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Palaeoecological responses to environmental changes on South Pacific islands

Volume 1 of 1

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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South Pacific island ecosystems are exposed to numerous disturbances, which are both abiotic and human-driven in nature. However, little is known about the long-term responses (>100 year) of these ecosystems to such events. Palaeoecological methods can provide information about responses, recovery times, and extend our knowledge of vegetation change beyond recent history through centuries and millennia. Focusing on the South Pacific islands this thesis aims to understand how periods of environmental disturbance such as climate variability, fire regime change, human arrival, relative sea level change, and volcanic eruptions have altered ecosystems.

Specifically, three of the thesis aims are to understand 1) how local vegetation responded to volcanic eruptions and sea-level change during the Mid-Late Holocene in the Tongan archipelago. 2) To quantify at high resolution (~5 years) how the forests surrounding Lake Emaotul, Efate, Vanuatu, and the lake ecosystem responded to the 1450s CE Kuwae eruption and a shift towards drier climate conditions ~1100 cal. years BP. 3) A regional analysis of 15 sites on 13 islands, where the aim is to analyse regional patterns of biotic similarity throughout the past 5000 years.

Methods used to investigate the aims of the thesis are biomarker analysis, charcoal, chironomids, fossil pollen and spore analysis, magnetic susceptibility, radiocarbon dating, tephra analysis, and XRF. Additionally, statistical techniques such as Bray-Curtis similarity, cluster analysis, ordination, and regression models were used. Data from published pollen records was also incorporated.

Results show that in Tonga, relative sea level was a more important driver of change for local vegetation than volcanic eruptions. In addition, smaller, low-elevation island littoral, mangrove, successional, and wetland vegetation may be more vulnerable to sea level changes than vegetation on larger or higher elevation islands or inland vegetation habitats such as rainforest. Analyses from Lake Emaotul, Vanuatu, shows that vegetation turnover increased following the 1450s CE Kuwae eruption. Vegetation and chironomid turnover also increased following a shift towards drier climate conditions ~1100 cal. years BP. The Lake Emaotul analyses also reveal that a recent increase in burning regime led to an increase in vegetation turnover during the last ~85 years. Biotic similarity analyses across South Pacific islands revealed a 5000 year long trend of biotic homogenisation which accelerated ~3150 cal. years BP synchronous with human arrival to many Southwestern Pacific islands.

Four major conclusions can be determined from this work; 1) volcanic eruptions alter vegetation communities in some instances and this can be captured with high-resolution pollen sampling strategies (e.g., the Lake Emaotul record); 2) coastal vegetation communities on low-elevation and/or small islands may be more at risk from sea level rise; 3) vegetation and chironomid communities are sensitive to decreases in precipitation, and 4) human presence on South Pacific islands may have led to enhanced biotic homogenisation. These analyses extend our knowledge of ecological change on South Pacific islands and highlight the importance of environmental disturbances as drivers of ecosystem change.

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Research Thesis: Declaration of Authorship

Print name: NICHOLA ANN STRANDBERG

Title of thesis: Palaeoecological responses to environmental changes on South Pacific islands

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission.

Signature: .... Date: 24th May 2023

Acknowledgements

> ‘When a flower grows wild it can always survive’ from the song ‘Wildflowers’ written by Dolly Parton.
>
> ‘En gång fanns rosor här där nu en stad fort växer fram’ from the song ‘Lyckliga gatan’. Swedish lyrics written by Britt Lindeborg and performed by Anna-Lena Löfgren.

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Finally, I will say that I did not find this PhD easy, the pandemic sadly stole away many of the more enjoyable experiences for me and those in my cohort, but I am proud that I maintained momentum and did not compromise on the ambitious aims of my project despite the challenges and uncertainty of the past few years. I hope that this work will make a genuine contribution to our understanding of the ecosystems of South Pacific islands and adds some threads to the tapestry of our knowledge of ecosystems change.

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Definitions and Abbreviations

AP	Arboreal pollen
C/N	Carbon/ nitrogen
Cal. years BP	Calibrated years before present (1950 CE)
CCA	Canonical correspondence analysis
CE	Common era
DCA	Detrended correspondence analysis
ENSO	El Niño Southern Oscillation
GC-MS	Gas chromatography–mass spectrometry
Itrax	Core scanning equipment to obtain geochemical data
LM	Linear model
m.a.s.l.	Meters above sea level
MCA	Medieval Climate Anomaly
NAP	Non- arboreal pollen
R	Programming language
RSL	Relative sea level
SD	Standard deviation
SE	Standard error
Seda-DNA	Sedimentary DNA
Simper	Similarity percentage analysis
SPCZ	South Pacific Convergence Zone
TLE	Total lipid extract
Turnover	Replacement of taxa
WPWP	West Pacific Warm Pool
α-diversity	Mean local diversity
β-diversity	Differences or dissimilarities between sites

γ-diversity	Total diversity within a landscape

Chapter 1 Introduction

1.1 Thesis aim

South Pacific islands ecosystems are somewhat vulnerable to sea level rise, climate change, and tectonic activities. Human actions also impact these ecosystems via alterations of fire regimes and species composition changes via non-native introductions and native extirpations/ extinctions. The aim of this thesis is to investigate the impact of abiotic and human actions on South Pacific island vegetation over millennial timescales. A secondary aim is to investigate patterns of biotic similarity. What follows is an introduction of the geography, biodiversity, and human settlement history of the South Pacific.

1.2 Geography of the Pacific islands

The Pacific Ocean spans almost a third of the Earth's surface but only around 0.34 % of its area is land (Nunn et al., 2016). The boundary of the Pacific Ocean is the Pacific Rim, which is located along the east coasts of Asia, Australia and New Zealand, the west coast of North and South America and to the south Antarctica. The focus of this thesis is on islands south of the equator in the geographical regions of Melanesia and Polynesia (Figure 1-1) particularly the countries of Chile (Rapa Nui), Fiji, French Polynesia, New Caledonia, New Zealand, Samoa, Tonga, and Vanuatu.

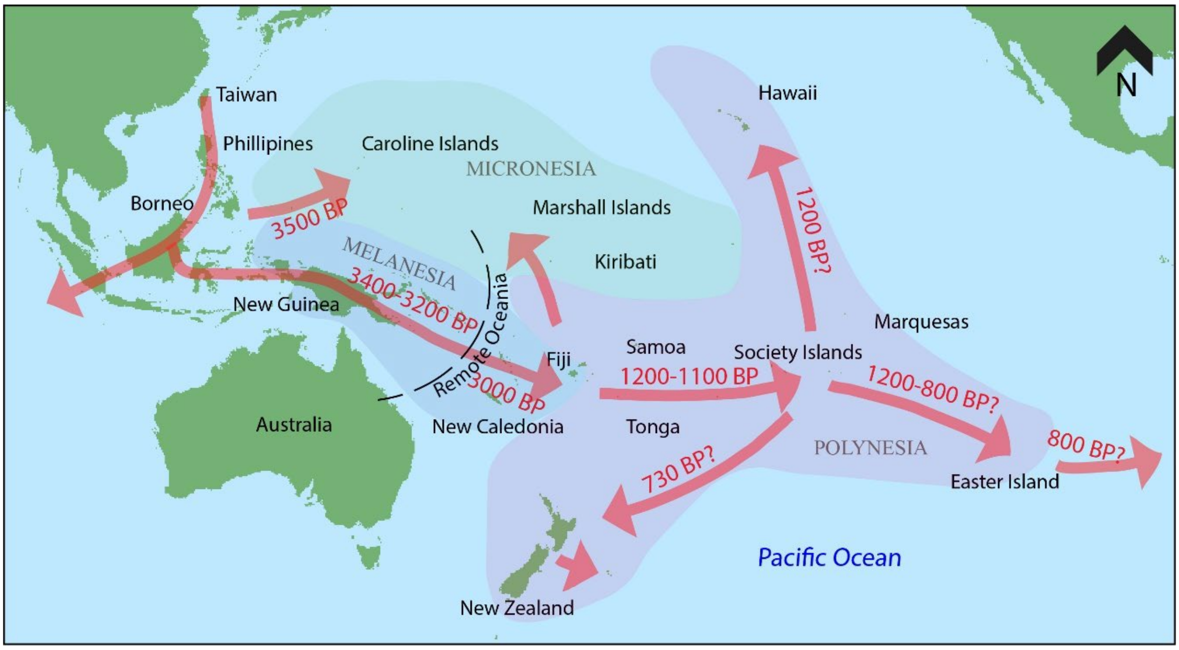

Figure 1-1 Remote Oceania and paths of colonisation, redrawn from Matisoo-Smith (2015).

1.3 Biodiversity of the Pacific islands

The source of many plants and animals on Pacific islands is New Guinea/Malesia, New Caledonia, and Australia (Keppel et al., 2009) and the main dispersal mechanisms for plants are wind, birds, and ocean rafting (Gillespie et al., 2012). Biodiversity decreases away from these source areas i.e. west to east (Keppel et al., 2009) creating a biodiversity gradient. For example, New Caledonia is known to have ~2379 native flowering species whereas Fiji has around 1302 (Jaffré, 1993), and Tonga has ~320 (Franklin, 2003). However, distance from the closest continent, or large island, is not the only control on biodiversity since biodiversity is also linked to island area and age with larger and older islands being more diverse (Keppel et al., 2009).

Islands are known to have relatively high rates of endemism for both plants and animals and these species can be considered highly specialised for their habitats (Macarthur and Wilson, 1967; Whittaker and Fernández-Palacios, 2007). However, these specialised island species are vulnerable to both human and natural disturbances due to their small population sizes, lack of genetic diversity, and low levels of α diversity (local diversity) (Frankham, 1998; Mueller-Dombois, 2008; Keppel et al., 2014). Some terrestrial ecosystems of Pacific islands include coastal forests, freshwater lakes and streams, grass savannahs, mangrove forests, open woodlands, salt marshes, mudflats and tropical montane rain forests (SPREP, 2012). However, many of these ecosystems are currently at risk from human impacts and natural hazards.

Today on Pacific islands, in terms of human impacts, the degradation and loss of habitat, arrival of invasive species, overexploitation of resources, disease, pollution, and human induced climate change have greatly impacted island biodiversity (Gibbons et al., 2000; Kingsford et al., 2009). Rainforest taxa are particularly at risk, for example in Tonga in the island group of Vava’u. It is estimated that ~90% of native vegetation has been modified and that native patches of rainforest are restricted to areas of steep terrain (Whistler, 1992). In Vanuatu, the loss of rainforest is detrimental to local communities who rely on the forests for food, medicine, building materials, cultural and spiritual requirements (Siwatibau et al., 1998). The loss of forests can also lead to a lack of income and to a loss of cultural identity and to small Pacific island communities becoming more globalised (Siwatibau et al., 1998).

Coastal ecosystems are also under threat in many Pacific islands as mangroves are cleared to make way for developments ('Aholahi, 2013). These mangroves are important habitats for fish and also protect against coastal erosion ('Aholahi, 2013). Mangroves trap sediment and promote clear water and the wood of the mangroves can be used to dye tapa cloth and for firewood (CBD, 2014). Sea-level rise is also a threat to mangroves and a recent study has shown that some mangrove species cannot keep pace with a rapid rise in sea-level (greater than 6.1 mm per year) (Saintilan et al., 2020) which is likely to be exceeded within the next 30 years according to the high emissions scenario (Church et al., 2013). Table 1-1 summarises some of the main threats to Pacific island terrestrial ecosystems.

Table 1-1 Summary of threats to terrestrial to flora and fauna on Pacific island ecosystems.

Main threats	**Impacts**
Climate change and sea-level rise	Plant and animal species often cannot migrate to find new suitable habitat conditions as climate conditions change (Hills et al., 2011). Mangroves cannot keep pace with rapid sea-level change (Saintilan et al., 2020) and mangrove species with narrow elevational ranges are most at risk (Ellison et al., 2022).
Governance	Poor policies and policy implementation processes regarding environmental protection (Hills et al., 2011).
Population increase	Between 1960 and 2021 the population of small Pacific states increased by over 1.7 million people (World-Bank, 2019). As populations continue to rise, there is increased pressure on resources such as fuel, food and freshwater (Hills et al., 2011).
Natural hazard events	Many Pacific islands, such as atolls, are low lying and topographically relatively simple, which leaves them vulnerable to natural hazards such as cyclones, droughts, earthquakes, floods, and tsunamis. These events can lead to loss or degradation of habitats and reduced opportunities for animals

Main threats	**Impacts**
	to find food, reproduce, and an increased risk from predation (Hills et al., 2011).
Introduction of exotic or invasive species	This is the largest cause of extinctions on Pacific islands through competition, disease, and predation. These factors impact biodiversity and alter ecosystem processes (Hills et al., 2011).
Threats to terrestrial systems	
Change of land-use	Habitats are lost due to land-use change to anthropogenic landscapes such as urban areas and farmland. Major causes of land-use change are forest burning to clear land and from logging (Hills et al., 2011)
Hunting of native animals	Negative impacts on specific species and ecosystems (e.g., fruit bat hunting, Coconut crab hunting and Pigeon hunting) (Hills et al., 2011)
Threats to freshwater systems	
Pollution and saline intrusion	Threats come from pollution, erosion causing sediments to enter the water system and saline intrusion of sea water (Hills et al., 2011).

1.4 Pacific islands and environmental change

The vegetation communities of South Pacific islands are impacted by short-term events such as cyclones (Franklin et al., 2004), El Niño Southern Oscillation (ENSO) climate variations (Haberle and David, 2004), volcanic ash falls (Cronin et al., 2004; Wallin and Martinsson-Wallin, 2010), and tsunamis (Chague-Goff et al., 2016). These dynamic ecosystems are also shaped and influenced by the ongoing extinction, extirpation, competition, and migration of new species (Fall, 2010). For many of these ecosystems the arrival of humans and the plants and animals they brought with them is considered to have been the largest ecosystem alteration in their recent history (Hope, 2001). The ecosystem changes of the past, i.e. caused by the arrival of people to South Pacific islands, contact with Europeans and subsequent ecosystem changes have caused large scale ecosystem modifications in terms of both flora (Fall, 2010) and fauna (Steadman, 1993).

Anthropogenic and natural changes to the ecosystems of Pacific islands, are referred to as **environmental changes** and **disturbances** in this thesis. These past environmental changes (Table 1-2) can be investigated and used as analogues for modern day and future vegetation changes. This thesis focuses on human impacts, climate change, RSL (relative sea level) change and volcanic eruptions.

Table 1-2 Definitions of environmental change or disturbances in this report, duration of the change and example studies.

Environmental change	**Duration of change event**	**Example studies**
Human impacts	Variable depending on whether the island became permanently settled or was abandoned (up to ~3000 years of impacts)	Mo’orea in French Polynesia (Stevenson et al., 2017), Samoa (Gosling et al., 2020), Tonga (Fall, 2005), New Zealand (Argiriadis et al., 2018), New Zealand, Norfolk Island (Australia) Henderson and Pitcairn (Prebble et al., 2019)
Climate change (usually precipitation)	Long-term change (decadal-millennial scale)	Efate, Vanuatu (Wirrmann et al., 2011; Combettes et al., 2015; Maloney et al., 2022), Fiji (Hope et al., 2009)
El Niño–Southern Oscillation (ENSO)	Can be long (increased frequency of ENSO events) or short-term (annual)	New Guinea and Northern Australia (Haberle and David, 2004)
Cyclones	Short-term (days/ weeks)	Vava’u, Tonga (Franklin et al., 2004)
Relative sea-level change	Centuries/ millennia (or rapid when earthquakes occur changing the land elevation)	Tonga and Mangaia (Cook Islands) (Ellison, 1988; Ellison, 1989; Ellison, 1994)
Tsunamis	Short-term (days)	Mangaia, Cook Islands (Chague-Goff et al., 2016). Tonga (Terry et al., 2022)
Volcanic eruptions and tephra/ ash falls	Short-term (days, years decades)	Efate, Vanuatu (Wirrmann et al., 2011) and Tonga (Terry et al., 2022)

1.5 Human arrival on Pacific islands

The colonisation of the Pacific islands represents the last great migration of humans into unoccupied lands. Oceania can be delineated into two geographical areas based on the period in which they were colonised (Green, 1991) (Figure 1-1). The portion which was colonised earlier is termed Near Oceania and includes New Guinea, colonised around 50,000 cal. years BP (Summerhayes et al., 2010), Australia, colonised around 45,000 cal. years BP (O'Connell and Allen,

2004) and the northern Solomon Islands, colonised around 30,000 cal. years BP (Wickler and Spriggs, 1988).

Archaeological evidence suggests that the first people to colonise the South Pacific islands were the Lapita, the ancestors of Polynesians (Kirch and Green, 2001). Linguistic studies indicate the Lapita's origins to be somewhere between Taiwan and the Bismarck Archipelago (Blust, 1996) and genetic studies support this (see Matisoo-Smith, 2015 for discussion). The Lapita left Southeast Asia and Melanesia and travelled by voyaging canoe to colonise new islands (Kirch, 1997; Spriggs, 1997). The size and exact design of these canoes is unknown, but the canoes must have been large enough to transport founding populations (Irwin, 2008). The Lapita people also took with them their tree and root vegetable agricultural systems, such as *Colocasia esculenta* or taro (Kirch and Ellison, 1994) and animals (Steadman, 1995b). Settlers altered the ecosystems of the islands they settled in various ways. Land covered by rainforest was cleared by burning and converted into agricultural land (Ellison, 1994; Kirch, 1996; Argiriadis et al., 2018). The Lapita brought with them animals such as *Sus scrofa* (pig), *Canis familiaris* (dog), *Rattus exulans* (Pacific rat), *Gallus gallus* (chicken) (Steadman et al., 2002) and their arrival coincided with the loss and extinction of birds and other animals (e.g., Olson and James, 1982; Steadman, 1995a; Steadman et al., 2002).

The earliest suggested dates for the settlement of Remote Oceania are based on archaeological findings and are dated to about 3500 cal. years BP for initial settlement of the Mariana Islands, in Western Micronesia, although there is no associated evidence of Lapita culture (Rainbird, 1994). Human colonisation of the Bismarck Archipelago occurred 3400–3200 cal. years BP (Summerhayes, 2010), 3000 cal. years BP for Efate, Vanuatu (Petchey et al., 2014), 3000 cal. years BP for Fiji (Denham et al., 2012), 2850 cal. years BP for Tonga (Burley et al., 2015) and 2750 cal. years BP for Samoa (Clark et al., 2016).

After a pause of approximately 1500−2000 years, the proto-Polynesian colonisation continued into other parts of the Pacific. Short timescales for colonisation of Eastern Polynesia after 950 cal. years BP have been suggested (Commendador et al., 2014; Kahn et al., 2015a; Kahn and Sinoto, 2017). However, a two-phase expansion has also been suggested (Wilmshurst et al., 2011). This two-phase expansion was suggested to have begun ∼925–830 cal. years BP when the proto-Polynesians colonised the Society Islands and then after a pause of 70–265 years continued to colonise other remaining islands (Wilmshurst et al., 2011). Sear et al. (2020) suggest that drought conditions in the Western Pacific may have been the impetus for incremental human dispersal into other parts of Polynesia.

