2 Other potential drivers

Both the multidimensional and CONISS analyses indicate the ongoing community changes after the onset of aerial topdressing (Figures 5.16, 5.17 & 5.18). The intensive agriculture zone for Lake Alice is separated slightly on the NMDS2 axis, which is also reflected in the CONISS analysis (Figures 5.16 & 5.17). This suggests another community shift not explained by nutrient application or earlier changing land-use, and could also explain the relatively weak explanatory power of Cd within the PERMANOVA and dbRDA when compared to Lake Wiritoa. The Lake Wiritoa CONISS analysis also showed one further division, which may be reflected in the slightly wider variation in the intensive agriculture zone (Figure 5.18). There is no evidence in the proxy records to explain the shift, but it could be a further intensification of fertiliser application not reflected by Cd (Gray & Cavanagh, 2022).

Alternatively, it could be the effects of exotic fish and waterfowl. Goldfish were likely introduced with other *Cyprinus* species, and were established in ornamental ponds around the 1980s AD (Collier & Grainger, 2015). If the sediment accumulation rate is constant throughout the intensive agriculture phases, then goldfish were likely established within the lakes around the time of this secondary community shift. Toxigenic and bloom-forming taxa may therefore have had an increased competitive advantage within the

lake by goldfish predating on zooplankton, dislodging macrophytes, increasing nitrogen cycling and resuspending sediment-bound phosphorous (Abell et al., 2019; Collier & Grainger, 2015; Hobbs et al., 2021). Goldfish are particularly damaging within shallow lakes (Collier & Grainger, 2015), and so while this may explain the ongoing changes in Lake Alice, depth makes this more implausible in Lake Wiritoa. Additional nutrient loading from waterfowl such as paradise shelducks (*Tadorna variegata*) has been linked to *Microcystis* blooms in a paleolimnological study of Alexander Lake in New Zealand (Woodward, 2013). Extensive numbers of waterfowl are reported both historically in Lake Alice and in the field observations during summer sampling in this research, while less were seen on Lake Wiritoa. Impacts of waterfowl and goldfish may therefore be driving additional cyanobacterial community shifts in Lake Alice, and could be investigated with further molecular analysis.

Climate change is another potential driver of increased cyanobacterial blooms (Hobbs et al., 2021; Paerl & Paul, 2012), although little is known about the effect of temperature on cyanobacterial community composition (Wood, Borges, et al., 2017). Climate change is expected to both warm waters and extend the stratification period (Paerl & Huisman, 2009), potentially favouring different cyanobacteria taxa over diatoms and green algae (Puddick et al., 2022). Aotearoa New Zealand's annual average temperature has risen by 1.13C (± 0.27) between 1909 and 2009 AD, with warming occurring at approximately 0.9C per century (Ministry for the Environment & Stats NZ, 2020b; Mullan, Stuart, Hadfield, & Smith, 2010). Much of this warming occurred from the mid-20th Century (Ministry for the Environment & Stats NZ, 2020b). Central Pacific El Niño events have also increased in frequency in the latter half of the 20th Century (Freund et al., 2019), bringing cooler temperatures and higher rainfall in Aotearoa New Zealand's west (Ministry for the Environment & Stats NZ, 2020b). This could provide further advantage to bloom-forming cyanobacteria through increased rainfall in western Aotearoa New Zealand, with rapid washing of nutrient loads from paddocks into lakes (Phlips, Badylak, Nelson, & Havens, 2020; Puddick et al., 2022). *Microcystis* has been identified in some studies as especially tolerant of warmer temperatures and is associated with thermally stratified waters (Imai, Chang, Kusaba, & Nakano, 2008; Paerl & Huisman, 2009; Reynolds & Fogg, 1973; Robarts & Zohary, 1987). *Microcystis* was present in both lakes over the contemporary sampling period peaking in April, although this was after peak summer temperatures and stratification (Figures 5.2 & 5.5). However the surface water DNA however indicates no clear relationship between water temperature and *Microcystis* abundance, and *Microcystis* proliferation is also linked to nutrient availability and other environmental variables (Rinta-Kanto et al., 2009; Wood, Borges, et al., 2017; Yang, Gao, Glibert, Wang, & Tong, 2017). Other thermally-tolerant taxa including *Raphidiopsis* species, were also not detected in either lake core or contemporary sampling (Puddick et al., 2022). While warming and alterations to the El Niño-Southern Oscillation may be playing a part in this secondary community shift, particularly in the increase of

bloom-forming taxa ASV reads during the intensive agriculture zone, this research is unable to conclude whether climate change is driving either taxonomic or quantitative change.