1.6 Detection of human occupation within sediment cores

Palaeoecological records such as that produced by Fall (2005); Stevenson et al. (2017) and Prebble et al. (2019) can reveal a wealth of information about past human activities and impacts on landscapes. However, this evidence is largely indirect and difficult to disentangle from abiotic drivers of change such as wildfires, climate changes, and volcanic eruptions. Faecal biomarker analysis offers a direct method, or a ‘smoking gun’, to detect if higher mammals, particularly humans, were abundant in a past ecosystem (e.g., D’Anjou et al., 2012; Argiriadis et al., 2018). Faecal biomarker 5β-coprostanol is the most abundant sterol in human faeces since it constitutes around 60% of the total sterol content (Leeming et al., 1996; Bull et al., 2002) and when 5β-coprostanol undergoes epimerization (a change in the configuration of the molecule) it becomes 5β-epicoprostanol (Birk et al., 2011). These biomarkers are also common in porcine (pig) excretions (Bull et al., 2002) and it is known that pigs were first introduced to across Pacific islands by humans (Steadman, 1995b). Therefore, any increase in these faecal biomarkers in the sedimentary record may indicate the arrival of humans. Both 5β-coprostanol and 5β-epicoprostanol typically reach sediment basins via runoff (Meyers, 1997) and therefore reflect the catchment scale. This is advantageous given that pollen analysis, which is often used to detect human presence, often reflects a more regional scale (D’Anjou et al., 2012). 5β-coprostanol and 5β-epicoprostanol are usually well preserved in sediments since they are hydrophobic (Tolosa et al., 2014) and therefore suitable to use in palaeoecological studies where sediment cores are analysed. Since 5β -stanols adsorb to organic matter particles, they are not prone to leaching (Lloyd et al., 2012).

Although this method has typically been limited to temperate regions (Prost et al., 2017), this technique has been used successfully in other parts of the South Pacific such as New Zealand (Argiriadis et al., 2018) and the Cook Islands (Sear et al., 2020). In New Zealand, faecal biomarker analysis has indicated the first arrival of humans, which was synchronous with deforestation ~1350 CE and the transient occupation of watersheds (Argiriadis et al., 2018). In the Cook Islands, the detection of faecal biomarkers has indicated that human colonisation may have occurred earlier than previously thought (Sear et al., 2020).

1.7 Past human impacts on island biodiversity

The human introduction of exotic flora and fauna on South Pacific islands lead to complex ecosystem changes (Steadman, 1993; Fall, 2010). For example, in Rapa Nui (Easter Island) it has been suggested that introduced rats may have consumed fruits and seeds and thus prevented the germination of new plants and ultimately impeding the growth of new forest (Hunt, 2007). Perhaps one of the most noticeable features of human arrival seen in South Pacific pollen diagrams is the introduction of exotic taxa such as *Colocasia esculenta* (taro) and/or *Ipomoea batatas* (sweet potato). *Colocasia esculenta* pollen in pollen records from across the Pacific has shown that it was introduced to New Zealand 1280 CE (Prebble et al., 2019), the Society Islands 1060–980 cal. years BP (Stevenson et al., 2017), Hawaii 1331 CE (Athens and Ward, 1997) and French Polynesia 1100 CE and 1400 CE respectively (Kennett et al., 2006; see Prebble, 2008 for review; Prebble and Wilmshurst, 2009).

Human arrival also coincided with the loss of taxa: for example, the loss of birds and bats in Tonga may have impacted the dispersal mechanisms of some native trees with large fruits, such as *Calophyllum inophyllum*, *Cerbera odollam*, *Pouteria garberi*, *P. membranacea*, *Pometia pinnata*, *Syzygium quadrangulatum, S. richii*, and *Terminalia catappa* (Fall, 2010). Human arrival to Pacific islands is also linked with a decline in palm pollen, for example *Pritchardia,* and is often associated with an increase in charcoal particles and pollen from non-native weeds and cultivated taxa (Prebble and Dowe, 2008).

Anthropogenic landscapes of South Pacific islands were characterised by changed fire regime, which is seen in charcoal and pollen records. A marked increase in charcoal is usually seen at the time of human arrival, as in New Zealand 1350 CE (Argiriadis et al., 2018), the Society Islands 1060–980 cal. years BP (Stevenson et al., 2017) and Tonga 2600 cal years BP (Fall, 2005) to name a few studies. The increase in burning, caused by traditional slash and burn farming techniques (Pole, 2014) also results in an increase in *Pandanus*, a relatively fire-resistant native tree (Prebble et al., 2005).

To summarise, human colonisation and settlement of Pacific islands is associated with:

1) the introduction of plants for agriculture, medicine, or construction (Prebble, 2008; Fall, 2010),
2) increased burning regime to clear land (Fall, 2005; Stevenson et al., 2017),
3) the extinction and extirpation of native or endemic plants and animals (Steadman, 1995a; Prebble and Dowe, 2008).

1.8 Main abiotic drivers of change on Pacific islands

Previous pollen studies in the Pacific (see supplementary Table 5-1) have shown the extent to which this region has been studied in terms of past vegetation change. Most of the studies within the region focus on human impacts or the arrival of humans on vegetation; however, some have also focussed on the effects of natural environmental changes such as sea-level change (Ellison, 1988; Ellison, 1989; Ellison, 1994) and climate change (Hope et al., 2009; Wirrmann et al., 2011; Combettes et al., 2015).

1.8.1 Holocene climate change and cyclones

Climate in the Pacific region, and indeed globally, has not been stable during the Holocene and is therefore an important factor to consider when identifying palaeoenvironmental changes on South Pacific islands. One reason for this climate variability is the movement and variability of the SPCZ (South Pacific convergence zone) which is a rain band which delivers precipitation to the islands of the South Pacific Ocean (Hassall, 2017; Sear et al., 2020). The impacts of past dry periods on South Western Pacific islands may have been severe and it has been suggested that drought coupled with other societal pressures may have been the catalyst for Polynesians to explore the Eastern Pacific islands (Sear et al., 2020).

A study by Sear et al. (2020) combined regional climate records to identify a drier climate phase 1150 to 1300 CE in Vanuatu, Samoa, and Atiu (Cook Islands) and, used faecal stanols as markers for human presence. This dry phase was linked with the Polynesian exploration of islands in the Eastern Pacific. Similarly, Hassall (2017) identified a migration or shift of the SPCZ towards the southeast Pacific during the Mid-Holocene (*c*. 5600–2700 cal years BP) associated with reduced ENSO variability (Cobb et al., 2013).

The response of vegetation to climate change has been studied in the South Pacific at several sites in Fiji (Hope et al., 2009) and Emaotfer Swamp, Vanuatu (Wirrmann et al., 2011; Combettes et al., 2015). Wirrmann et al. (2011) identified an increase in ENSO events in Vanuatu *c.* 3250–2500 cal. years BP whereas Combettes et al. (2015) identified a vegetation change caused by ENSO event increases between 3790–3600 cal years BP. Hope et al. (2009) identified a possible dry phase and an increase in ENSO events around 5000 years ago in Fiji with the response of an increased fire regime. These climate records show the movement of the SPCZ created precipitation changes on South Pacific islands throughout the Holocene. Changes in precipitation, for example, known dry phases, likely impacted vegetation but there is still much uncertainty about responses. Although there have been attempts to detect climate changes in pollen records from the South Pacific none have combined pollen with other proxies from the same site to measure precipitation.

Warm and humid conditions created by the SPCZ are ideal conditions for cyclones (e.g., Vincent et al., 2011). Although vegetation responses to cyclones are not the focus of this study, they offer a useful insight into the response and recovery of these ecosystems following rapid and often high intensity disturbances. Cyclones are a regular occurrence on Pacific islands (e.g., Chague-Goff et al., 2016) and some post cyclone observations and surveys are available in order to investigate the impacts of these storms on vegetation. On the 3rd March 1982 cyclone Isaac passed over the Ha'apai and Tongatapu island groups in Tonga killing six people, devastating buildings and destroying crops (Woodroffe, 1983). Coastal scrub vegetation including coconut palms were stripped and *Pandanus* trees were felled, however 11 –15 weeks after the cyclone struck some shrubs had begun to recover (*Messerschmidia argentea*, *Hibiscus tiliaceus*, and *Bikkia tetrandra*). On 31st December 2001 tropical cyclone Waka passed directly over Vava'u, Tonga (Franklin et al., 2004). Since vegetation plots had already been established in Vava'u in 1995, a pre and post-cyclone survey comparison was made possible (Franklin et al., 2004). Characterisation of the forest plots followed those by Franklin et al. (1999) and due to human impacts on the forests of Vava'u forest types were grouped classified on a successional gradient rather than into topographic or habitat preferences. Tree mortality related to the cyclone was lower in late successional lowland forest species (6%) compared with early successional lowland forest species (8 – 16%) (Franklin et al., 2004). Uprooting and snapped stems were found to have occurred on 25% of stems measured within the plots. Uprooting was relatively high amongst the large trees (> 20 cm diameter) and the greatest level of damage was to the largest trees (> 35 cm diameter) which were found in early successional plots (Franklin et al., 2004). Prior to cyclone Waka and over a 6 year period, background mortality was 1.4% and most of the plots has not been impacted by any human activities (Franklin et al., 2004). This contemporary example shows how a cyclone can change the make-up of a forest system, preferentially removing older and larger trees and increasing tree mortality; however, no study has been done on the impacts of cyclones on native forests, unmodified by people, in this part of the world. Without an analogue for the effects of cyclones of native forest types it is difficult to identify the potential ecosystem changes and to identify these in pollen records. It is still unclear whether native forests are more or less resilient to cyclone damage than human modified forests.

An example of vegetation change related to cyclones in pollen records was from Mangaia in the Cook Islands. Clay deposits from weathered laterites in Lake Tiriara, Mangaia, have been found to coincide with decreases in tree pollen and increases in fern spores (Dawson, 1990). These spores may be related to soil erosion of the volcanic slopes around the lake during the heavy rainfall associated with cyclone events (Lamont, 1990). However, the use of palaeoecological records to reconstruct cyclone activity in the past may be problematic given that they occur on short timescales (Table 1-2) and may appear similar to other erosional events. A high resolution study would be required to investigate such levels of detail within sediment cores and a multi-proxy approach is preferred ideally using grain size and Itrax (Croudace et al., 2006) to identify sedimentary changes related to in wash of material during cyclones.

1.8.2 Sea-level change during the Holocene

During the Mid-Holocene sea levels in the Pacific were higher than today; this was caused by equatorial ocean siphoning (Mitrovica and Milne, 2002) which is a function of global isostatic adjustment and the transfer of water from glaciers to the world's oceans (Dickinson, 2014). Sea levels peaked around 4000 years ago and these conditions persisted for 1000–2000 years (Dickinson, 2003). Around Tonga and Fiji sea levels were 2–2.5 m higher than today during the high stand and to the east and west in Polynesia and Micronesia 1.5–2 m higher than today (Dickinson, 2014). Ellison (1988) identified the timing of the Mid-Holocene high stand to around 4500–2500 can years BP in Tongatapu, Tonga by identifying mangrove pollen from sediment cores. Relative sea-level histories for islands across the Pacific may differ due to their differing isostatic histories i.e. uplift or subsistence rates (Woodroffe and Horton, 2005), for example the northern islands of Tonga have subsided at a rate of around 0.5mm/ year (Dickinson, 2014). This means that the relative sea-level change may be less (1–1.5 m) than for other islands within the region. After the Mid-Holocene high stand sea levels fell until present day levels (Ellison, 1989). Most recently, several sea-level curves have been modelled for the island of Tongatapu in Tonga, one of these estimates is shown in Figure 1-2 (Fukuyo et al., 2020).

Understanding past sea levels in the Pacific during the Holocene is important for understanding the human settlement patterns of islands and for reconstructing coastal vegetation. Dickinson and Burley (2007) have correlated Lapita archaeological sites with shoreline reconstructions in Tonga and have found that they are broadly found along palaeoshorelines. Gosling et al. (2020) who produced a pollen and charcoal record from central Upolu, Samoa also suggest decreasing human impacts away from coastlines. This suggests a preference for living is coastal locations and that in the past, disturbances may have been most intense in coastal areas.

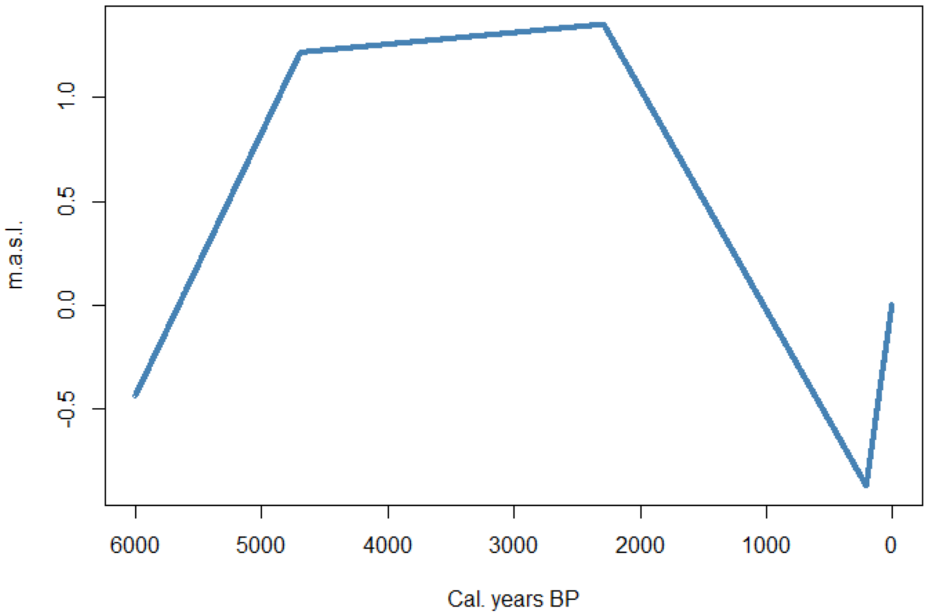

Figure 1-2 Sea level change for Tongatapu over the past 6000 years digitised from Fukuyo et al. (2020). The model output used was with lithospheric thickness of 65 km, lower mantle viscosity of 2 (10^{20} PaS), and upper mantle viscosity 1 (10^{22} Pa S).

1.8.3 Volcanism and tsunamis during the Holocene

Every year around 60 volcanoes erupt globally and around 20% of these eruptions occur on land (Dale et al., 2005). These eruptions have impacts on vegetation from lava flows, pyroclastic flows, avalanches, mudflows, tephra deposition and blowdowns (Dale et al., 2005). Examples of impacts wrought on vegetation vary from whole island sterilisation such as the 1883 CE Krakatoa eruption in Indonesia (Whittaker et al., 1989) to blanketing an island in volcanic ash such as occurred in Hawaii during the Kilauea Iki 1959 CE eruption (Smathers and Mueller-Dombois, 1974). These events allow for the investigation of the varying impacts of disturbance on vegetation such as the modification of vegetation to the colonisation of plants on freshly created substrates from lava flows (Dale et al., 2005). The vegetation changes that occur depend on the distance from the eruption, nutrients released during the eruption, and the types of vegetation and propagules that survive (Dale et al., 2005). The depth of the ash fall also appears to play an important role and this is linked to the distance from the eruption (Eggler, 1963). Where tephra deposits are deep, plants may not be able to penetrate the surface. Lesser impacts may occur further away from the epicentre of the eruption such as ash impeding photosynthesis (Bilderback and Carlson, 1987) or windblown tephra causing plants to drop their leaves (Black and Mack, 1984).

Perhaps one of the most notable volcanic eruptions to occur in the South Pacific was the Kuwae eruption, which has been estimated to have occurred in either late 1452 or early 1453 CE (Gao et al., 2006). A song (oral tradition) in Vanuatu mentions two women who went searching for *Boa*, a type of edible plant with tubers similar to yam, that was only collected during times of need, who happened across a man buried alive and helped him out, this song has been linked with the Kuwae eruption (Hoffmann, 2007).

Wirrmann et al. (2011) provided a pollen record from Emaotfer Swamp, Efate, Vanuatu (~100 km south of the eruption site). They identified a tephra layer from the Kuwae eruption but found no evidence of related vegetation changes. However, the resolution of the pollen sampling was relatively low with one sample per ~380 years. A higher resolution pollen sampling strategy may be required to identify vegetation change associated with volcanic eruptions. Further investigation is required to understand whether impacts from the eruption altered vegetation and impacted the lives of those who lived there. However, other palaeoecological studies from South America indicate that volcanic eruptions may be followed by a decrease in local forest taxa and an increase in herbs (e.g., Montoya et al., 2021) or even the onset of primary succession (e.g., Fesq-Martin et al., 2004).

A major source of earthquakes and tsunamis in the Pacific Ocean is the Tonga-Kermadec Trench (Goff et al., 2011) and submarine slope failures (e.g., Goff et al., 2011). For example, in 2010 a tsunami hit the uninhabited southern coast of Mangaia in the Cook Islands and was caused by a sub-marine slope failure (Goff et al., 2011). A more recent example is the January 2022 tsunami which was caused by the Hunga Tonga–Hunga Haʻapai submarine eruption and caused wave amplitudes >60 cm (Terry et al., 2022). Additionally, the 1450s CE Kuwae eruption in Vanuatu is known to have left tsunami deposits at least 30 m.a.s.l. on islands close by and as far away as Wallis and Futuna (1500 km away) (Goff et al., 2012). However, distinguishing between cyclone deposits, tsunami deposits and erosional events within sediment records is not straightforward but grain size measurements of sediments may assist in the identification of tsunami deposits (Chague-Goff et al., 2016). Additionally, the response of ecosystems to tsunamis is relatively unknown.

1.8.4 Ecosystem responses and similarity

As discussed in the previous sections, South Pacific island ecosystems encounter a number of environmental disturbances over time. In palaeoecology, fossil assemblages mirror the communities which produced them and to some degree the environmental disturbances that they have endured (Correa-Metrio et al., 2014). Statistical techniques are required to investigate these fossil assemblages and associated changes. For example, multivariate techniques offer a way to summarise fossil datasets (e.g., Bush et al., 2004; Correa-Metrio et al., 2014; Castilla-Beltrán et al., 2021a; Nogué et al., 2021). Although insights can be gained from observing individual taxon changes within a dataset, multivariate techniques are more robust and can provide understanding of a wide range of ecological changes (Orlóci et al., 2006). Detrended correspondence analysis (DCA) is a multivariate technique which is relatively easy to interpret in terms of understanding responses (Hill and Gauch, 1980) and DCA axes are presented in units of standard deviation (SD) which makes it possible to interpret distances between samples in terms of turnover (Orlóci et al., 2006).

While turnover offers a useful way to measure changes within fossil assemblages, it is also possible to calculate recovery rates following disturbances (e.g., Cole et al., 2014; Matthews-Bird et al., 2017; Montoya et al., 2021). For example, Cole et al. (2014) investigated re-establishment times of tropical forests taxa following disturbances. Results suggest that forests which are exposed to natural, large, and infrequent events recover faster than climatic and human induced disturbance events and that increased frequency of disturbance events increases the recovery time. Investigation of community changes following disturbances have also proven useful. For example, a study of lakes in the tropical Andes of Ecuador has investigated the impact of volcanic ash falls on chironomid communities, and at one lake, Laguna Baños, it has been shown that communities have not recovered 1500 years after ash deposition.

Both abiotic disturbances and human impacts can also lead to increases in similarity between distinct ecosystems. This increase in similarity between ecosystems is called biotic, or taxonomic homogenisation (McKinney and Lockwood, 1999) and has been identified in plants (Castro and Jaksic, 2008; Castro et al., 2010; Finderup Nielsen et al., 2019), insects (Shaw et al., 2010), birds (Rosenblad and Sax, 2017), fish (Magurran et al., 2015; Liu et al., 2017) and corals (Burman et al., 2012). This is a concerning trend given that reduced diversity can pose a threat to ecosystems, since it may remove the functional ability of communities to respond to disturbances (Gámez-Virués et al., 2015). The process of biotic homogenisation is caused by the introduction of non-native species to multiple locations (Castro and Jaksic, 2008) and by the extinction or extirpation of native or endemic species (Fraser et al., 2022). A third mechanism which drives biotic homogenisation is the filtering associated with disturbances. For example, drought conditions have been known to homogenise pond communities (Chase, 2007) and scouring events have been known to homogenise macroinvertebrate communities in the Scandinavian mountains (Lepori and Malmqvist, 2009). In both instances, only the species which are tolerant of the extreme conditions persevere. Tree falls in rainforests have also lead to biotic homogenisation (Connell, 1978) since a limited number of taxa excel at rapidly colonising forest gaps. Palaeoecology has been used occasionally to investigate patterns of similarity (e.g., Feurdean et al., 2010; Blarquez et al., 2014; Birks et al., 2016b; Salgado et al., 2018; Wengrat et al., 2018; Fraser et al., 2022) despite its potential to uncover long-term patterns.

1.8.5 Ecosystem recovery, resilience, and resistance

Resilience, recovery, and resistance are key concepts in ecology (Van Meerbeek et al., 2021). Recovery can be defined as returning to an ecological condition following a disturbance (Westman, 1978; Hillebrand et al., 2018; Domínguez-García et al., 2019). Van Meerbeek et al. (2021) identified two definitions of resilience. The first is resilience sensu Holling (1973) and is defined as the ability of an ecosystem to remain unchanged and maintain ecosystem relationships despite absorbing the impacts of disturbance, this is also sometimes called ecological resilience (Holling, 1973). The second definition is sometimes called engineering resilience and was put forward by Pimm (1991) and Grimm and Wissel (1997) and states that resilience can be defined as a period of recovery after a disturbance event. Hodgson et al. (2015) argue that both perspectives should be included, and that resilience covers a broad range of factors relating to the recovery of an ecosystem and the time it takes to recover, the resistance to change and the general precariousness of an ecosystem. The term resistance is also used to refer to the ability of an ecosystem to remain unchanged following a disturbance (Justus, 2007).

Some ecological models suggest that heterogenous and diverse landscapes may be more resilient to stress (Virah-Sawmy et al., 2009) and that these diverse and heterogenous ecosystems may recover quicker (Gunderson, 2000). Palaeoecology offers a method to test such models (e.g., Virah-Sawmy et al., 2009) and to extend the timescales of our understandings of ecosystems and measure recovery times (e.g., Cole et al., 2014) and gain insights into resilience and resistance.

1.9 Outstanding questions

There is a considerable body of knowledge related to the palaeoecology of the Pacific islands and many of these studies focus on human impacts (see supplementary information Table 5-1). However, far less is known about responses to different environmental changes (e.g., climate changes, sea level changes, and volcanic eruptions). In addition, there are other questions which require more research:

1) what are the effects of long-term versus short term disturbances on vegetation?
2) Are ecosystems becoming more similar or different over time due to disturbances or human impacts?

Understanding past vegetation responses is important for predicting the response of vegetation to future human disturbance, sea-level change, climate change, and volcanic eruptions. In addition, understanding patterns of biotic similarity may help us understand large scale patterns in diversity and therefore ecosystem resilience.

1.10 Study setting

To investigate these questions about South Pacific island ecosystems, wetlands or lakes where sediments or organic materials accumulate forming a palaeoecological record are required with the following desirable attributes:

1. Sites located on islands with different physical characteristics, for example different elevations and areas, to investigate the whole landscape change,
2. Sites with evidence of natural disturbance (e.g., tephra layers from past volcanic eruptions), and
3. Sites on islands which have been colonised by humans where the timing of colonisation is well understood.

To address the outstanding questions posed above, this thesis will focus on Tonga, and specifically the island of ‘Uta Vava’u, and the island of Efate, Vanuatu (Table 1-3) since these sites meet the site selection criteria. The final aim is to improve the regional knowledge of vegetation response to environmental change and disturbances by analysing published datasets from 15 locations, including one within this thesis, to make larger-scale comparisons of vegetation change and trajectories of homogenisation and differentiation.

Table 1-3 Summary of selected sites for case studies.

	Ngofe Marsh, ‘Uta Vava’u, Tonga	**Lake Emoatul, Efate, Vanuatu**
Location	18°39'46.8"S 174°02'36.4"W	17°43'58.3"S 168°24'52.3"E
Elevation (m.a.s.l.)	4	110
Distance to coastline (km)	0.8	7
Island size (Nunn et al., 2016)	12719.52 ha	99278.3 ha
Island type	Limestone high island	Composite high island
Maximum elevation of island (m)	88	647
Distance to closest mainland (Weigelt and Kreft, 2013)	(Late, Tonga closest available island) 3395.726 km	(Matthew, Vanuatu, closest available island) 1886.709 km
Human colonisation date	2850 cal years BP (Burley et al., 2015)	3000 cal years BP (Petchey et al., 2014)
Evidence of abiotic environmental change?	Multiple tephra layers, reported sea-level fall around 2000 years ago	Kuwae tephra (1450s CE). Drier conditions indicated by dinosterol record (Sear et al., 2020)
Length of record	~7500 years	~1600 years

1.11 Research questions

The overarching research questions are as follows:

1. What is the effect of relative sea-level fluctuations and volcanic eruption drivers on island vegetation change in Tonga?
2. What are the relative effects of the 1450s CE Kuwae eruption, ~1100 cal. years BP drying trend, and changing fire regime on vegetation?

3. Have South Pacific islands plant communities become more similar or dissimilar during the past 5000 years?

Additionally, faecal biomarker analysis of samples from the Ngofe Marsh sediment cores was used to detect the timing of human arrival to the island of ‘Uta Vava’u in Tonga and to compare this with the timing of human arrival based on archaeological findings (e.g., Burley et al., 2015) (for methodology, results, and discussion see appendix E page 147).

Chapter 2 Influences of sea level changes and volcanic eruptions on Holocene vegetation change in Tonga.

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2.1 Abstract

Here, we investigate Mid- to Late-Holocene vegetation changes on low-lying coastal areas in Tonga and how changing sea level and recurrent volcanic eruptions have influenced vegetation dynamics on four islands of the Tongan archipelago (South Pacific). To investigate past vegetation and environmental change at Ngofe Marsh (‘Uta Vava’u) we examined palynomorphs (pollen and spores), charcoal (fire), and sediment characteristics (volcanic activity) from a 6.7-m long sediment core. Radiocarbon dating indicated the sediments were deposited over the last 7700 years. We integrated the Ngofe Marsh data with similar previously published data from Avai’o’vuna Swamp on Pangaimotu Island, Lotofoa Swamp on Foa Island, and Finemui Swamp on Ha’afeva Island. Plant taxa were categorised as littoral, mangrove, rainforest, successional/ disturbance, and wetland groups and linear models were used to examine relationships between vegetation, relative sea-level change, and volcanic eruptions (tephra). We found that relative sea-level change has impacted vegetation on three of the four islands investigated. Volcanic eruptions were not identified as a driver of vegetation change. Rainforest decline does not appear to be driven by sea-level changes or volcanic eruptions. From all sites analysed, vegetation at Finemui Swamp was most sensitive to changes in relative sea level. While vegetation on low-lying Pacific islands is sensitive to changing sea levels, island characteristics, such as area and elevation, are also likely to be important factors that mediate specific island responses to drivers of change.

2.2 Introduction

Pacific islands are subject to volcanic eruptions and sea-level change, which may put their populations and ecosystems at risk (Nakicenovic et al., 2000; Cronin et al., 2004). The January 2022

Hunga Tonga-Hunga Ha'apai volcanic eruption, and associated tsunami inundation of parts of Tonga, exemplifies the need to improve our understanding of how island ecosystems respond to environmental dynamics. This research analyses four palaeoecological records from Tonga, one new in this study and three extant records, to quantify how vegetation (littoral, mangrove, rainforest, successional/ disturbance, and wetland; Table 2-1) responded to both sea-level changes and volcanic eruptions over the last 5000 –7000 years.

It is well established that the timing and sources of past volcanic eruptions can be derived from tephra layers preserved in the stratigraphy of sediment records (Lowe, 2011). Such layers allow researchers to identify how ecosystems responded to volcanic events, especially when recovery periods exceed the timescales of modern observations, i.e., centuries rather than decades. Evidence for the impacts of volcanic eruptions on vegetation from other ecosystems world-wide indicates variable responses, recovery times and initial conditions (Strandberg et al., 2023b). For example, in Ecuador a palaeoecological reconstruction showed an increase in grass pollen and a decrease in forest pollen, presumably indicating a shift in vegetation cover (Montoya et al., 2021), whilst in Chile, Fesq-Martin et al. (2004) recorded a primary succession sequence. In other cases, impacts on vegetation may not be detected at all (e.g., Gosling et al., 2020), they may be brief, e.g., lasting up to a few decades (Lotter and Birks, 1993; Urrutia et al., 2007) or longer lasting, e.g., several hundred years; (Fesq-Martin et al., 2004).

Evidence of past volcanic activity in Tonga includes a stratigraphic tephra and pollen record from Lotofoa Swamp, Foa, Ha'apai group (Figure 2-1), which shows an increase in mangrove taxa *Excoecaria* (Tongan name fetaʻanu) for ~3000 years following an eruption ~3840 cal. years BP (Flenley et al., 1999). However, it is difficult to disentangle the effect of volcanic eruptions from those of relative sea-level rise (RSL) and other environmental changes.

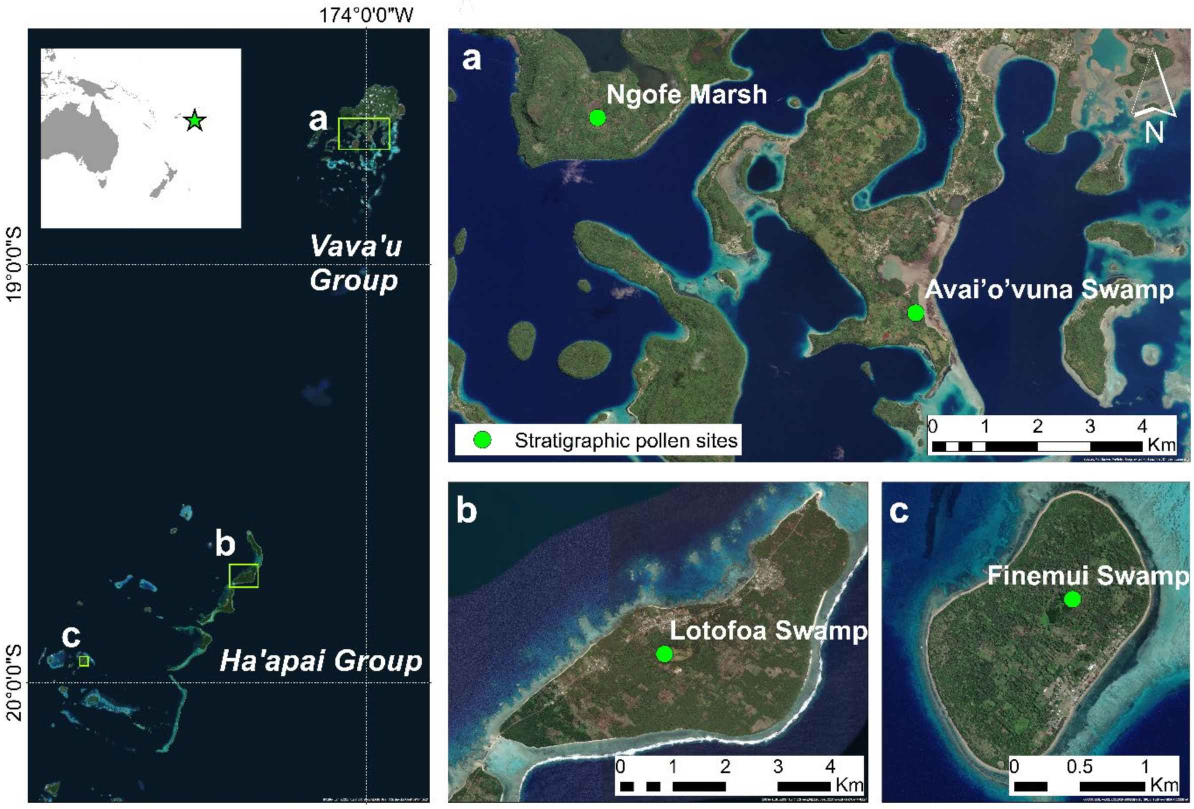

Figure 2-1 Left panel: the Northern Tongan Island groups and locations of study sites. The stratigraphic pollen sites are; a) Ngofe Marsh on ‘Uta Vava’u Island (this study) and Avai’o’vuna Swamp on Pangaimotu Island (Fall, 2005), b) Lotofoa Swamp on Foa Island, and c) Finemui Swamp on Ha’afeva Island (Flenley et al., 1999). Satellite imagery is from ESRI (2022).

Ecosystems in Tonga have also been influenced by changes in RSL; for example, a Holocene sea-level high stand was identified using sediment cores from Folaha Lagoon, Tongatapu and Avai’o’vuna Swamp, Vava’u and dated between ~5000–2000 cal. years BP (Ellison, 1989; Fall, 2005). Sea levels reached near-present levels in the South Pacific by ~7300 cal. years BP, then were up to 2 m higher than present by the Mid- Holocene, ~4000 cal. years BP, before falling towards present day levels thereafter (Nunn and Peltier, 2001). Similar patterns of change have been identified from modelled RSL changes from Tongatapu (Fukuyo et al., 2020). Changes in sea level altered coastal environments, resource availability, and the size and shape of the islands (Nunn, 2009; Margalef et al., 2018). In particular, mangrove vegetation zones retreated and advanced with sea-level rise and fall (Ellison, 1989). Mangrove species with narrow elevation ranges (~0.4 m), including those with a preference for the landward zone (e.g., *Nypa fruticans),* may also be more at risk than those with broad ranges, e.g., *Bruguiera gymnorhiza* (tongo lei) (Ellison et al., 2022). In addition, sediment accretion rates show that mangrove communities in tropical coastal regions are not able to keep pace with projected future sea-level rise (Saintilan et al., 2020). Despite the importance of RSL changes there has been limited regional analysis to determine how littoral vegetation, occurring along the shore or landward of mangrove forests, e.g., *Barringtonia* (futu), *Casuarina* (toa), and *Pandanus* (fafa), and rainforest taxa, e.g., *Syzygium* (fekika) and *Dysoxylum* (moʻota), may be impacted by changes in sea level.

Using the most complete records of RSL and tephra deposition available, we investigated how changes in these drivers have impacted the vegetation of Tonga during the Mid and Late Holocene, also taking into consideration the role of island size and elevation. We first describe a new palaeoecological record from Ngofe Marsh on the island of ʻUta Vava'u (Vava'u group). We then present a regional analysis of four sites: Ngofe and three published records from Tongan islands (Flenley et al., 1999; Fall, 2005).

2.3 Methods

For faecal biomarker analysis of the Ngofe Marsh sediments see appendix E on page 158.

2.3.1 Study sites

The Tongan archipelago lies on the eastern margin of the Asia-Australian Plate, which is uplifting as the Pacific Plate subducts under it; this causes volcanic activity (Crane, 1979). The 169 islands in the Tonga group mostly consist of raised limestone or coral sand cays. The larger islands, such as Tongatapu, have fertile soils due to nutrient inputs from ash falls over time (Roy, 1990). Raised limestone karstic islands are permeable and have freshwater lenses (Roy, 1990); their surface elevation is controlled by sea-level position (White and Falkland, 2010). The climate in Tonga is mild marine tropical, and South Pacific trade winds dominate for most of the year (Fall, 2010). Precipitation averages around 2340 mm per year and the average annual temperature is 23.5°C (Thompson, 1986).

Tonga is part of the South-Western Pacific, Indo-Melanesian floristic area (van Steenis, 1979). In a review, Fall and Drezner (2020) identified 1020 vascular plant species in Tonga with 450 of these being native. Fewer than 2% of the 1020 species identified are endemic (Fall and Drezner, 2020).

2.3.2 Coring site at Ngofe Marsh on ‘Uta Vava’u Island

Ngofe Marsh is a land-locked wetland on the island of ‘Uta’ Vava’u, in the Vava’u island group (18°39'49.27"S 174° 2'35.57"W; 4 m a.s.l.). Recently, the flora of Ngofe Marsh has been dominated by the sedges *Eleocharis dulcis* (kutu) and *Lepironia articulata* (kutu kofe), and the swamp tree *Erythrina variegata* (ngatae) (Fall, 2010). In May 2017, a 670 cm sediment core was retrieved from Ngofe Marsh from the centre of the basin. The core segments were collected using a 5-cm diameter Russian peat corer with a 50-cm long sampling chamber. The cores were retrieved with 10-cm overlaps to avoid missing any part of the sequence, boxed carefully to avoid movement during transit, and transported back to the UK within 48 hrs after collection. All cores were stored at 5°C at the University of Southampton cold core storage facility, UK.

2.3.3 Radiocarbon dating for Ngofe Marsh

Three macrofossil and three bulk-sediment samples were dated using AMS (accelerator mass spectrometry) radiocarbon techniques at the SUERC NERC Radiocarbon Laboratory. Radiocarbon dates were calibrated using the Southern Hemisphere calibration curve (Hogg et al., 2020). The age-depth model for Ngofe Marsh was created using the *rbacon* package in R Studio (Blaauw and Christen, 2011; RStudio Team, 2015; R Core Team, 2017) (see Table 5-3).

2.3.4 Palynomorph and charcoal extraction, identification, and counting

Sixty-one core sediment subsamples were prepared for analysis following standard procedures (Erdtman and Wodehouse, 1944) giving an approximate resolution of one sample per 120 years for the Ngofe Marsh main core. Subsamples of 1-cm^3 volume were taken from the core and *Lycopodium* tablets (batch #3862, *n*= 9666 and batch #140119321, *n*=19,855) were added in order to calculate charcoal concentrations (Stockmarr, 1971). See the supplementary information for detailed description of the pollen preparation methods. Pollen grains were counted at 400x magnification with detailed identification and photography of grains at 1000x magnification (Figure 5-4). Pollen identification was carried out using the pollen reference collection of Prof. John Flenley stored at the Department of Geography, Geology and Environment, University of Hull, and three pollen keys (ANU, 2007; Gosling et al., 2013; Poliakova and Behling, 2016). The pollen percentage diagram was created in Tilia 2.0.41, and pollen assemblage zones were determined using CONISS, a cluster analysis technique included in Tilia (Grimm, 1987; Grimm, 1990).

To investigate fire history around Ngofe Marsh, we counted micro- and macro-charcoal fragments at ~10 cm intervals. Micro-charcoal particles (<125 µm), indicating a regional fire signal, were identified in the pollen slides as opaque, black, and angular fragments. The micro-charcoal particles were counted alongside pollen grains and the exotic *Lycopodium* spike across regularly spaced transects on each slide (Wang et al., 1999). Macro-charcoal samples, counted to reconstruct local fire history, were prepared by sieving 1-cm^3 sediment samples at 125 µm and retaining the >125-µm fraction; this was bleached with 6% H_2O_2 until the reaction stopped. All macro-charcoal fragments in a sample were counted using a stereo microscope.

2.3.5 Palaeoecological information of the additional pollen records

We augmented the Ngofe Marsh pollen data with three pollen datasets: 1) Avai'o'vuna Swamp, a coastal wetland on Pangaimotu Island in the Vava'u island group (Fall, 2005), 2) Finemui Swamp on the small island of Ha'afeva, and 3) Lotofoa Swamp on the island of Foa (Flenley et al., 1999) (Figure 2-1). All sites are relatively low lying (<7 m a.s.l.) and hence have the potential to be impacted by changes in RSL. For these sites the age-depth models were re-calibrated using the SHCal20 calibration curve (Hogg et al., 2013). We digitised the pollen percentage diagrams and core stratigraphies from Lotofoa Swamp (basal age 7200 cal. years BP) and Finemui Swamp (basal age 5200 cal. years BP) of Flenley et al. (1999) using ImageJ software (Schneider et al., 2012). We used the original counts from Avai'o'vuna Swamp (basal age 4800 cal. years BP) from Fall (2005).

2.3.6 Vegetation groupings

We classified all pollen taxa into one of the following groups: littoral, mangrove forest, rainforest, successional/ disturbance, wetland, and other, see Table 2-1; following Whistler (1992) and Ellison (1990). Mangrove taxa have been listed previously for Tonga (Ellison, 1990), and littoral taxa were identified with reference to the flora of Malinoa island (21° 2'12.33"S 175° 7'43.84"W). The census flora list of Malinoa island was used as an example of a littoral habitat ecosystem due to the island's small (~0.66 km^2) area and low elevation (< 7 m.a.s.l.). Genus and family names with the prefix cf. were omitted. Uncertain pollen and spore identifications also were omitted. Taxa with the notation "comp." (favourably comparable) and "sim." (similar to) were included (Benninghoff and Kapp, 1962).