Threshold shifts from cumulative effects rather than individual drivers are also a possibility. Anthropogenic impacts can compound within a lake system, each slightly reducing the resilience of an ecosystem until a threshold is reached or a stochastic event such as a storm occurs (Schallenberg & Saulnier-Talbot, 2016; Scheffer et al., 2001). Abrupt ecosystem changes are common responses to surpassed thresholds within a lentic system (Wagner & Adrian, 2009). Endogenous feedbacks can then maintain a lake within a new state (Dent, Cumming, & Carpenter, 2002) which biota populations can still fluctuate within (Scheffer & Carpenter, 2003). Significant destabilisation of the in-lake conditions were shown with ongoing anthropogenic impacts on the lakes, including in oxygen regime, biota assemblage and nutrient concentration. A threshold for cyanobacterial community composition may therefore exist in a combination of these interacting components that is not represented by one proxy. Thresholds are difficult to statistically detect (Gal & Anderson, 2010) but have been demonstrated in both shallow and deep lakes for water quality, particularly with the loss of macrophytes (Hilt, 2015). Shifts from oligotrophic to eutrophic conditions can occur in as little as three years when a critical threshold is reached (Tay, Teh, Koh, Mohd, & Zhang, 2021). As the surface water sampling within this research demonstrated that each sediment layer likely represents multiple years of cyanobacterial communities, crossing of a threshold could be captured in one or two samples. If a threshold shift has occurred in both lakes from cumulative effects, the ecosystem change detected here may be permanent (Carpenter et al., 1999; Hilt, 2015; Wagner & Adrian, 2009).

6.3.3 Implications for management of Lake Alice and Lake Wiritoa

The results from both lakes indicate that the cyanobacterial communities and blooms that occur today reflect the cumulative impacts of anthropogenic pressure, particularly since the advent of intensive agriculture. In both lakes, fertiliser application is associated with significant increases in cyanobacteria and the expansion of potentially toxigenic genera. This likely occurred just before the earliest quantitative water quality measurements in the coastal dune lakes (Cunningham, 1957), further underscoring the value of paleolimnology in setting appropriate baseline targets for lake management. The high percentages of diazotrophic taxa in both the contemporary surface water and throughout the intensive agriculture era indicates that phosphorous management is key to reduce the threat of cyanobacterial blooms (Figures 5.5, 5.13 & 5.14).

If hysteresis effects are occurring in either lake, nutrient loads will need to be reduced beyond the levels at the onset intensive agriculture era (likely c. 1950 AD) to reduce blooms (Scheffer & Carpenter, 2003). The need for quick nutrient load reductions may be hurried by the prevalence of *Egaria densa* in both lakes, an invasive macrophyte that is prone to sudden collapse (Waters et al., 2018). As shallow lakes are often partly

regulated by their macrophyte cover, a devegetation event in Lake Alice could make a return to the likely more oligotrophic state identified in the Māori subsistence phase much more difficult (Schallenberg & Sorrell, 2009; Scheffer, 2001; Scheffer & Carpenter, 2003). While Lake Wiritoa as a deeper lake is likely more resistant to hysteresis effects, internal nutrient loading with stratification has been identified as a likely process within Manawatū-Whanganui dune lakes (Waters et al., 2018). Lake Wiritoa has previously been found to have total phosphorous concentrations of around 4.0 ± 1.4 g kg^{-1} dry weight in the upper 4 cm of its benthic sediment, compared to the national average of 1.77 ± 1.42 g kg^{-1} dry weight (Woodward & Gibbs, 2019). While this is not conclusive evidence of internal phosphorous loading within Lake Wiritoa, internal loading has also been identified as a key driver of poor water quality in other lakes within the Manawatū-Whanganui dune complex with similarly high sedimentary phosphorous levels, including Lakes Horowhenua, Pauri, Dudding and Waipu (Gibbs et al., 2022; Waters et al., 2018; Woodward & Gibbs, 2019). Further consideration comes from Lake Wiritoa being a medium-depth lake overall, with potential regulation from both stratification and macrophyte cover (Hilt, 2015; Milan et al., 2022). Both lakes may therefore have different internal mechanisms that affect recovery times and require further research to identify potential secondary drivers that would contribute to the maintenance of a turbid state in each lake (Milan et al., 2022; Scheffer, 2001).

There is some evidence that Lake Alice was more productive in its baseline state than Lake Wiritoa. Although the absence of pre-human stratigraphy makes definitive conclusions difficult, the retention of significant overlap in its cyanobacterial communities across the three available land-use zone suggests a lesser magnitude of change than in Lake Wiritoa (Figure 5.16). This is further supported by the proximity of early intensive agriculture DNA samples to the previous two eras, suggesting a delayed response to the high-volume application of superphosphate. Further consideration comes from the relatively high percentages of *Pediastrum* in the Lake Alice pollen sum when compared to Lake Wiritoa (Figures 5.8 & 5.9). While this could indicate that *Pediastrum* – similar to the cyanobacteria described in Section 6.1 – may be more likely to be preserved in the shallow lake sediments, it also suggests that that Lake Alice was more constrained by light availability in its baseline state than Lake Wiritoa (Wetzel, 2001; Woodward, 2013). Utilising the same restoration or rehabilitation targets between the two lakes may therefore be inappropriate (Gann et al., 2019).

The common understanding of lentic vulnerability to eutrophication is that shallow lakes are more susceptible, in part due to their greater surface sediment to water ratio (Feuchtmayr et al., 2009; Hilt, 2015). Results presented here, however, imply this is an over-simplified approach for dune lakes. While both lakes have experienced significant cyanobacterial community change over time, the changes in Lake Wiritoa represent a greater departure from baseline conditions (Figure 5.16). As Lake Alice was likely more eutrophic than Lake Wiritoa – but still not to the extent seen today – it is possible that less overall change

that had to occur for today's cyanobacterial blooms. Therefore, while Lake Alice is likely more vulnerable to the high biomass of blooms associated with cultural eutrophication, the cyanobacterial community was much more responsive to nutrient enrichment in Lake Wiritoa. This is further supported by the other proxy indicators of in-lake change, which were broadly more variable in Lake Wiritoa than Lake Alice. While the shallow lake is more affected by the visible effects of eutrophication such as poor water clarity, the deep lake had more signs of continued ecosystem destabilisation with similar anthropogenic impacts. This implies that deep and shallow lakes may have different vulnerabilities to cultural eutrophication, and more significant impacts may be occurring even though they are less visible to people.

7 Chapter 7 – Conclusions

Cyanobacterial blooms are one of the most important water quality issues worldwide (Paerl et al., 2001). Although linked with cultural eutrophication both in Aotearoa New Zealand and globally (Conley et al., 2009), limited monitoring data can make lake management decisions difficult (Larned et al., 2018; Verburg et al., 2010). Paleolimnology has long been used to establish baseline states for lakes, and describe the changes that have occurred from anthropogenic pressures (Smol, 2008; Abell et al., 2019). This research utilised molecular techniques to explore how cyanobacterial communities have changed during the past millennium in two Manawatū-Whanganui dune lakes, Lakes Alice and Wiritoa. Paleolimnology proxies were used to both reconstruct the environmental changes that have occurred within and around the lakes, and investigate the probable drivers of the cyanobacterial blooms. This was complemented by molecular analysis of water and surface sediment samples within both lakes to explore how representative the sedimentary record is of the pelagic community composition.

Lakes Alice and Wiritoa had similar but statistically significantly different cyanobacterial communities during the 2021/2022 AD summer. Potentially toxigenic and bloom-forming taxa such as *Dolichospermum* and *Microcystis* were dominant. This is consistent with the warm water temperatures and the lakes' elevated TLI scores (Conley et al., 2009; Land Air Water Aotearoa, 2023a, 2023b; Paerl & Huisman, 2008). Alpha diversity metrics and multidimensional analysis indicated the community turnover and variability was higher in Lake Alice than Lake Wiritoa. The community composition of the surface sediment samples was taxonomically and proportionally similar to the water samples over the whole summer season. Despite the shallower Lake Alice likely having conditions more conducive to microbial degradation of DNA, sediment and water samples were more dissimilar in Lake Wiritoa. Lower sedimentary proportions of *Planktothrix* and *Cyanobium* in Lake Wiritoa suggest that genera ecology and interference from the metalimnion affect the sedimentation of cyanobacteria (Nwosu et al., 2021). Sedimentary samples also likely reflect multiple years of pelagic blooms.