Table 2-1 List of the six vegetation groups used to classify the fossil pollen taxa: littoral, mangrove, rainforest, successional, or disturbance, wetland, and others. Information on the vegetation classifications and description is inferred from on contemporary vegetation ecology based on Whistler (1992), and Ellison (1990).

Vegetation group	**Description and ecology**	**Typical fossil pollen taxa**
Littoral	Includes coastal back-beach herbs, shrubs, and trees, also plants of coastal raised rocky shorelines. These are usually narrow vegetation zones affected by marine influences such as part-saline groundwater, reduced freshwater availability and perhaps salt spray. Taxa are often water dispersed (Fall and Drezner, 2011).	*Barringtonia*, *Casuarina, Cocos nucifera,* and *Pandanus.*
Mangrove forests	Taxa growing around mean tide elevations up to high tide. Taxa are mostly water dispersed (Fall and Drezner, 2011).	*Acrostichum*, *Excoecaria*, *Rhizophora* and Rhizophoraceae.
Rainforest type	Includes coastal forest (further inland than the littoral forest), lowland forest, and montane forest with canopies up to 30 m in height. According to Fall (2010), this was the dominant vegetation type before human arrival in most areas, apart from those that have experienced recent volcanic activity (Whistler, 1992).	Anacardiaceae, *Canarium*, *Diospyros*, *Dysoxylum*, *Elaeocarpus*, Myrtaceae, and Sapotaceae.
Successional, or disturbance-adapted secondary forest	Includes managed land, secondary scrub, and secondary forest. Many species are considered anthropochores.	*Homalanthus*, *Macaranga, Plantago* and *Trema.*

Wetland	This includes inland freshwater wetlands (which may be close to the coast) and upland wetlands that are dominated by herbaceous taxa.	Cyperaceae, *Polygonum*, *Potamogeton*, *Stenochlaena*, and *Typha*.
Other	Includes grasses, lowland volcanic scrub, upland scrub, and taxa which cannot be otherwise classified due to taxonomic uncertainty/ lack of botanical information.	Monolete fern spores, Poaceae, and trilete fern spores.

2.3.7 Sediment and tephra analysis

We used two methods to detect tephra falls from volcanic eruptions: 1) tephra content and tephra shard geochemistry, and 2) the stratigraphic description from sedimentary sequences.

2.3.8 Tephra content and tephra shard geochemistry

For Ngofe Marsh, we determined the sediment elemental variations and Ti/incoherent-scatter using an Itrax core scanner (BOSCORF, National Oceanography Centre) using established procedures (Croudace et al., 2019). The Scanner used a Mo-X-ray tube and analysis was carried out at a 200-µm step-size and a dwell time of 30 seconds. We also used magnetic susceptibility to detect layers with higher magnetism that might include potential tephra layers with a predicted higher Fe-Ti content/mineralogy. These data were obtained using a Bartington MS2 scanner (Dearing, 1994). Sections of the cores that displayed relatively higher values of magnetic susceptibility and Ti/incoherent-scatter (Tephra layers T1-T5; determined from Itrax scanner, see Figure 5-3) were subsampled and analysed for tephra content and tephra shard geochemistry. See the supplementary information for the tephra geochemistry method.

2.3.9 Stratigraphic descriptions of sedimentary sequences.

For Lotofoa Swamp (Figure 2-1b), and Finemui Swamp (Figure 2-1c), we used the stratigraphic description from Flenley et al. (1999) to indicate the locations of tephra layers. For Avai’o’vuna Swamp (Fall, 2005) no tephra layers were identified during the analysis of sediment cores. However, given the close proximity (6 km) of the two sites, we match the Ngofe Marsh tephra dataset to the Avai’o’vuna sedimentary sequence (see Figure 5-3).

2.3.10 Holocene sea-level change

Sea-level change for the Tongan archipelago over the past 6000 years was obtained from Fukuyo et al. (2020). The model output we digitised to be used in the linear models was with lithospheric thickness of 65 km, lower mantle viscosity of 2 (10^{20} PaS), and upper mantle viscosity 1 (10^{22} Pa S). The same sea level model was used for all four sites.

2.3.11 Statistical analysis

The analyses are based on percentage data of the vegetation groups (Table 2-1), in which the 'other' group was removed and the data for the five remaining vegetation groups were rescaled to 100%. For the Ngofe Marsh pollen record, Cyperaceae, belonging to the wetland habitat group, dominated the pollen record (up to 80% of the pollen and spore sum), potentially masking other interesting shifts within habitat groups, for this reason Cyperaceae was removed from the Ngofe Marsh analysis. Pollen percentage data were log-transformed to normalise distributions. Linear models were used to investigate the relationship between the pollen taxa from littoral, mangrove, rainforest, successional/ disturbance, wetland vegetation groups, RSL, and volcanic eruptions (tephra) at each site separately. The tephra variables consist of 0s and 1s for absence or presence of tephra layers, respectively. Tephra layers were assigned dates from the age-depth models (Figure 5-2). Temporal changes of vegetation groups were visualised for each island using local polynomial regression fitting (Figure 2-3).

2.4 Results

2.4.1 *Pollen, spores, and charcoal records for Ngofe Marsh*

The core stratigraphy, radiocarbon dates (Table 5-3), and calibrated age-depth models (Figure 5-2), are presented in supplementary information. The pollen diagram (Figure 2-2) was divided in three zones based on CONISS cluster analysis (Grimm, 1987).

2.4.1.1 Pollen assemblage zone one: 639–414cm (7440–4920 cal years BP):

This pollen zone contains 24 samples. Mangroves (Rhizophoraceae 31%), rainforest (*Elaeocarpus*-type 12%, *Syzygium* 9%), disturbance taxa (*Trema* 12%), and ferns (monolete fern spores 5%) dominate the record. A ~300-year peak in *Trema* starts at around 3900 cal. years BP and is associated with a tephra layer. There are also minor occurrences of coastal taxa such as *Terminalia*-type (1%) and rainforest taxa such as Arecaceae, Burseraceae, *Calophyllum*, Fabaceae, *Homalium*, *Ixora*, Melastomataceae, Meliaceae, and Sapotaceae. The disturbance taxa *Homalanthus* and *Rhus* are found in abundances of <1% and 5%, respectively. Macro- and micro-charcoal concentrations are low (<1 fragment per cm^3 and ~15700 fragments per cm^3 respectively).

2.4.1.2 Pollen assemblage zone two: 414–206cm (4920–2040 cal years BP)

This pollen zone contains 22 samples. There are evident peaks in *Trema* 17%, *Stenochlaena* fern spores 17%, *Macaranga* 15%, monolete fern spores 14%, and cultivated Poaceae grains > 40 µm 2%. The primary rainforest taxa *Elaeocarpus* and *Syzygium* decrease to 4 % and 1 %, respectively. The successional taxon *Rhu*s also decreases to 1%. Micro-charcoal concentrations increase to around 725,000 fragments per cm^3. Macro-charcoal concentrations remain low (~2 fragments per cm^3) or zero.

2.4.1.3 Pollen assemblage zone three: 206–44 cm (2040–430 cal years BP)

This pollen zone contains 15 samples and coincides with reed peat in the stratigraphy. There is increased pollen from Cyperaceae 80%, *Pandanus* 17%, *Macaranga* 14%, and Poaceae 13%. For most samples, pollen from rainforest taxa and mangroves is absent. Micro-charcoal concentrations are lower (140,000 fragments cm^{-3}) than in Pollen assemblage zone two, but macro-charcoal is present with high concentrations of ~100 –600 fragments per cm^3.

2.4.2 Tephra falls from volcanic eruptions

Analysis of samples (T1-T5) from Ngofe Marsh confirmed that these sediment layers contain tephra. The samples have not been geochemically matched to specific eruption events.

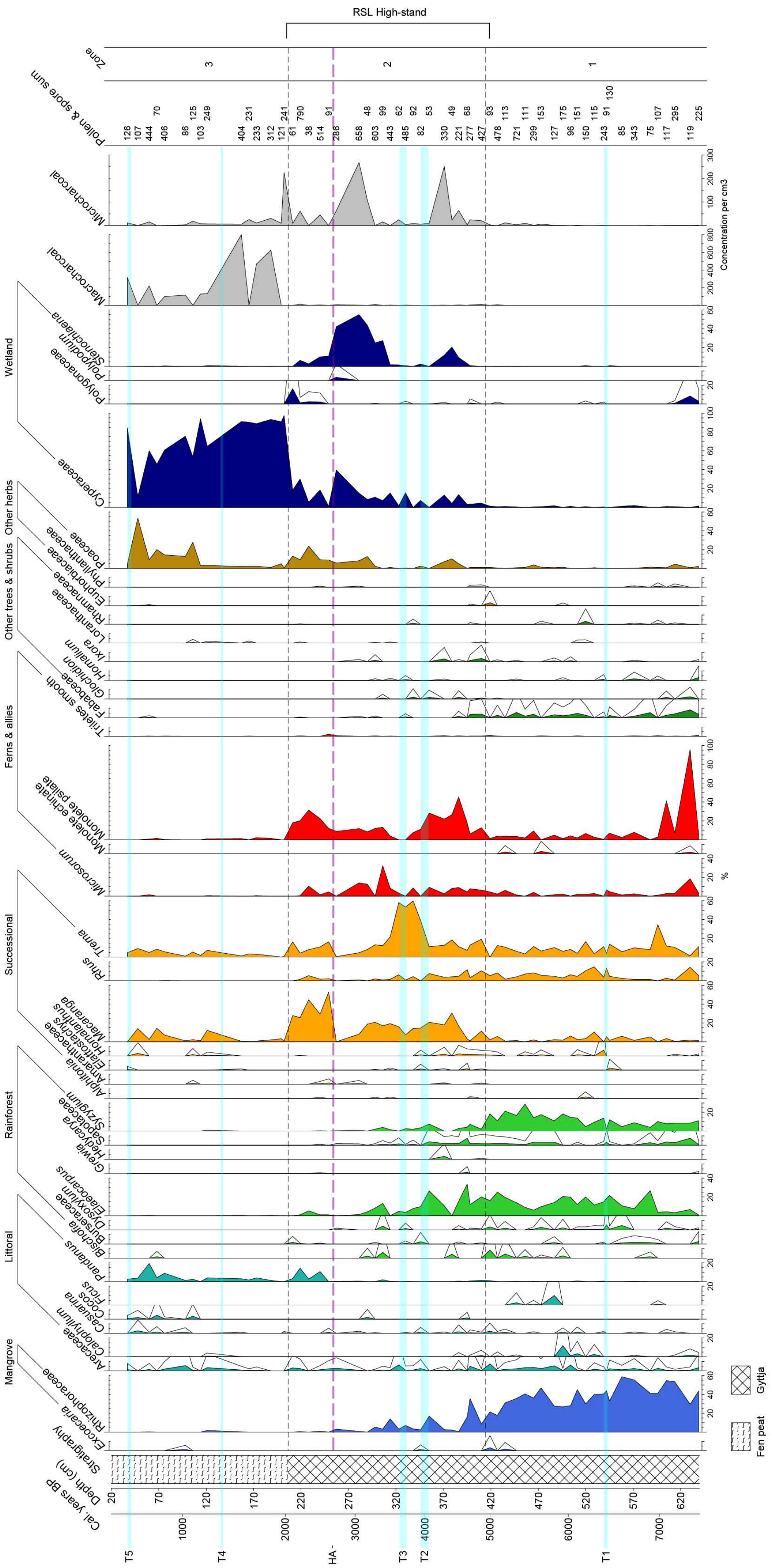
RSL High-stand
Zone
3
2
1
Pollen & spore sum
126
107
444
70
406
86
125
103
249
404
231
233
312
121
241
61
790
38
514
91
286
658
48
603
99
443
62
485
92
82
53
330
49
221
68
277
427
93
478
113
721
111
299
153
127
175
96
151
150
115
243
91
130
85
343
75
107
117
295
119
225
Microcharcoal
Macrocharcoal
Concentration per cm3
Wetland
Stenochlaena
Polypodium
Polygonaceae
Cyperaceae
Other herbs
Poaceae
Other trees & shrubs
Phyllanthaceae
Euphorbiaceae
Rhamnaceae
Loranthaceae
Ixora
Homalium
Glochidion
Fabaceae
Triletes smooth
Ferns & allies
Monolete psilate
Monolete echinate
Microsorum
%
Successional
Trema
Rhus
Macaranga
Homalanthus
Elattostachys
Amaranthaceae
Alphitonia
Rainforest
Syzygium
Sapotaceae
Hedycarya
Grewia
Elaeocarpus
Dysoxylum
Burseraceae
Bischofia
Littoral
Pandanus
Ficus
Cocos
Casuarina
Calophyllum
Arecaceae
Mangrove
Rhizophoraceae
Excoecaria
Stratigraphy
Depth (cm)
Cal years BP
20
70
120
170
220
270
320
370
420
470
520
570
620
1000
2000
HA
3000
4000
5000
6000
7000
T5
T4
T3
T2
T1
Fen peat
Gyttja

Figure 2-2 Pollen, spores, and charcoal from Ngofe Marsh; pollen and spore percentages display taxa >2%. Pollen and fern spores are included in the total sum. Uncertain identifications have been omitted from the CONISS calculations (Grimm, 1987). Zonation is based on the CONISS dendrogram and represented as fine dashed lines. Tephra layers are indicated as T1-T5 on the left-hand side and are shaded in blue. The potential timing of human arrival (HA) is represented as a purple dashed line based at ~2670 cal. years BP. The timing of the Mid-Late Holocene RSL high stand, according to Fukuyo et al. (2020), is shown on the right-hand side.

2.4.3 Regional analyses of multiple pollen records from Tonga

According to the linear model results of all four study sites, tephra falls from volcanic eruptions do not significantly explain the dynamics of littoral, mangrove, rainforest, successional/ disturbance, or wetland vegetation at different points in time, (p>0.05, see Table 2). Meanwhile, RSL significantly explains vegetation group dynamics at Ngofe Marsh (littoral, $p < 0.001$, $R^2 = 0.3$; wetland, $p < 0.001$, $R^2 = 0.4$), Lotofoa Swamp (mangrove, $p < 0.01$, $R^2 = 0.4$; wetland, $p < 0.05$, $R^2 = 0.4$), and Finemui Swamp (littoral, $p < 0.01$, $R^2 = 0.03$; mangrove, $p < 0.001$, $R^2 = 0.7$; successional/ disturbance, $p < 0.01$, $R^2 = 0.3$; wetland, $p < 0.001$, $R^2 = 0.7$) (Table 2-2). The model coefficients show that successional/ disturbance and littoral taxa have a negative relationship with RSL, whereas mangroves taxa have a positive relationship with RSL. Wetland taxa show mixed coefficients.

Table 2-2 Temporal trends of littoral, mangrove, rainforest, successional/ disturbance, and wetland vegetation groups as revealed by linear models. R2 are reported to show the strength of relationships and p-values indicating significance are given in parentheses For significant results, the directions of the coefficients are given (positive or negative relationship).

Site	**Drivers of change**	**Littoral**	**Mangrove**	**Rainforest**	**Successional / disturbance**	**Wetland**
Ngofe Marsh ('Uta Vava'u Island, Vava'u Group)	RSL	$R^2 = 0.3$ ($p<0.001$) Negative coefficient	($p>0.05$)	($p>0.05$)	($p>0.05$)	$R^2 = 0.4$ ($p<0.001$) Positive coefficient
Ngofe Marsh ('Uta Vava'u Island, Vava'u Group)	Tephra	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)
Avai'o'vuna Swamp (Pangaimotu Island, Vava'u Group)	RSL	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)
Avai'o'vuna Swamp (Pangaimotu Island, Vava'u Group)	Tephra	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)

Lotofoa Swamp (Foa Island, Ha’apai Group)	RSL	($p>0.05$)	$R^2 = 0.4$ ($p<0.01$) Positive coefficient	($p>0.05$)	($p>0.05$)	$R^2 = 0.4$ ($p<0.05$) Negative coefficient
Lotofoa Swamp (Foa Island, Ha’apai Group)	Tephra	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)
Finemui Swamp (Ha’afeva Island, Ha’apai Group)	RSL	$R^2 = 0.3$ ($p<0.01$) Negative coefficient	$R^2 = 0.7$ ($p<0.001$) Positive coefficient	($p>0.05$)	$R^2 = 0.3$ ($p<0.01$) Negative coefficient	$R^2 = 0.7$ ($p<0.001$) Positive coefficient
Finemui Swamp (Ha’afeva Island, Ha’apai Group)	Tephra	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)	($p>0.05$)

The analysis of how vegetation groups change over time shows that Ngofe Marsh’s mangrove and rainforest taxa were relatively abundant between ~7000–4000 cal. years BP after which their abundances declined (Figure 2-2 and Figure 2-3a). Successional/ disturbance, wetland and littoral taxa all increased within the last ~4000 years (Figure 2-3a). Percentage data from Avai’o’vuna Swamp shows that littoral taxa were relatively abundant at ~5000 cal. years BP and declined in abundance subsequently. Wetland taxa increased toward the present, and rainforest, successional/ disturbance and mangrove abundances were all relatively stable (Figure 2-3b). For the other sites, the vegetation groupings show that at Lotofoa Swamp, wetland taxa constituted the most dominant vegetation type at ~7000 cal. years BP, but decreased at ~3000 cal. years BP, then increased again to become the most dominant group towards the present. Mangrove taxa increased until ~3000 cal. years BP, but then began to decline. Littoral, rainforest, and successional/ disturbance taxa were somewhat stable (Figure 2-3c). Finemui Swamp mangrove taxa dominated the record until ~500 cal. years BP, after which successional/ disturbance, littoral and wetland taxa increased. Rainforest taxa remained at relatively low abundances throughout the record (Figure 2-3d).