Both lakes have undergone extensive changes in their cyanobacterial communities with changing land-use. The pre-human undisturbed era was only captured within the Lake Wiritoa core, however zones characterised by Māori subsistence living, intensifying European agriculture and intensive agriculture were successfully identified in cores from both lakes. The cyanobacterial community in both lakes responded to each land-use phase, with the proliferation of toxigenic and bloom-forming taxa only detected after the onset of aerial superphosphate topdressing, circa 1950 AD. Deforestation was the next most significant driver of cyanobacterial community change, but likely did not cause the blooms currently observed. The extent of change is underscored by the increasing destabilisation of the lakes' ecosystems, shown by in-lake indicators such as Mn/Fe and $RABD_{660–670}$ hyperspectral scanning. The community compositions detected in

the intensive agriculture era broadly matched the average community composition detected in the contemporary water samples, with *Dolichospermum* more prevalent in Lake Alice and *Microcystis* more prevalent in Lake Wiritoa. Clustering detected within the CONISS analysis suggests further drivers of cyanobacterial change during the intensive agriculture era. These could include exotic fish, climate change or cumulative effects causing a threshold shift (Carpenter et al., 1999; Wagner & Adrian, 2009). Without a representative proxy, however, these remain speculative.

As age control was unavailable at the time of writing, timelines of eutrophication were limited to the previously mentioned zones delineated by pollen and Cd concentrations. Similar cyanobacterial community changes were recorded at each stage between the lakes. Lake Alice also showed signs of being more eutrophic in its baseline state than Lake Wiritoa, with earlier detections of *Dolichospermum*, significant overlap in cyanobacterial community composition between land-use phases, and higher historic amounts of *Pediastrum*. Lake Wiritoa also showed a greater and more rapid response to intensive nutrient enrichment, challenging the general assumption that deep lakes are more resilient to cultural eutrophication. The potential presence of other drivers that are not detected within this study's proxies suggests multiple, complementary management strategies alongside external nutrient reduction will be necessary to reduce the impacts of cyanobacterial blooms in these lakes (Hobbs et al., 2021; Mehner et al., 2008; Schallenberg & Sorrell, 2009; Scheffer, 2001).

With the extensive insights gained in this research from sediment core eDNA, future study exploring the cyanobacterial settling dynamics would be beneficial. Understanding which genera are likely under- or -over-represented could improve confidence in molecular results and facilitate identification of potentially spurious detections. Longer term sampling of contemporary pelagic cyanobacterial communities would also assist this, as inferences are limited from one summer period. Replication of this research in other dune lakes would be valuable, as it is difficult to determine if the unusual XRF results and increasing diversity with eutrophication are limited to this study or a feature of dune lakes due to the limited literature available. Further coring of Lake Alice to obtain the pre-human period would also be useful. Exploration of additional drivers or thresholds is also important, and broader eDNA usage in the cores could potentially track the effects of fish or other bacterial community changes. Insight to these processes could both refine paleolimnological studies and improve advice for lake managers.

8 Chapter 8 – References

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9 Chapter 9 – Appendix

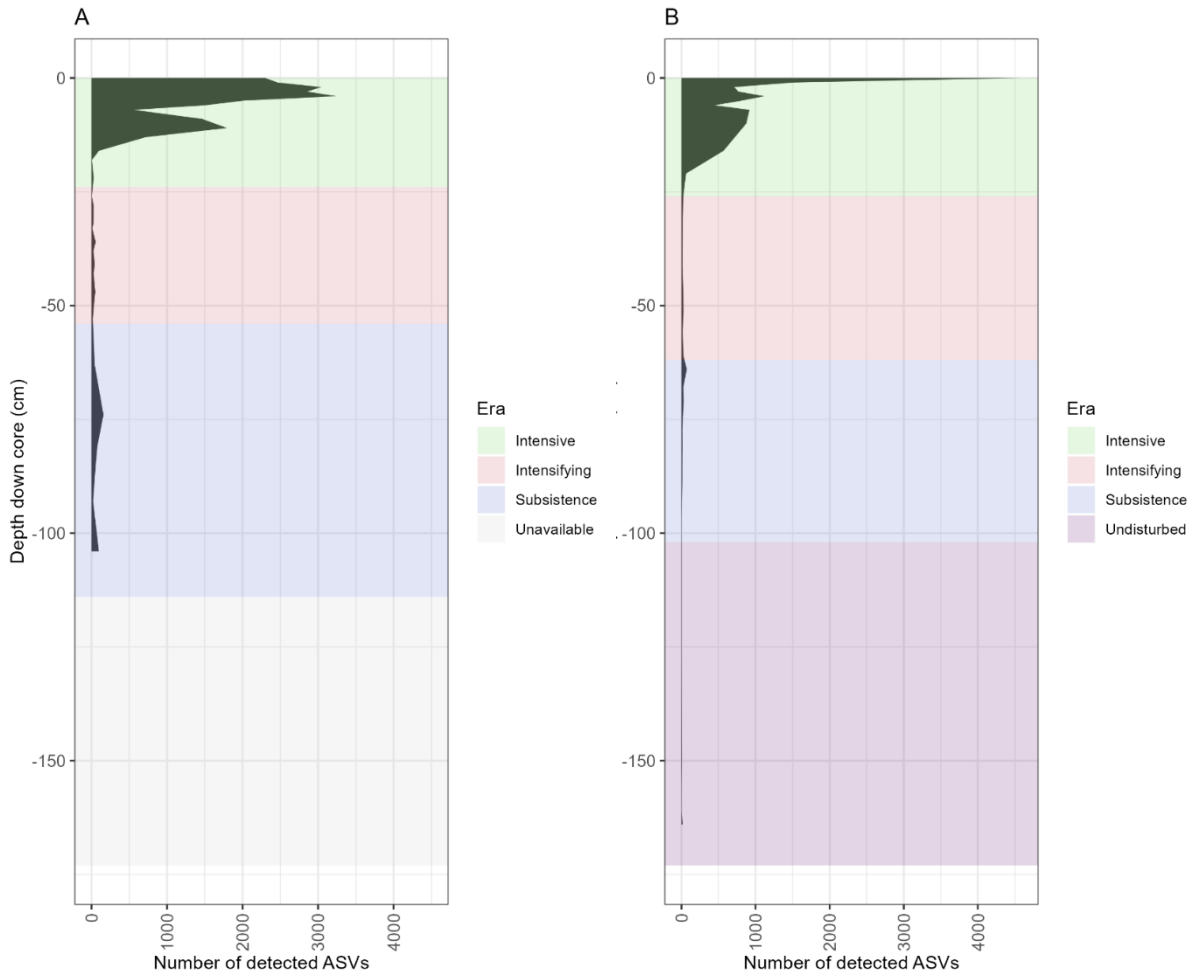

Figure 9.1 *The number of detected photosynthetic cyanobacteria ASV reads in the sediment core metabarcoding for Lake Alice (A) and Lake Wiritoa (B).*

Table 9.1 *Table of the ASV read totals for photosynthetic cyanobacteria for each metabarcoding sample in the Lake Alice sediment core. Samples highlighted grey were removed from multivariate analysis due to zero reads.*

Upper core (0-18 cm depth):														
Sample ID (descending core depth)	Al17	Al18	Al19	Al20	Al21	Al22	Al23	Al24	Al26	Al28	Al30	Al33	Al34	Al35
ASV read total	2299	2464	3041	2854	3243	2001	1509	560	1466	1793	719	98	54	6

Middle core (22-53 cm depth):														
Sample ID (descending core depth)	Al39	Al40	Al43	Al45	Al47	Al49	Al50	Al53	Al55	Al58	Al60	Al64	Al67	Al70
ASV read total	30	23	5	29	29	27	11	56	27	44	29	51	33	18

Lower core (63-104 cm depth):														
Sample ID (descending core depth)	Al80	Al91	Al98	Al2.2	Al2.10	Al2.21	Al2.31							
ASV read total	43	159	77	56	22	98	0							

Table 9.2 *Table of the ASV read totals for photosynthetic cyanobacteria for each metabarcoding sample in the Lake Wiritoa sediment core. Samples highlighted grey were removed from multivariate analysis due to zero reads.*

Upper core (0-36 cm depth):														
Sample ID (descending core depth)	Wi9	Wi10	Wi11	Wi12	Wi13	Wi14	Wi15	Wi16	Wi20	Wi25	Wi30	Wi35	Wi40	Wi45
ASV read total	4549	1472	648	713	1060	747	388	862	845	545	44	20	17	0
Middle core (41-97 cm depth):														
Sample ID (descending core depth)	Wi50	Wi55	Wi60	Wi65	Wi70	Wi73	Wi77	Wi80	Wi86	Wi90	Wi92	Wi98	Wi2.3	Wi2.6
ASV read total	13	19	27	13	27	71	25	30	12	13	12	11	0	4
Lower core (101-164 cm depth):														
Sample ID (descending core depth)	Wi2.10	Wi2.14	Wi2.25	Wi2.30	Wi2.35	Wi2.41	Wi2.46	Wi2.54	Wi2.59	Wi2.65	Wi2.70	Wi2.73		
ASV read total	0	0	0	4	0	0	0	0	8	4	3	15		