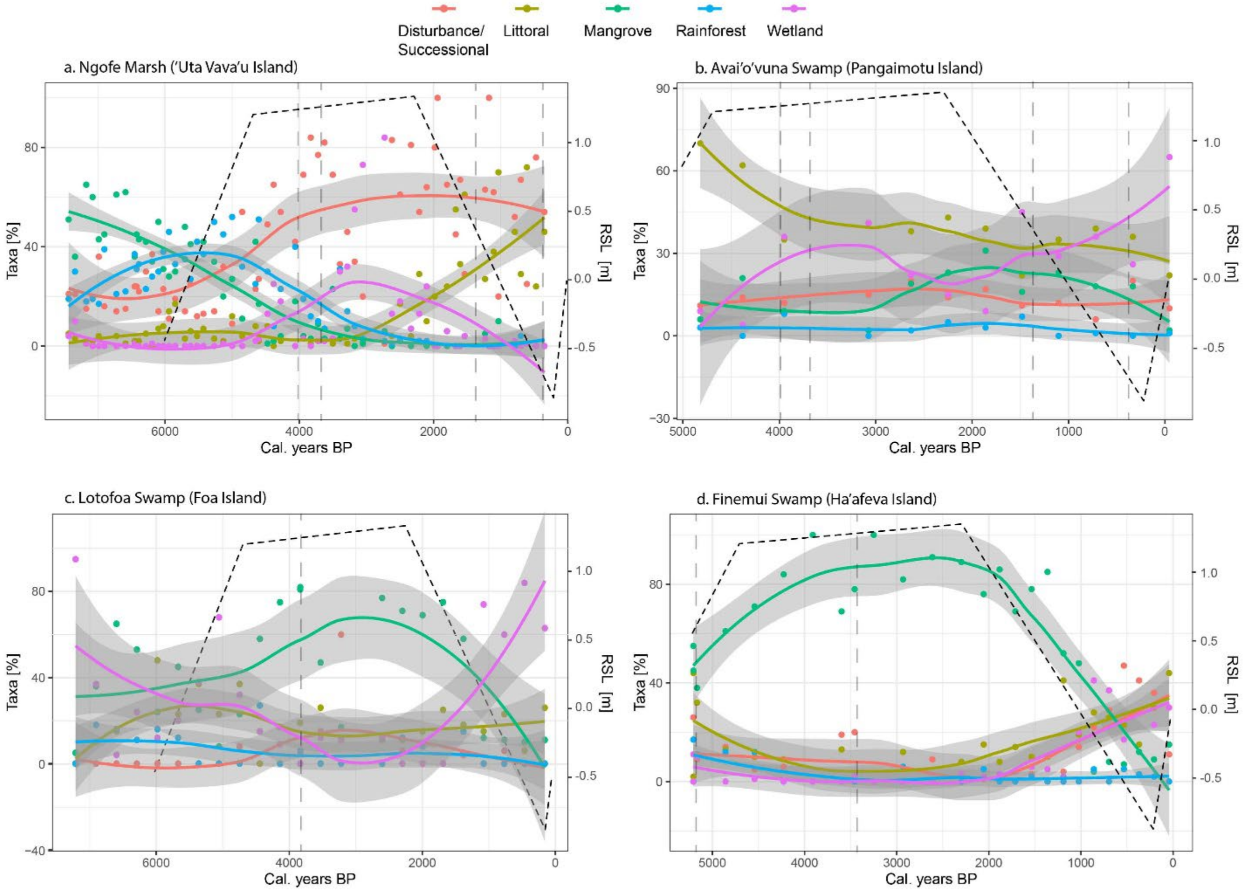

Figure 2-3 Temporal change of vegetation groups for each island using local polynomial regression fitting. The four sites are organised from north to south: a) Ngofe Marsh ('Uta Vava'u Island), b) Avai'o'vuna Swamp (Pangaimotu Island), c) Lotofoa Swamp (Foa Island) and d) Finemui Swamp (Ha'afeva Island). Trend lines indicate changes in fossil pollen percentages for successional/disturbance related taxa (pink), littoral taxa (olive green), mangrove taxa (green), rainforest taxa (blue) and wetland taxa (purple). Confidence intervals of 95% are shown in grey. The RSL curves (dashed black line) are redrawn from Fukuyo et al. (2020) for each site. Tephra layers are shown as vertical dashed lines.

2.5 Discussion

2.5.1 Regional trends and drivers of vegetation change

Vegetation groups within the Tongan archipelago show different patterns of change throughout the Mid-Late Holocene Figure 2-3. Our analyses suggests that RSL has been an important driver of change for littoral, mangrove, successional/ disturbance, and wetland vegetation at Ngofe Marsh, Lotofoa Swamp, and Finemui Swamp (Table 2-2). In contrast, volcanic eruptions have not been a driver of change for any of the vegetation groups from any of the islands included in the analysis (Table 2-2).

One explanation for the non-significant results for tephra deposition is that vegetation in Tonga might be resilient or resistant to volcanic activity. However, tephra layers deposited at Lotofoa Swamp and Finemui Swamp were relatively thick (50 and 37 cm respectively) and might be expected to have caused vegetation changes, given that the magnitude and persistence of ecological impacts are often related to ash thickness (Dale et al., 2005). Mangroves for example, can suffer mortality after their roots have been buried in sediments 50 cm deep (Ellison, 1999). Further research tying tephra geochemical data to known regional eruption dates and locations will bring improved information on the understanding of sources of tephra ash and distances from the sites. In addition, the temporal resolution of pollen records may present a challenge for capturing rapid vegetation changes or recoveries following volcanic eruptions. For example, the Avai'o'vuna Swamp pollen record has one pollen sample every ~440 years, Lotofoa Swamp has one sample every ~ 300 years, Finemui Swamp has one sample every ~200 years, and Ngofe Marsh has one sample every ~120 years, potentially limiting the identification of vegetation responses and recoveries following short-lived eruption events, which can occur on shorter timescales (see Strandberg et al., 2023b). Our results, however, suggest that volcanic eruptions did not have multi-centennial scale impacts on vegetation of these islands.

An additional challenge encountered was related to the classification of certain fossil pollen taxa according to vegetation groups. For example, *Cocos nucifera* and *Casuarina,* which may be considered as introduced in some parts of the South Pacific (see Fall, 2010 for discussion), may also be considered a coastal or littoral taxa (Whistler, 1992). In our analysis *Cocos nucifera* and *Casuarina* have been included in the littoral taxa group. *Pandanus* is another example of a genus which can be placed into two vegetation types since it is both a coastal and littoral tree (Whistler, 1992) and is also somewhat fire tolerant (Prebble et al., 2005), indicating that it may be considered a disturbance or successional taxon. In our analysis we have placed *Pandanus* in the littoral group.

Although in this study we focus on RSL and volcanic eruptions, we would like to highlight that Holocene proxy precipitation and temperature records from Tonga are currently absent and data linking vegetation responses to climate events are limited. Exceptions come from Efate, Vanuatu, where a decline in rainforest vegetation was interpreted as being caused by drier conditions between 3790–3600 cal. years BP (Combettes et al., 2015). Another study from Vanuatu shows increased vegetation turnover associated with a shift from wetter to drier conditions 1100 cal. years BP (Strandberg et al., 2023b). In Fiji a possible dry phase and change in fire regime may indicate a response to an increase in ENSO events 5000 ca. years BP (Hope et al., 2009).

The same limitations occur with datasets of human-related impacts, such as anthropogenic fires. Micro-charcoal datasets, which indicate regional fires, or fire intensity, are only available from Ngofe Marsh and Avai'o'vuna Swamp. For example, for Ngofe Marsh, micro-charcoal particles increased after ~5000 cal. years BP, prior to human arrival, which is dated 2805–2760 cal. years BP for Vava'u (Burley et al., 2015). However, fire cannot be considered a regional event since at Avai'o'vuna Swamp, located ~6 km away, micro-charcoal particles were first detected at 2850-2410 cal. years BP (2620 ^{14}C years BP) (Fall, 2005). There are also no tephra layers associated with the first peaks in micro-charcoal ~5000 cal. years BP and pre-human fires may have been caused by lightning strikes. In addition, local fires data (i.e., macro-charcoal particles) are only available for Ngofe Marsh. These data indicate that high concentrations of macro-charcoal are only found from 2040 cal. years BP, indicating a potential association with human-related impacts (Figure 2-2). Fire history for Tonga is therefore far from being resolved, and this currently prevents further regional analysis. It is also still unclear to what degree macrocharcoal fragments indicate spatial variation in burning or differences in fire intensity.

2.5.2 Relative sea-level and direction of vegetation changes

We found different relationships between RSL and vegetation groupings, from a non-significant relationship for rainforest taxa to significant relationships for littoral, mangrove, successional/ disturbance, and wetlands. While the non-significant relationship for rainforest taxa might be explained by rainforest habitat being located on the inland portion of the islands, the explanation for the other vegetation groups is more complex. For example, wetland taxa display a complex pattern of responses to RSL change, demonstrated by both positive and negative coefficients (Table 2-2). When RSL was higher (5000 –2000 cal. year BP), more wetland taxa were present at Finemui Swamp and Ngofe Marsh (excluding Cyperaceae for Ngofe Marsh). However, wetland taxa increased at Lotofoa Swamp when RSL started to decline ~2000 years ago. These results indicate that site-specific factors, such as local hydrology (e.g., driven by climate changes), as well as hydroseral development, may be important for the development of Tongan wetlands (Table 2-2). For example, RSL was at a similar level to today at Ngofe Marsh ~5500 cal. years BP but mangrove pollen was found to be present at that time but is missing from recent samples. Sediment infilling of the Ngofe Marsh basin may be the cause of this difference in vegetation.

Mangrove responses are more straightforward to interpret, for example, mangrove forests were relatively more abundant at Lotofoa and Finemui Swamps, when RSL was higher during the Mid-Late Holocene high-stand ~5000–2000 cal. years BP (Figure 2-3) (Ellison, 1989; Fall, 2005). Two scenarios may provide possible explanations for this. The first scenario is that rising sea levels caused landward migration of mangrove taxa. The second, is that higher RSL led to increased water height and salinisation of the wetlands through the permeable limestone bedrock. Since *Excoecaria agallocha* pollen (native mangrove), usually reflects local presence (Pandey and Holt, 2018), the second scenario is perhaps more plausible.

While lower RSL corresponds with increases in the littoral group at two sites (Ngofe Marsh and Finemui Swamp), higher sea levels led to the decline of the successional/disturbance taxa group at Finemui Swamp (Figure 2-3). During the same time period, however, there was an increase in human impacts in the region, 2805–2760 cal. years BP (Burley et al., 2015), noted by (Ellison, 1989; Fall, 2005) to coincide with a fall in sea level, and this may suggest an alternative driver, or perhaps two drivers, of change.

2.5.3 A summary of 7400 years of vegetation change at Ngofe Marsh, Uta Vava’u Island, Vava’u group

Between 7400 and 5000 cal. years BP, Ngofe Marsh, which is currently a sedge wetland, was likely a freshwater lake surrounded by mangroves (Rhizophoraceae) and diverse primary rainforest, with Arecaceae*, Elaeocarpus* (ma‘ama‘alava), Sapotaceae, *Syzygium*, and *Rhus* (tavahi). After 5000 cal. BP, mangroves declined, and there was an increase in ferns, including *Microsorum*, *Stenochlaena,* possibly *S. palustris* (pasivaka), and unidentified fern taxa (monolete spores). Sedges (Cyperaceae), grasses (Poaceae), the trees *Macaranga*, *Trema*, and the tree-like-monocot *Pandanus* have dominated over the last two millennia after the transition from lake to sedge wetland, and the increasing occurrence of grass pollen indicates opening up of the landscape around Ngofe Marsh, with forest being replaced by agricultural land and settlements, as is seen today on ‘Uta Vava’u.

The tephra layers (T2 ~3970 cal. years BP and T3 ~3670 cal. years BP in Figure 2-2) coincide with a 300-year period of high *Trema* pollen values. *Trema*, a native successional tree, is associated with volcanic ash falls and is classed as a successional/ disturbance taxon in our regional analysis (Flenley et al., 1999; Wallin and Martinsson-Wallin, 2010). However, our regional analysis (Table 2) did not identify tephra as a driver of change in the successional/ disturbance group.

At around 2670 cal. years BP, native secondary forest taxa *Macaranga* and *Pandanus* increased, but some other native forest taxa, many of which are considered to be primary rainforest taxa, such as *Bischofia*, *Dysoxylum, Elaeocarpus*, Fabaceae, *Rhus*, Sapotaceae, and *Syzygium,* declined (Figure 2-2). This forest decline likely reflects human arrival and its impacts. In addition, *Macaranga*, which is a secondary forest taxon common on disturbed land (Whistler and Atherton, 2015), increased after the arrival of humans at ~2670 cal. years BP (Figure 2-2). An increase in *Macaranga* and *Pandanus* (which can indicate disturbance, see above) after human arrival was also observed at Avai'o'vuna Swamp (Fall, 2005) and Finemui Swamp (Flenley et al., 1999). Our analysis shows that rainforest-type vegetation is not impacted by volcanic eruptions or RSL change; however, we may attribute the decline in native rainforest taxa to human impacts, such as deforestation and/ or burning after ~2670 cal. years BP. No introduced taxa, other than *Casuarina* (see Fall, 2010 for discussion), are associated with initial human arrival in this study (Ngofe Marsh), suggesting that the area in the vicinity of Ngofe Marsh was not heavily populated by people or used for taro/talo (*Colocasia esculenta*) cultivation; indeed, to the best of our knowledge to date, no archaeological findings from the colonisation period have been reported in this area of southwest 'Uta Vava'u Island.

2.5.4 Island size and vulnerability to relative sea level changes

Recently, islands have gained considerable focus due to concerns over their vulnerability to sea-level rise (Fernández-Palacios et al., 2021). Small areas and low elevation are features generally considered to increase the vulnerability of an island to sea-level rise and other natural hazards, such as coastal flooding (Veron et al., 2019). The island of Ha'afeva is the smallest island included in this study (135 ha), and it is also low-lying (14 m a.s.l. maximum elevation) making it the most vulnerable to RSL change of the islands (Table 5-2). Our results are consistent with this description and show that the island vegetation (littoral, successional/ disturbance, mangrove, and wetlands) seems to be particularly sensitive to RSL changes (Table 2-2). Additionally, small islands have smaller population sizes making them more vulnerable to loosing taxa (Mueller-Dombois and Fosberg, 1998; Frankham, 2001; Keppel et al., 2014). On the contrary, results from the sites located on somewhat larger and higher islands, do not display such a strong association with RSL change (Table 2-2). It is important to highlight that the Avai'o'vuna Swamp, located on Pangaimotu Island, showed no significant associations. Vegetation groups at this site appeared to be less variable than the other sites, perhaps indicating that vegetation at this wetland, or on this island is somewhat buffered from environmental changes.

2.6 Conclusions

Considering projections of future sea level rise across the Pacific islands, studies like this demonstrate the complex influences on island biodiversity and specifically on coastal habitats. Our results highlight that RSL was a driver of vegetation change at three out of four of our study sites, with the smallest island (Ha'afeva) the most impacted. A better understanding of past periods of higher sea level may help to anticipate how ecosystems in Tonga are likely to react to future sea level rise.

Although results indicate the non-significance of tephra deposition as a driver of change on Tonga's vegetation, vegetation responses may have not been detected for several reasons. It may be, for example, that factors such as the distance of sites from the sources of eruptions served to minimise effects, though some observed tephra layers were moderately thick. Furthermore, as volcanic events are, while large, highly infrequent, there are few datapoints to test. If responses occurred but were short-lived (i.e., decades), the fairly coarse temporal resolution of these pollen datasets is not ideal. If this were the case, however, Tongan ecosystems appear in the longer term (centuries) to have been resilient in the face of regional volcanism.

2.7 Acknowledgements

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without his contributions to the field. Permission to undertake research on Ngofe Marsh in 2017 was given by the Office of the Prime Minister of Tonga.

2.8 Author contributions

NS and SN designed the study. DS and PL did the fieldwork. NS, AC-B, IWC, and SC did the laboratory analysis. NS, MJ, and AW analysed the data. NS and AW constructed the figures. NS wrote the manuscript with substantial input from SN, ME, JCE, and WDG. All authors contributed to the writing of the manuscript.

Chapter 3 Island ecosystem responses to the Kuwae eruption and precipitation change over the last 1600 years, Efate, Vanuatu

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3.1 Abstract

Introduction: Islands of the Southwest Pacific are exposed to geologic and climate-related disturbances that occur on a range of timescales and which probably affect, to varying degrees, their terrestrial ecosystems. Over the past ∼1100 years we know of two major events in the region: the Kuwae eruption which is thought to have occurred ∼500 cal. years BP and a shift to drier conditions which began ∼1100 cal. years BP.

Methods: We investigated terrestrial and lacustrine ecosystem responses to these events and also to a changing fire regime, likely human-caused, using a multi-proxy (C/N, charcoal, chironomids, pollen, and tephra) record from Lake Emaotul, Efate, Vanuatu.

Results: Tephra from the Kuwae eruption was found across a 6 cm layer which our age-depth model suggests was deposited 650–510 cal. years BP (95% confidence). Forest and chironomid community turnover increased during the wet-dry shift 1100–1000 cal. years BP; subsequently, chironomid turnover rates decreased again within <135 years and vegetation had partially (but not fully) recovered after ∼80 years. Following Kuwae volcanic tephra deposition, vegetation turnover increased again, reflecting a reduction in small trees and shrubs and an increase in grasses. Subsequently, the forest vegetation did not regain its previous composition, whereas chironomid community composition remained fairly stable before and after tephra deposition. Within the last ∼90 years, enhanced local burning drove another increase in vegetation turnover.

Discussion: Terrestrial and freshwater ecosystems in Efate are sensitive to changes in hydroclimate, volcanism, and anthropogenic fires, although to different degrees; while recent human impacts are often obvious, volcanic eruptions and climatic shifts have also structured Pacific-island ecosystems and will continue to do so.

3.2 Introduction

Islands are often home to high levels of endemism compared with mainland ecosystems, and they also contribute disproportionately by land area to total terrestrial diversity (Kier et al., 2009; Losos and Ricklefs, 2009). Palaeoecological records from islands around the world have shown that human arrival is generally associated with accelerated turnover in floristic diversity (Nogué et al., 2021) and faunal extinctions (Steadman et al., 2002; Bedford and Spriggs, 2014; Gosling et al., 2017). Under such dramatic anthropogenic changes, the impacts of natural disturbances and climate change are challenging to identify, yet they also influence ecosystem dynamics. South Pacific islands are often exposed to natural hazards: cyclones, droughts, landslides, tsunamis, earthquakes, and volcanic eruptions (Siméoni, 2009; Bedford and Spriggs, 2014). Such events would have been the main drivers of change prior to human settlement. High-resolution palaeoecological records, such as the one presented here, provide valuable data on the rates and patterns of recovery of terrestrial ecosystems following natural disturbances.

The January 2022 Hunga Tonga–Hunga Haʻapai eruption is a timely reminder of how Pacific islands can be exposed to volcanic hazards. Responses to eruptions often relate to substantial tephra falls and have been documented previously in palaeovegetation records from both continental and island locations (Table 5-8). For example, in the tropical Andes of Ecuador, a lake-sediment record from a páramo (alpine grassland) landscape showed a slight increase in herb pollen, a decrease in local and long-distance forest taxa, and a relatively quick (<100 years) recovery following volcanic tephra deposition, whereas in a forested, pre-montane landscape, the forest opened up after tephra deposition and took around 150 years to return to the pre-eruption state (Montoya et al., 2021). On the eastern Atlantic Ocean island of Brava, Cabo Verde, repeated tephra deposition between 1800 and 650 cal. years BP coincided with an expansion of fern-rich, woody scrubland and the decline of previously dominant Urticaceae and Poaceae (Castilla-Beltrán et al., 2021b). In southern Italy, pollen records have shown a decrease in vegetation productivity following eruptions (Allen and Huntley, 2018). Generalisations about recovery rates are difficult to make, as the extent of the impact depends on a range of factors: the volume of ash ejected, thickness of ash (Allen and Huntley, 2018), the height of vegetation, ground surface roughness (Arnalds, 2013), how long ash persists in the catchment (Hickman and Reasoner, 1994), distance from the eruption, the nutrients released, the types of vegetation and propagules that survive (Dale et al., 2005), and local climate conditions (Wilmshurst and McGlone, 1996).

Lacustrine ecosystems are also impacted by volcanic eruptions. Nutrient enrichment can alter their ecology, but, as with terrestrial ecosystems, aquatic responses to ash falls can vary depending on lake and catchment characteristics. Volcanic ash may deposit elements such as sulphur and decrease soil pH, which in turn may release acid-soluble metals into soil solution (Cronin et al., 1997) as well as to groundwater and lacustrine environments. Low inputs of tephra can also have a fertilising effect on soils (Arnalds, 2013). The 2011 eruption of the Puyehue volcanic complex in Chile ejected large amounts of ash and pumice, and in some lakes, this resulted in increases in suspended solids, light exclusion, increased phosphorus and increased biomass of phytoplankton in relation to the pre-eruption conditions (Modenutti et al., 2013). Also in Chile, at Lake Galletué, palaeoecological reconstructions indicated that tephra deposition in 1957 CE resulted in a transient increase in nutrients, identified through diatom analysis (Urrutia et al., 2007). Montoya et al. (2021) suggested that the vegetation surrounding a lake or within a catchment may be important for creating a barrier against deposition and to reduce tephra runoff into lakes. Laguna Baños, on the Ecuadorian Andean flank, is surrounded by open páramo and thus not protected by a forest barrier, making it susceptible to tephra in-wash (Montoya et al., 2021). Here, there was also a significant shift in chironomid assemblage composition after ash deposition that may have been caused by shallowing of the lake. According to the results of Matthews-Bird et al. (2017); and Montoya et al. (2021) the chironomid regime shift has still not recovered today, 1500 years later.

With regards to the Pacific islands, hydroclimate changes are another source of environmental variation; they are strongly related to movement of the South Pacific Convergence Zone (SPCZ), a rain band that delivers precipitation to the islands of the South Pacific Ocean (Hassall, 2017; Sear et al., 2020). During El Niño events, the SPCZ moves northwards, which can lead to severe droughts in more southerly islands, including Vanuatu. For example, during the 1994/1995 CE drought in Vanuatu there was no rain for nine months, and communities experienced water shortages and the loss of livestock and crops (McNamara and Prasad, 2014). The impacts of dry periods on South Western Pacific islands in the past may have been severe, and it has been suggested that drought coupled with other societal pressures may have been the impetus for Polynesians to explore the Eastern Pacific islands (Sear et al., 2020). In particular, a drier climate phase has been identified around 1100–500 cal. years BP in Vanuatu, Sāmoa, and Atiu (Cook Islands) (Sear et al., 2020; Maloney et al., 2022).

People settled Vanuatu 3000 years ago (Lipton et al 2020), meaning they have been part of the ecosystem for the duration of this record. An increase in charcoal fragments has been identified in a palaeoecological record from Aneityum island, Southern Vanuatu, and is associated with human arrival (Hope and Spriggs, 1982). Evidence of burning throughout the last 2000 years has also been detected in another palaeoecological record from the island of Erromango (Hope et al., 1999) but the effects of fire on vegetation turnover remain unknown.

Here we investigate a 1600 year record that gives insight into how terrestrial vegetation and components of the lacustrine system responded to this past drier climate phase (precipitation record previous published by Maloney et al., 2022), to the Kuwae eruption, and to changes in fire regime.

3.3 Materials and methods

3.3.1 Site description

The nation of Vanuatu in the Southwest Pacific stretches 1000 km from north to south and comprises over 83 islands, which formed as a result of uplift and volcanism associated with the New Hebrides Arc, where eastward subduction of the Indo-Australia Plate beneath the Pacific Plate occurs (Stewart et al., 2010b). Around 90% of the islands of Vanuatu are less than 1.8 Ma years old (Mallick, 1975). Here we focus on Efate, Central Province, the location of Port Vila, the capital city of Vanuatu. Efate has a volcanic core (Ash et al., 1978), but the surface geology is dominated by uplifted coral sequences and the Efate Pumice Formation, which form the main topography of the centre of the island (Raos and McPhie, 2003). A series of now uplifted coral terraces formed within the last 300,000 years along the island coast (Taylor et al., 1987).

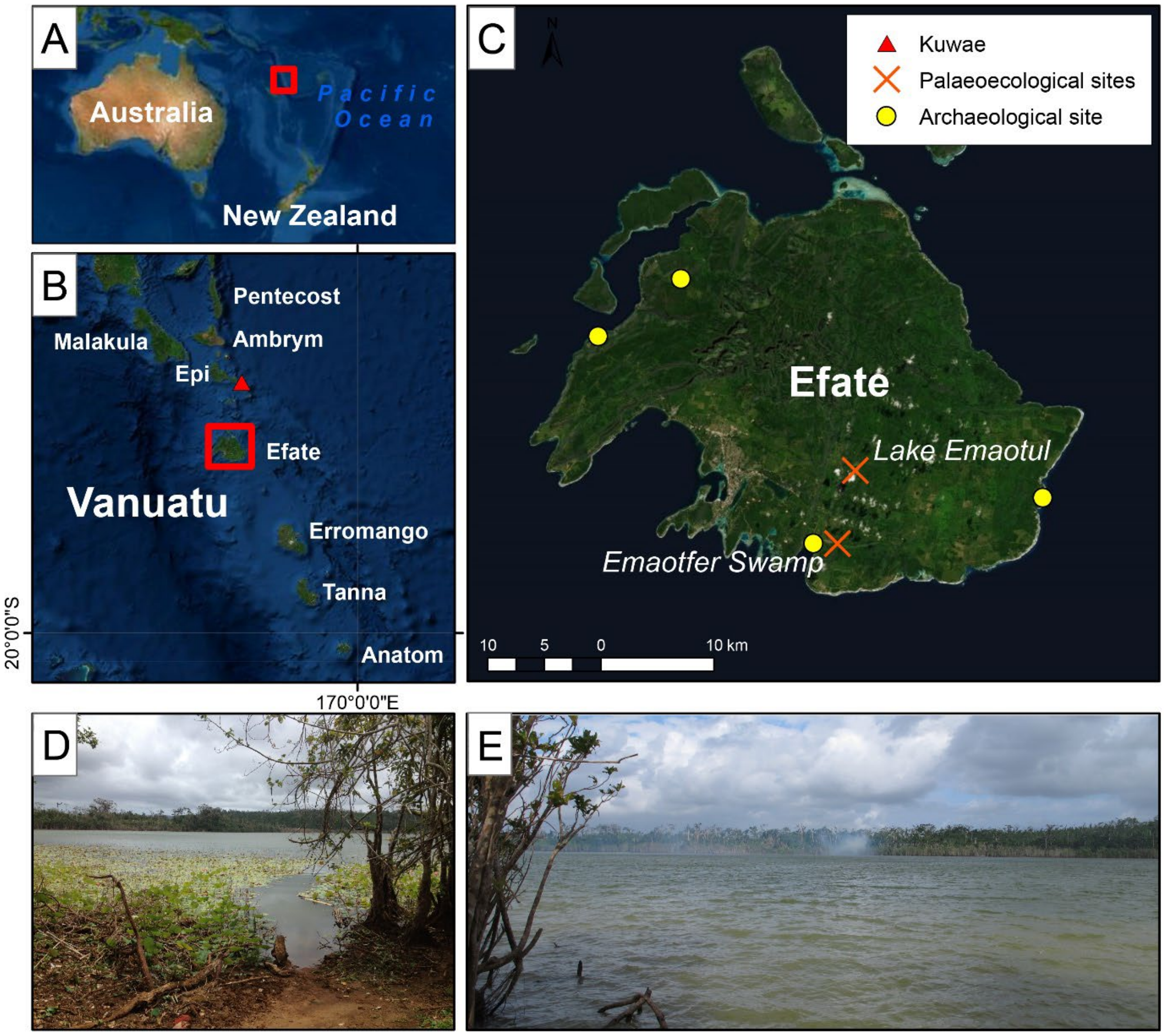

Figure 3-1 A) The location of Vanuatu within the Pacific Ocean; B) the Southern and central islands of Vanuatu, the red triangle indicates the location of the Kuwae submarine caldera; C) The island of Efate. Yellow circles indicate the location of archaeological sites and the red crosses indicate palaeoecological sites including Lake Emaotul (Wirrmann et al., 2011, Combettes et al., 2015). D and E are photographs taken from the shore of Lake Emaotul in October 2015.

3.3.2 Climate and regional vegetation

The climate of Vanuatu is tropical, with temperatures ranging between 23–33°C (Singh et al., 2019). The main climate influences are the position and variability of the West Pacific Warm Pool (WPWP) and SPCZ (Vincent, 1994). Summers are relatively wet and often feature cyclones, while winters are drier. South-westerly trade winds prevail for most of the year. Mean annual rainfall on Efate varies from 3000 mm on the eastern coast of the island to 2400 mm on the western coast (Cillaurren et al., 2001); however, yearly rainfall totals vary in relation to the state of ENSO (the El

Niño Southern Oscillation), a pattern of inter-annual climate variability linked to changes in sea-surface temperatures and precipitation (Wyrtki, 1975). During El Niño events the SPCZ is in a more northerly position, and during La Niña events it extends to a more south-easterly position. Typically, during an El Niño phase the climate of Vanuatu is drier than average, while during the opposite La Niña phase it is wetter than average (Wirrmann et al., 2011; Combettes et al., 2015).

The vegetation of Vanuatu varies with human impacts, soil type, leeward or windward locations, and altitude (Mueller-Dombois and Fosberg, 1998). The vegetation can be generally classified as lowland rain forest, montane cloud forest, seasonal forest, scrub, grassland, pioneer species growing on new volcanic surfaces, coastal taxa including mangrove forests, and secondary and cultivated vegetation (see Mueller-Dombois and Fosberg, 1998 for detailed descriptions).

3.3.3 The Kuwae eruption

The Kuwae submarine caldera is located between the islands of Epi and Tongoa in Vanuatu (Figure 3-1B), around 100 km north of Efate (Figure 3-1). Evidence from multiple ice cores, historical records, and tree rings from the Northern and Southern hemispheres suggested a single eruption of Kuwae in either 1452 or 1453 CE (Gao et al., 2006). However, evidence from ice cores from the Law Dome site, Antarctica, has identified a large sulphate signal dating to ~1458 CE which may been from the Kuwae eruption (Plummer et al., 2012). Yet, South Pole ice cores containing cryptotephra which was deposited ~1458 CE do not match with Kuwae tephra (Hartman et al., 2019) and Kuwae tephra is get to be detected within Antarctic ice cores. Locally, the geology of the mainly submarine Kuwae volcano is represented by a complex sequence of andesitic to dacitic pyroclastic deposits covering the islands of Epi, Tongoa, Laika and other nearby islets. Németh et al. (2007) suggest that terrestrial deposits were consistent with pyroclastic flows from median to small eruptions but dismissed the likelihood of a large eruption in the 1400s CE. Using an assumed erupted volume of ~40 km^3 (from Robin et al., 1994), and based on analysis of melt inclusions, Witter and Self (2007) estimated sulphur release of 175–700 Tg from the eruption. If this was during a single event, it amounts to five times the climate-forcing ejection produced by the 1815 CE Tambora eruption (Indonesia) (Cole-Dai et al., 2000). The volume of material ejected is around six times that ejected during the 1991 CE Pinatubo eruption in the Philippines (Pang, 1993). Given the scale of this eruption, we would expect to see evidence of tephra deposition and an effect on vegetation in Efate.

3.3.4 Human arrival and settlement

Archaeological and genetic evidence suggests that people first settled Vanuatu *c*. 3000 years ago (Petchey et al., 2014). Later Mangaasi-style ceramics are identified in numerous coastal and inland sites from 2300–1200 cal. years BP. The 500–510 cal. years BP Kuwae eruption had an important cultural impact since many ni-Vanuatu, the indigenous people of Vanuatu, were forced to migrate away from the affected Sheppard and Epi islands (Hoffmann, 2007). Garanger (1972) has documented long-standing oral traditions of the movement of people from these islands to Efate in the post-eruption period. Furthermore, Bedford et al. (2018) has inferred from a large expanse of agricultural features documented from recent LiDAR aerial surveys, that rapid population expansion on Efate took place within the last 1000 years. This period is associated with Lapita ceramic-ware culture, and these ceramics have been discovered at the coastal Teouma Cemetery, to the west of Emaotfer Swamp on Efate (Figure 3-1C).

3.3.5 Sample collection

Sediment samples were recovered from Lake Emaotul (sometimes called Duck Lake; 17°43'57.48"S, 168°24'53.58"E) on Efate. Lake Emaotul was selected because it is a confined lake system likely to be sensitive to changes in the precipitation-evaporation balance. It is relatively insulated from marine processes compared with other sites on the island due to its elevation (119 m above sea level). The lake sits within a raised coral reef dated at *c*. 120,000 BP (Sear et al., 2020). It has a maximum depth of 7.1 m and is meromictic. A chemocline at 6 m results in a suboxic hypolimnion with dissolved oxygen at 5% saturation (Sear et al., 2020).

Hydrologically, the lake is a closed system. It measures 0.3 km^2 in area and has a catchment covering 0.98 km^2. The lake is fringed by grass-dominated wetlands to the east and west, with the swamp-forest taxa *Barringtonia*, *Hibiscus,* and *Pandanus*. The lake surface is mostly open but has some cover of water lilies, such as *Nelumbo nucifera*, *Nymphaea* spp., and *Nymphoides* spp. The wetland areas are bordered by *Phragmites.* Beyond the wetland, the lake catchment is covered by secondary tropical forest that supports patches of subsistence gardening and cattle grazing (Sear et al., 2020). Secondary lowland forest taxa include *Metroxylon warburgii* (Kalfatak and Jaensch, 2014).

The Lake Emaotul cores were retrieved between the 9th and 11th October 2015. The 3.4-m sedimentary sequence of overlapping cores was retrieved using a UWITEC gravity corer and a piston corer (Geo-Core, Columbus, Ohio, USA) from the deepest part of the lake. Deeper coring of the sediments was impeded by stiff clay. This precluded recovery of sediments that predated human arrival. All six recovered cores were stored in airtight tubes during transportation and subsequently at +4 °C at the School of Geography and Environmental Sciences (SOGES) at the University of Southampton (UK).

3.3.6 Tephra analysis and dating

Three subsamples of the core that displayed discrete and high magnetic susceptibility were extracted from 173–171 cm, 169–167 cm, and 166–160 cm. To identify the depth range over which tephra was deposited small amounts of sediment were smeared on glass slides and examined under an optical microscope. All samples contained shards; however, particularly high counts of fresh volcanic glass particles occurred between 166–160 cm. To obtain the geochemical signature of volcanic glass samples from all three horizons were cleaned in deionised water, and the coarsest grains (~63–125 μm) were hand-picked, mounted in an epoxy round, cut, and polished. The polished samples were sputter-coated in carbon. An initial suite of three samples was analysed using a Jeol JXA8230 Superprobe at the University of Iowa, with repeat analyses and an additional eight samples using a JXA8530F Hyperprobe at the University of Auckland. For both instruments, points were analysed using an accelerating voltage of 15 kV and a 2-nA electron beam current. A defocussed 10-μm beam was used in order to minimise Na loss, with a 5-μm diameter required for a few smaller grains. Analysis was completed with 10-s peak and 10-s total background dwell times for all elements. To test for Na migration, some analyses were collected in two 1-s accumulated peak measurements with 1-s dwell time on background for the second measurement. The accumulated Na measurements showed that post-measurement correction of Na migration was not required. Analyses were calibrated and quality cross-checked against secondary glass standards ATHO-G (MPI-DING), BCR-2G, (USGS) and VG-568 (NMNH 72854).

The age-depth model is based on the radiocarbon ages of seven plant macrofossils and 34 ^{210}Pb analyses; see Maloney et al. (2022). All ^{14}C dates were re-calibrated using the Southern Hemisphere calibration curve (Hogg et al., 2020) to years before present (cal. years BP). To build the age-depth model we used *rbacon* v2.2 (Blaauw and Christen, 2011).

3.3.7 Carbon-to nitrogen ratio

We analysed 188 sediment samples (every 2 cm) for carbon-to-nitrogen (C/N) ratio, which is used as an indicator of the source of organic material in a lake (Rice and Hanson, 1984). See supplementary information appendix C page 129 for full C/N method. The C/N ratio can vary, since algae are more enriched in nitrogen and depleted in carbon compared with terrestrial vascular plants (Tyson, 1995). A C/N ratio of >20 usually indicates a system in which terrestrial organic material is dominant (Jones et al., 2013), whereas a ratio of 10–20 likely signifies a mixture of terrestrial and aquatic organic inputs. A ratio of <10 is more likely to suggest more aquatic plants were present (García-Alix et al., 2012). C/N samples were measured at the British Geological Survey, in Nottingham, UK.

3.3.8 Pollen and spore analysis

To determine plant community changes, we analysed 32 samples of 1-cm^3 volume for pollen and spores. The sampling resolution is about 1 sample per ~70 years (14 cm) for the majority of the sequence and one sample every ~5 years (1 cm) above and below the Kuwae tephra layer (

Table 5-6). We followed a standard procedure to extract and count pollen and spores (Erdtman and Wodehouse, 1944).

Pollen grains were counted and identified at x 400 magnification with detailed identification and photography of grains at x 1000 magnification (Figure 5-10). Unidentified types were described, photographed, and assigned a code; obscured or damaged grains were grouped as unknown. Poaceae pollen grains were grouped as either < 40 µm, > 40 µm, > 60 µm or as multiporate grains. We used the ANU (2007) Australasian Pollen and Spore Atlas to identify the pollen and spores.

3.3.9 Charcoal analysis

Micro-particles of charcoal were quantified from 32 samples by counting in the size range 10–125 µm alongside exotic *Lycopodium* spores and pollen on pollen slides (Wang et al., 1999). Particles were identified in the pollen slides as opaque, black, and angular fragments. Macro-charcoal samples were prepared from the >125-µm sieved fraction created in pollen preparation and were bleached with 6% H_2O_2 until the reaction stopped. All macro-charcoal fragments in each 1 cm^3 sample were counted using a stereo microscope (Whitlock and Larsen, 2001).

3.3.10 Chironomid analysis

The head capsules of chironomid larvae were extracted by disaggregating 2 cm^3 samples of sediment with 10% KOH (following Brooks et al., 2007) The disaggregated samples were then sieved to < 90 µm. The head capsules were then picked and mounted with Hydro-Matrix onto microscope slides. The counting and identification was done at x 400 magnification and taxonomically identified using Brooks et al. (2007), Andersen et al. (2013), and more specifically with a focus on the Southern hemisphere, following Dieffenbacher-Krall et al. (2007) and the New Zealand subfossil chironomid taxonomy which can be found at https://climatechange.umaine.edu/perl/nzguide.html. Ten samples were analysed, with an average temporal resolution of *c*. 200 years.

3.3.11 Zonation and ordination analyses

To identify the occurrence and timing of transitions, we created the pollen and spores and chironomid diagrams using Tilia 2.9.1 software and numerically zoned them using depth-constrained cluster analysis (CONISS) (Grimm, 1987; Grimm, 1990). All pollen taxa with an abundance of >1%, apart from unknown types, were included in the CONISS calculations. The same analysis was carried out for the chironomid data. In addition, the arboreal (trees and shrubs) to non-arboreal (herbs) pollen ratio was calculated for all depths.

Using pollen and spore percentages and chironomid percentages we performed detrended correspondence analysis (DCA) in R (RStudio Team, 2015; R Core Team, 2017) with the vegan package (Oksanen et al., 2007) with the assumption that the DCA axis 1 scores represent turnover (Bush et al., 2004; Blarquez et al., 2014; Castilla-Beltrán et al., 2021a; Nogué et al., 2021). Unknown pollen types, which were assigned a code (Figure 5-10), were included in the DCA. DCA axis 1 scores were used since they are considered optimal for analysing percentage data which contains many zeros (Hill and Gauch, 1980).

Canonical correspondence analysis (CCA) was conducted on the pollen and spore percentage data also using the vegan R package. Micro-charcoal, macro-charcoal (regional and local fire, respectively), reconstructed precipitation rate (mm d^{-1}), Ti/ incoherent scatter (erosion), and magnetic susceptibility (tephra and erosional events) were incorporated into the CCA as environmental variables. To fill data gaps in the precipitation rate dataset (to facilitate comparisons with the other proxies) we interpolated between data points. See Maloney et al. (2022) for how precipitation rate values were calculated.

3.4 Results

3.4.1 Tephra analysis

The opportunity to carry out a detailed tephra analysis allowed us to assign the source of the main tephra horizon in the record with confidence. Samples between 166–160 cm contain dominantly clear, vesicular, angular, and un-weathered volcanic glass, with subordinate brown fresh volcanic glass, feldspar, and pyroxene grains (with adhering glass). The coarsest particles of 2–2.5 mm diameter, and highest concentration of volcanic particles were in the 162–160 cm core segment. While we recognise that a firm identification requires further data, the glass texture, associated minerals, and glass major-element composition shows a good match to glass analysed on the same instrument in this study from near-source sites around the Kuwae Caldera (Figure 3-2). The age-depth model (Figure 5-9) suggests that the 6 cm layer of Kuwae tephra was deposited 650–510 cal. years BP (95% confidence) which is close to estimates of the Kuwae eruption occurring in the 1450s CE (Gao et al., 2006; Plummer et al., 2012).

The sample from 169–167 cm contained mainly weathered and highly altered crystalline rock fragments (andesitic to mafic based on mineralogy) as well as rare fragments of clear and highly vesicular glass. The composition of these rare glass fragments is not similar to the Kuwae tephra, but instead matches the Efate Pumice Formation tephra (~1.7 Ma; Stewart et al., 2010a), which is a common contributor to colluvial and alluvial sediments on Efate (Figure 3-2). These early Pleistocene glass and older weathered lithic grains from basement rocks, cf. Ash et al. (1978), were likely reworked into the lake following earthquakes or during major rain events or cyclones. The 173–171 cm samples contained no fresh glass, but inorganic particles were dominated by weathered and altered crystalline rock fragments (Figure 3-2). Most compositional analysis was unsuccessful on this material, but two analyses showed an andesitic composition, consistent with basement rock on Efate (Ash et al., 1978).

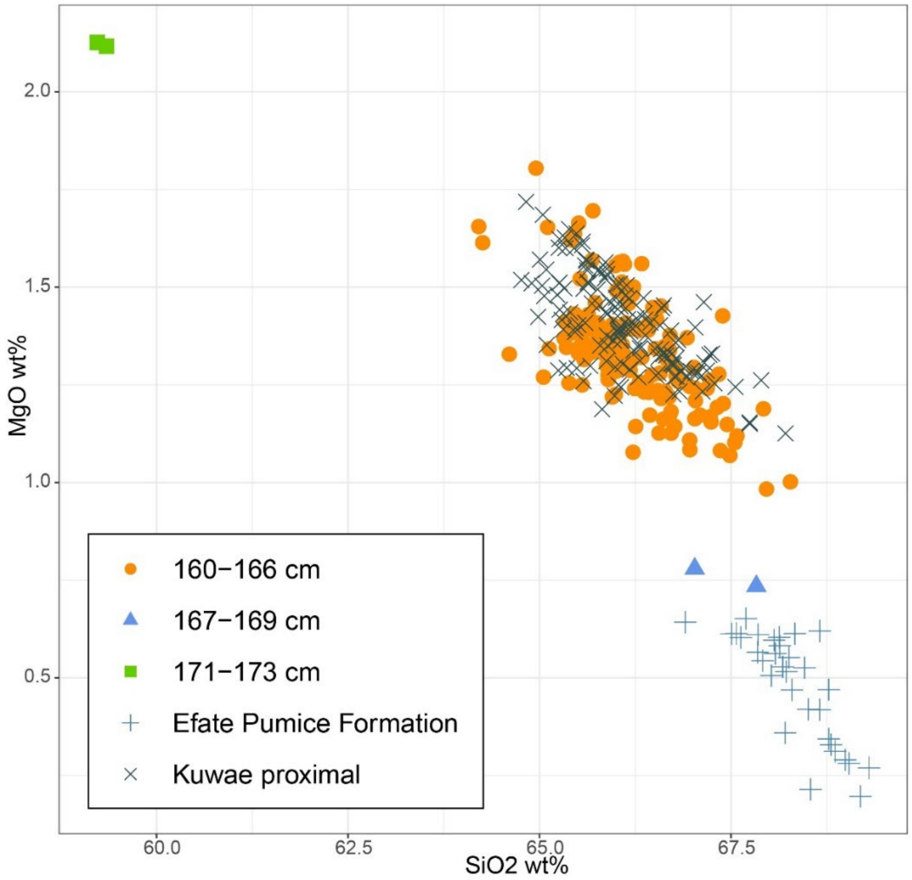

Figure 3-2 Major element composition of the volcanic glass identified between depth compared with known sources where possible.

3.4.2 Vegetation dynamics: pollen and spore zonation

Over 100 pollen types were identified, around 5% of which were assigned a code since they could not be identified. The pollen diagram is divided into four pollen assemblage zones based on the CONISS dendrogram (Figure 3-3). The following percentage values are calculated as means for each zone.

Zone one (341–258 cm, >1620–1120 cal. years BP) comprises of nine samples and is dominated by secondary forest taxa *Acalypha* (30%), *Pandanus* (4%), *Macaranga* (20%) *Trema* (13%), and *Homalanthus* (1%) with occurrences of Poaceae (7%), Cyperaceae (2%), trilete psilate fern spores (7%), and monolete psilate fern spores (1%).

Zone two (258–155 cm, 1120–560 cal. years BP) consists of 13 samples and has relatively high proportions of *Acalypha* (21%), *Macaranga* (19%), *Pandanus* (6%), *Trema* (9%), and *Homalanthus* (3%). Cyperaceae (4%), Poaceae (8%), psilate trilete spores (12%), psilate monolete spores (2%) also exhibit relatively higher proportions.

Zone three (155–24.5 cm, 560 cal. years BP to 1930 CE) consists of seven samples and shows a decline in secondary forest taxa *Acalypha* (to 16%) *Trema* (to 6%), *Macaranga* (to 16%) and an increase in *Persicaria*-type (to 2%), Poaceae (to 17%), *Nymphoides* (to 1%), *Pandanus* (to 9%), and trilete psilate spores (to 13%). Cyperaceae remains at 4% and monolete psilate fern spores declines to 1%.

Zone four (24.5–1 cm, 1930 – 2015 CE) consists of three pollen samples. In this zone, *Acalypha Trema*, *Macaranga,* and *Pandanus* decline to 12%, 0.5%, 14%, and 4% respectively. Herbaceous taxa Asteraceae (5% abundance), *Persicaria*-type (2% abundance) and Poaceae (17% abundance) increase. The aquatic plant *Nymphoides* increases to 2%, as do monolete (to 2%) and trilete fern spores (to 26%) whereas Cyperaceae remains at 4%.

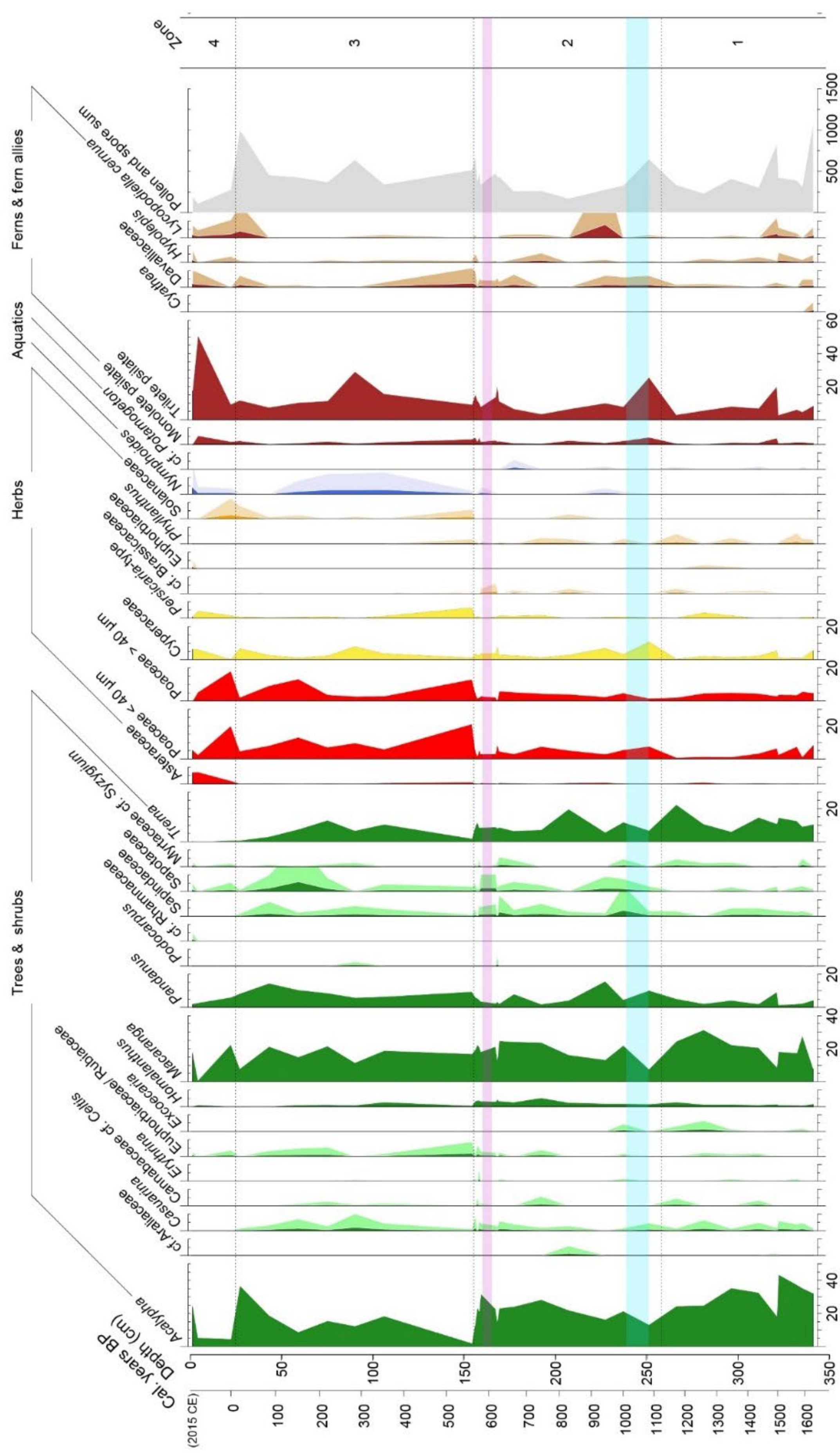
Trees & shrubs
Herbs
Aquatics
Ferns & fern allies
Zone
4
3
2
1
Cal. years BP
Depth (cm)
(2015 CE)
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
0
50
100
150
200
250
300
350
Acalypha
cf.Araliaceae
Casuarina
Cannabaceae cf. Celtis
Erythrina
Euphorbiaceae/ Rubiaceae
Excoecaria
Homalanthus
Macaranga
Pandanus
Podocarpus
cf. Rhamnaceae
Sapindaceae
Sapotaceae
Myrtaceae cf. Syzygium
Trema
Asteraceae
Poaceae < 40 µm
Poaceae > 40 µm
Cyperaceae
Persicaria-type
cf. Brassicaceae
Euphorbiaceae
Phyllanthus
Solanaceae
Nymphaceae
cf. Nymphoides
Potamogeton
Monolete psilate
Trilete psilate
Cyathea
Davalliaceae
Hypolepis
Lycopodiella cernua
Pollen and spore sum
20
40
20
40
20
20
20
20
20
20
40
60
500
1000
1500

Figure 3-3 Pollen percentage diagram for Lake Emaotul showing pollen and spores that have been taxonomically identified and have >1% abundance in any one sample. Taxa are grouped into trees and shrubs (green), dryland herbs (red), wetland herbs (yellow), other herbs (orange), aquatic plants (blue), and ferns and fern allies (brown). Taxa that occur in low abundances have been shown with x 5 exaggeration (paler shaded areas). The purple-shaded area represents the area where Kuwae volcanic tephra was identified, and the pale blue shaded area is the period of climate shift from wetter to drier conditions.

3.4.3 Chironomids

Ten chironomid taxa were identified. The chironomid diagram (Figure 3-4) is divided into three zones using CONISS (Grimm, 1987).

Zone one (357–252 cm, >1600–1090 cal. years BP) consists of four samples and is dominated by *Procladius* (46%) and *Tanytarsus funebris*- type (41%).

Sub-zone two (252–221.5 cm, 1090–910 cal. years BP) consists of one chironomid sample and has high proportions of *Chironomus anthracinus*-type (52%) and *Orthocladiinae* type 1 (similar to *Pseudorthocladius*) (8%). *Procladius* and *Tanytarsus funebris*- type decline to 4% and 24% respectively.

Zone three (221.5–61 cm, 910–160 cal. years BP) consists of five samples and is similar to zone one where *Procladius* increases to 36% and *Tanytarsus funebris*- type increases to 55%. *Chironomus anthracinus*-type decreases again to 2%.

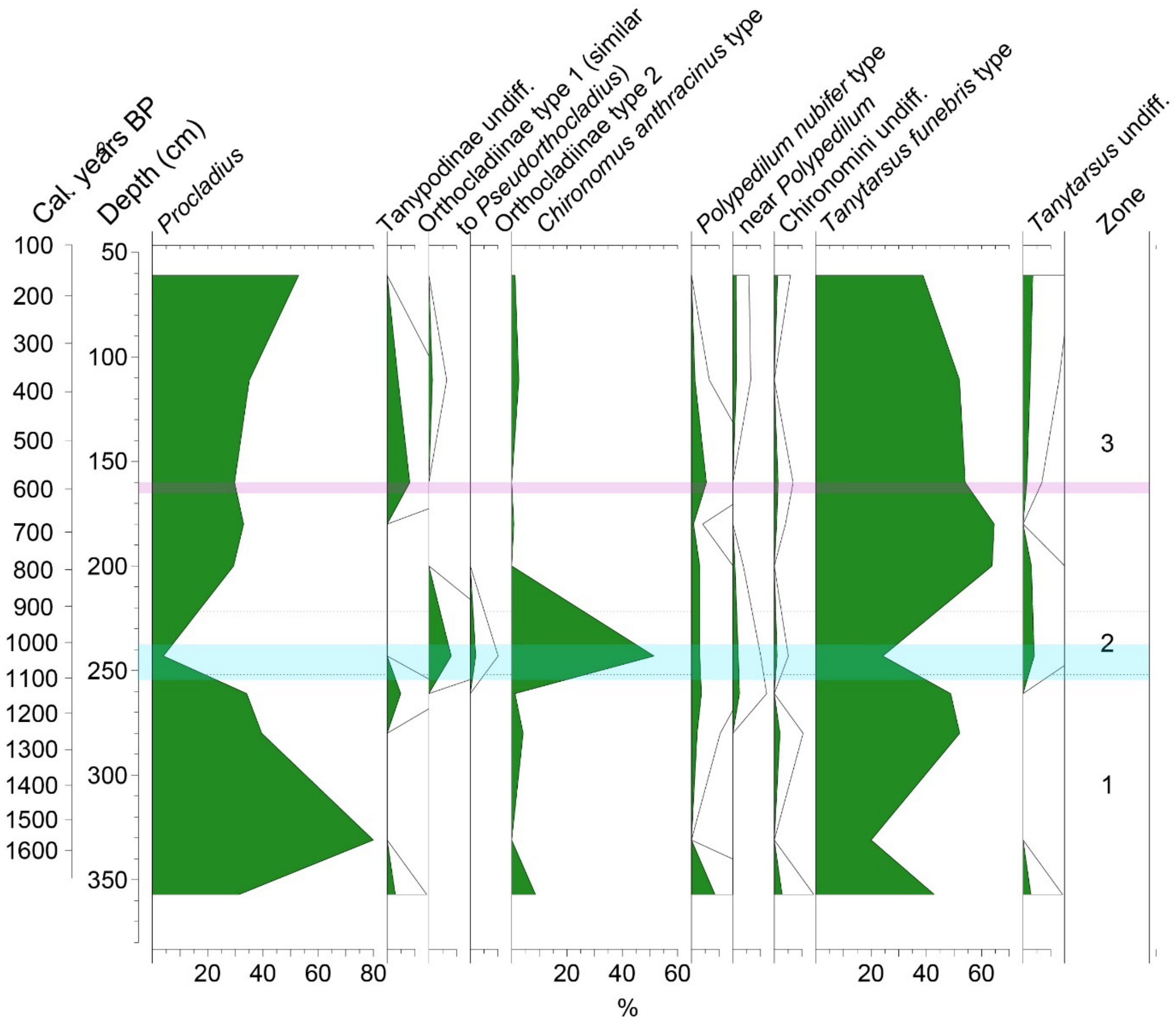

Figure 3-4 Chironomid percentage diagram, the period of climate transition from wetter to drier is shown in pale blue and the Kuwae tephra is shown as a purple shaded area.

3.4.4 Core stratigraphy, AP/NAP, and C/N dynamics

The core stratigraphy consisted of gyttja throughout. We structured this section following the pollen zones from Figure 3-3 (red dashed line). Micro-charcoal concentrations, as shown in Figure 3-5, are variable in pollen zone one and the mean value is 1300000 particles per cm^3, macro-charcoal concentrations are lower (7 particles per cm^3). In pollen zone two, micro-charcoal concentrations are relatively lower (1190000 particles per cm^3) and macro-charcoal particles are still 7 particles per cm^3. In pollen zone three, micro-charcoal particle concentrations decrease again to 790000 particles per cm^3 but there is a relative increase in macro-charcoal particle concentrations to 14 particles per cm^3. In pollen zone four, micro-charcoal particle concentrations remain relatively low at 205000 particles per cm^3 but macro-charcoal concentrations increase to 57 particles per cm^3. The ratio of arboreal to non-arboreal pollen varies throughout the record (between 0.4 and 1.96). The most notable shifts in the ratio occur after the Kuwae eruption and in the upper part of the record (pollen zone four). Following the Kuwae eruption, AP/NAP increases and then declines after ~20 years. The lowest AP/NAP is within pollen zone four. The C/N ratio fluctuates thorough the record but does not display any change during the shift to drier conditions (Figure 3-5). However, the ratio largely varies around between 12 and 16 with one notable decline to 7.8 at 185 cm (~700 cal. years BP), prior to the Kuwae eruption suggesting a greater proportion of algal material.

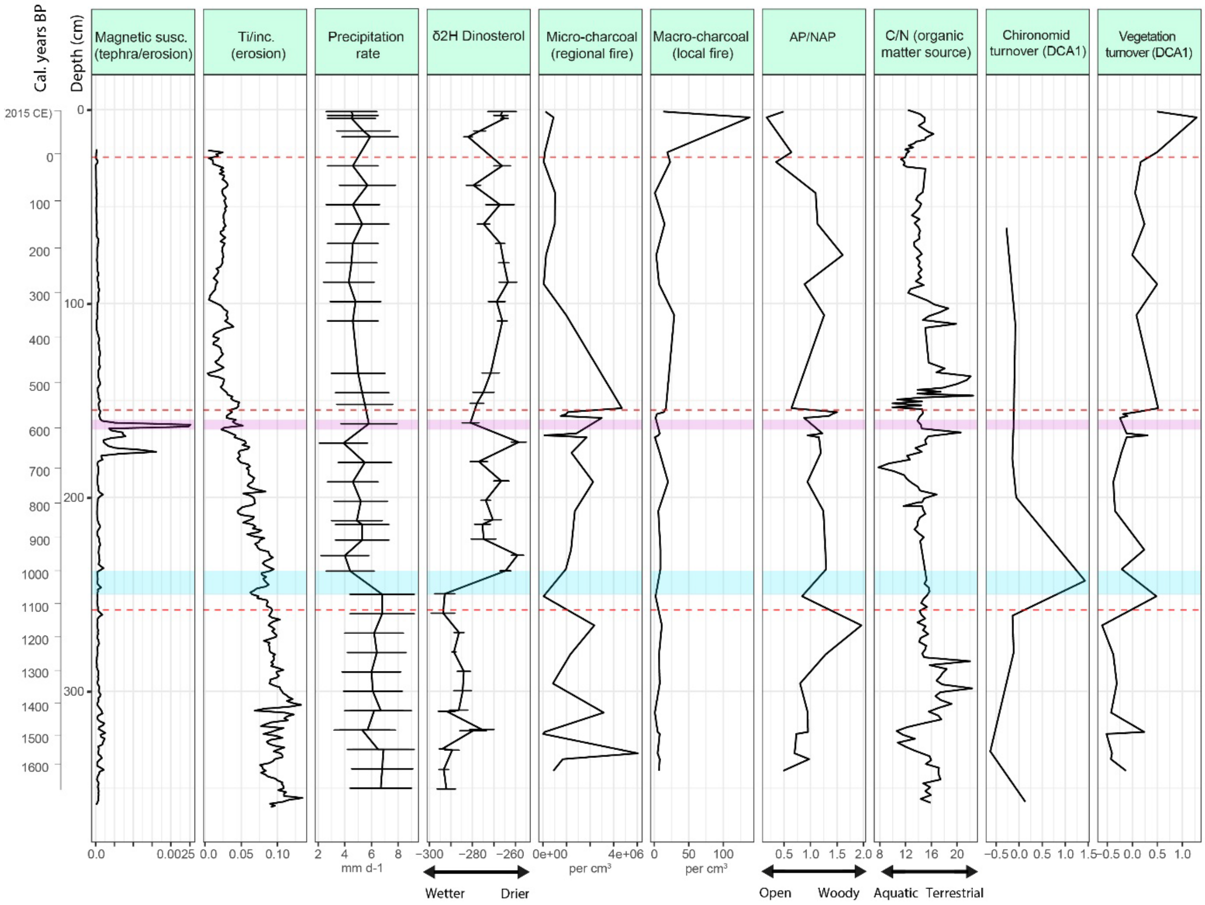

Figure 3-5 Summary diagram of methods used in the study. From left to right: magnetic susceptibility (tephra/erosion), Ti/ incoherent scatter (erosion), reconstructed precipitation rate mm d-1 and 2Hdinosterol all redrawn from Maloney et al. (2022). What follows is new data from this study; micro- and macro charcoal particle concentrations per cm^3, indicating regional and local fires. Arboreal pollen/ non arboreal pollen ratio (AP/NAP) indicating forest openness, C/N indicating organic matter source, and chironomid and vegetation turnover (DCA axis 1 scores). The purple shaded area represents samples where Kuwae volcanic tephra is present. The blue shaded area represents the transition from wetter to drier conditions during the onset of the 1100 cal. years BP shift to drier climate conditions. The red dashed lines are consistent with zonal

divisions within the pollen diagram. The mean temporal resolution, where 1 cm of sediment represents 5 years (1–8 year range) for all the palaeoecological proxies is shown in the supplementary information. The mean error for each 1 cm slice of the core was 140 years (95% confidence ranges).

3.4.5 Vegetation and chironomid turnover and Canonical correspondence analysis (CCA)

We used a turnover measure (DCA axis1) to assess the degree of change in the composition of both chironomids and pollen due to the shift to drier conditions (Maloney et al., 2022) and the Kuwae eruption (Figure 3-5). Both chironomid and vegetation turnover increased during the shift towards drier conditions ~1100 cal. years BP. While chironomid turnover showed no change following the Kuwae eruption, the vegetation values indicate greater taxonomic turnover following the eruption. There was also a sharp increase and then decline in the arboreal to non-arboreal pollen ratio (AP/NAP) following the eruption.

Canonical correspondence analysis (CCA) was used to determine which environmental drivers have dominant associations with each pollen zone. CCA axis 1 explained 39% of the variance (eigenvalue 0.05) and CCA axis 2 explained 22% (eigenvalue 0.04) (Figure 3-6). Environmental variables on the positive side of CCA axis 1 include regional fires, precipitation rate (mm d^{-1}), erosion (Ti/ incoherent scatter), and tephra/ erosional events indicated by magnetic susceptibility (correlation scores 0.47, 0.61, 0.9, 0.01 respectively, see Table 5-7). One environmental variable, macro-charcoal particles (local fires), was located on the negative side of CCA axis 1 (correlation score -0.5). Pollen taxa from zone one (in red) are mostly positioned in the positive half of the CCA axis 1 and associated with precipitation and erosion. Pollen zone two (in orange) transitions from the positive to the negative half of CCA axis 1 with tephra/ erosion (magnetic susceptibility) as the most influential environmental variable of this period and finally pollen zones three (in green) and four (in blue), which occur after 560 cal. years BP, are found in the negative side of CCA axis 1 and explained by local fires.

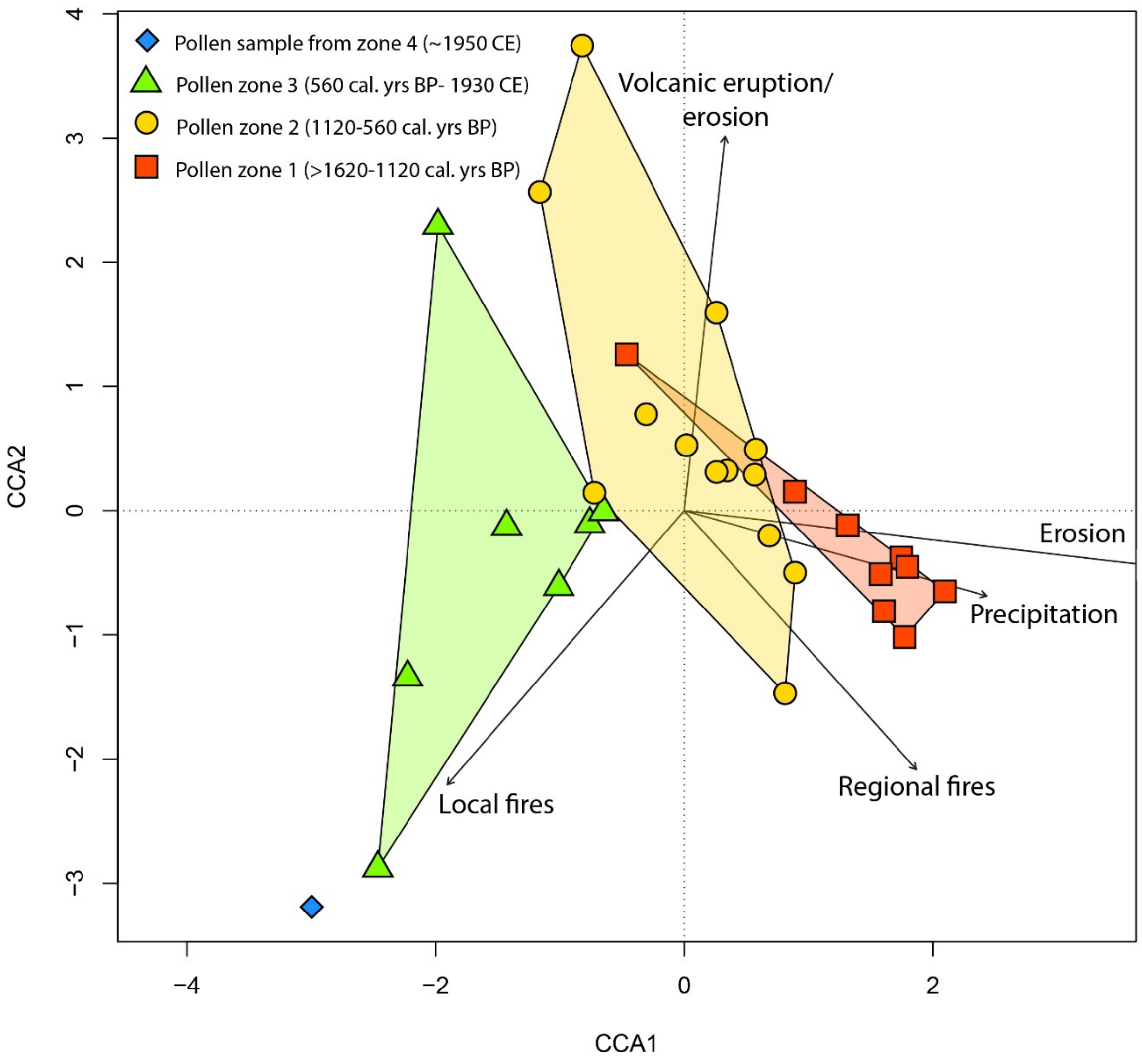

Figure 3-6 Canonical correspondence analysis (CCA) of pollen percentages. Environmental variables include regional fires (micro-charcoal), local fires (macro-charcoal), precipitation rate (mm d^{-1}), erosion (Ti/ incoherent scatter), and volcanic eruptions/ erosion (magnetic susceptibility). Pollen assemblages are coloured according to their zones.

3.5 Discussion

3.5.1 The impact of precipitation changes on terrestrial and lacustrine ecosystems

Drought in the SW Pacific islands is currently considered a threat to both island ecosystems and their human societies (e.g. Sear et al., 2020). After ~1100 cal. years BP, there was a shift towards drier climate conditions (Figure 3-5; Maloney et al, 2022). Precipitation values changed from around 6.8 mm d^{-1} to 4.4 mm d^{-1} over a period of ~70 years (Maloney et al., 2022), a significant shift in moisture availability. Both vegetation and chironomid turnover temporarily increased across the transition from wetter to drier climate conditions (Figure 3-5). The vegetation change was characterised by an increase in Cyperaceae, Poaceae, and ferns, which then declined to previous values within ~80 years (Figure 3-3). According to the CCA analysis, precipitation, and erosion plot with samples from pollen zone one (>1620–1120 cal. years BP) prior to the change to drier conditions, linking both environmental drivers of change as the most significant. Indeed, erosion (Ti/inc) is well known to be linked with sedimentary in-wash (e.g. Sear et al., 2020), which here corelates with higher precipitation. While there is a higher turnover at the transition to drier conditions, the individual taxon changes are subtle and somewhat transient (Figure 3-5).

The changes in the chironomid community show a strong response to the moisture shift, then recovery, but with different abundances of the dominant taxa than prior to the shift. While all main taxa declined during the transition, *Chironomus anthracinus* type increased; this caused high turnover in the short term (Figure 3-4 and Figure 3-5). *Chironomus anthracinus* is known to be able to withstand low levels of oxygen and can tolerate unfavourable conditions (Hamburger et al., 1994; Hamburger et al., 1995). The increase in *Chironomus anthracinus* and relative decrease in other taxa may suggest a decrease in oxygen or even anoxia following the climate shift. Turnover decreased within ~135 years, despite climate conditions remaining relatively dry. The C/N ratio shows no clear response to the climate transition, indicating that there was no detectable shift in the balance of terrestrial and algal input to the lake with the shift to drier conditions. This possibly suggests that the overall biomass in the catchment did not change much, and also that the organic input to the lake was not strongly driven by precipitation-driven in-wash.

3.5.2 The Kuwae eruption led to significant changes in vegetation diversity

The Kuwae eruption is considered one of the largest eruptions of the last millennium (Neukom et al., 2014), and it had far more impact on the forest of Efate than did the moisture change. The CCA picks out the Kuwae eruption as the most significant association with the fossil pollen assemblage in pollen zone two (1120–560 cal. years BP) (Figure 3-6). It is notable that vegetation turnover not only increased sharply after the Kuwae eruption, but it remained high throughout the subsequent record (Figure 3-5). It is generally accepted that after a volcanic eruption there may be changes in vegetation composition, such as an increase in grass abundance (see examples in Table 5-8). In Efate, after the Kuwae eruption sequence, an increase in grass pollen (Poaceae) is linked with a decline in AP/NAP, suggesting increased occurrence of open patches (Figure 3-5).

The tree and shrub post-eruption dynamics show *Acalypha* (native shrub or small tree) and *Trema* (native tree) decreasing within ~20 years of the deposition of the Kuwae tephra, while *Persicaria*-

type, Solanaceae, and *Nymphoides* increased together with grasses (Figure 3-3). Initially, damage to small trees and shrubs such as *Acalypha* and *Trema* could have created space for grasses and sedges to expand, and the increase in grasses may also be explained by its relatively short generation time compared with woody vegetation, which gives the group the ability to profit relatively quickly from nutrient enrichment following volcanic eruptions (Urrutia et al., 2007). It is important to note, however, that our results show that the forests surrounding Lake Emaotul were already disturbed at the start of this record, as indicated by the presence of *Acalypha*, *Macaranga* and *Trema,* which are considered secondary, disturbance, and early-successional taxa (Whittaker et al., 1989; Fall, 2010; Åkesson et al., 2021) and the continuous presence of fire, which is often associated with human occupation on Pacific islands (e.g. Fall, 2005; Stevenson et al., 2017). Although our results show that the Kuwae eruption impacted on the forest surrounding Lake Emaotul, local human impacts during the period of the Kuwae eruption cannot be ruled out as a driver for change. For example, there is archaeological evidence that human populations moved southwards from Sheppard and Epi islands to Efate following the eruption (Garanger, 1972), and an increase in population size could have led to some level of deforestation. However, there is no clear link between the declining taxa (*Acalypha* and *Trema*) and known human uses of them.

Despite numerous examples of change in vegetation composition (Table 5-8), recovery rates of vegetation following volcanic eruptions are poorly understood. Palaeoecological evidence of tephra deposition events have typically shown short-lived impacts (decades to centuries e.g. Lotter and Birks, 1993; Montoya et al., 2021). For example, the main patterns that emerge from analysing large datasets of pollen time-series from tropical forests suggest that forest recovery rates are faster for large, infrequent events, such as volcanic eruptions, than for human-induced burning (Cole et al, 2014). The analysis by Cole et al. (2014) also suggests that arboreal taxa typically recover to ~95% abundance after >200 years. On Efate, the arboreal taxa *Acalypha* and *Trema* had largely recovered their pre-eruption abundance in ~260 years. Prior to the eruption, *Acalypha* and *Trema* values were 23% and 9% of the total pollen sum, respectively. After 260 years, they reached 19% and 11%, respectively. These two taxa responded differently to other arboreal taxa such as *Macaranga*, *Pandanus*, Sapindaceae, and Sapotaceae, which showed no obvious decline after the eruption. Despite the partial recovery of *Acalypha* and *Trema*, turnover remained higher for all taxa ~625 years following the eruption (Figure 3-5).

While the forests of Efate showed changes linked to the volcanic eruption, Lake Emaotul chironomid communities remained unperturbed (Figure 3-4). Addition of volcanic tephra of basaltic/andesitic composition to the lake could be expected to deliver nutrients, including substantial S, Fe, and other cations (Cronin et al., 1998), and this may have led to algal blooms (e.g. Harper et al., 1986; Roberts et al., 1997; Eastwood et al., 2002; Telford et al., 2004), which might be expected to show as a change in C/N. The Emaotul C/N record shows short-term variability, but no clear directional change is evident following the eruption, with ratio values before and after being ~13 (Figure 3-5), a value indicative of a mixed source of organic matter (García-Alix et al., 2012); if there was a post-eruption increase in algal biomass, it is not detectable. As suggested for forested sites in Ecuador (see Montoya et al., 2021), the dense canopy of the forest trees surrounding Lake Emaotul may have partially shielded aquatic ecosystems from major impact by blocking some airborne tephra fall on to the lakes surface. The inconsistent responses of algal productivity to volcanic tephra-fallout recorded to date suggest site- or catchment-specific factors may be important in determining responses. At Lake Emaotul, chironomids also showed no significant change following the eruption. Either they recovered so quickly that changes were not identified in this record or they are not sensitive to volcanic tephra inputs at this site.

3.5.3 Recent changes in fire regime

Archaeological evidence indicates that people had been actively modifying the landscape of Efate ~1400 years prior to the start of this record (1600 cal. years BP), since the first human settled Vanuatu ~3000 years ago (Petchey et al., 2014; Bedford et al., 2018). Notably, the CCA analysis (Figure 3-6) shows an association between samples from the period 560 cal. years BP to 1950 CE and local fires, indicating that the local use of fires, suggested by the increase in macro-charcoal particles (Figure 3-5) could have been an important driver of change (Clark, 1988; Whitlock and Millspaugh, 1996). During pollen zone four (1930–2015 CE), an increase in Asteraceae, Poaceae, Solanaceae, and *Persicaria*-type pollen, and fern spores, a decrease in woody taxa (e.g., *Acalypha* and *Trema*), together with higher concentrations of macro-charcoal concentrations spanning the last ~90 years is strongly indicative of opening of the forest and transition towards the wetland areas and secondary forests we see today surrounding Lake Emaotul. These findings agree with other studies from Vanuatu; for example, human impacts are seen in pollen diagrams from ~3000 cal. years BP onward from Aneityum island, Southern Vanuatu (~320 km south of Efate). At Aneityum island, tree and shrub taxa (*Eugenia*, *Celtis* and *Trema*) were replaced by grasses (Poaceae), sedges (Cyperaceae), ferns, accompanied by an increase in charcoal particles (Hope and Spriggs, 1982). Another example is the palaeoecological record from the island of Erromango (Figure 3-1, ~150 km south of Efate), which shows evidence of burning throughout a 2000 year period during which humans were present (Hope et al., 1999). Human impacts may have been present prior to the last 1600 years, but despite their apparent impacts, the transition to drier climate ~1100 cal. years BP and the Kuwae eruption were both strong enough disturbances to affect the vegetation surrounding Lake Emaotul.

3.6 Conclusion

It can be difficult to isolate and disentangle multiple drivers of change and their effects on an ecosystem when they occur close together in time. Efate has been affected by a major volcanic tephra fall and a marked climate transition. The Kuwae eruption (650–510 cal. years BP) and the transition from wetter to drier conditions occurring ~1100–1000 cal. years BP are, however, well separated in time and both post-date colonisation, which provides the opportunity to examine each in turn (while assuming no major change in human impact). The Kuwae eruption appears to have had a more lasting impact on vegetation than the period of climate change. In contrast, the aquatic ecosystem, as represented by chironomid assemblages, appears more sensitive to the ~1100 cal. years BP shift to drier conditions than to the Kuwae eruption. While precipitation changes and the Kuwae eruption explained more variance in the pollen and spore data prior to the Kuwae eruption, local scale burning seems to have had a more important role within the last few centuries, over which there has been a major change in vegetation composition. Understanding legacies of volcanic and climatic impacts is relevant for the sustainable management of the islands and archipelagos natural resources.

3.7 Acknowledgements

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3.8 Author contributions

NS and SN contributed to conception and design of the study. NS wrote first draft of the manuscript and created the figures. SC, CL, AM, SB, TB, IC, ML, and JS contributed with sediment analyses. WG and MP helped with the content and structure of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

Chapter 4 Biotic homogenisation on South Pacific islands during the last 5000 years

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4.1 Abstract

The increasing similarity of plant species composition among distinct areas is leading to the biotic homogenisation of ecosystems globally. Human actions such as ecosystem modification, the introduction of non-native plant species, and the extinction or extirpation of endemic and native plant species are considered the main drivers of this trend. However, little is known about when biotic homogenisation began or about pre-human patterns of biotic similarity. Here we investigate vegetation trends during the past 5000 years across the tropical, sub-tropical, and the warm temperate South Pacific using fossil pollen records from 15 sites on 13 islands within the biogeographical realm of Oceania. The site comparisons show that biotic homogenisation began between 3400–2900 cal. years BP, synchronous with the timing of human colonisation of the Southwestern Pacific islands. Pairwise Bray-Curtis similarity results also show that when two islands were settled in a given time interval, their similarity is greater than when one or neither of the islands were settled. Importantly, higher elevation sites tended to show less biotic homogenisation. While biotic homogenisation is often referred to as a contemporary issue, we find that initial human settlement of islands was a driver.

4.2 Introduction

Biotic homogenisation threatens global biodiversity, as increasing similarity of species composition among regions leads to the overall decline of larger-scale diversity (Smart et al., 2006; Blowes et al., 2022). Homogenisation is often linked to anthropogenic impacts such as habitat loss and range expansion of generalist introduced taxa, which can lead to range contractions and/or population decline of native/endemic species (McKinney and Lockwood, 1999; Püttker et al., 2015; Kress and Krupnick, 2022; Xu et al., 2023). It may also affect ecosystem function and services and thus (socio)ecosystem resilience in the face of further anthropogenic impacts (Olden et al., 2004; Isbell et al., 2015; Castilla-Beltrán et al., 2021a).

In many ways, islands are ideal models for studying biodiversity changes (Vitousek, 2002). Insular biotas are particularly vulnerable to human-mediated drivers that are known to be causes of the biotic homogenisation process, such as species introductions, habitat loss, and climate change (Sax et al., 2002; Pyšek and Richardson, 2006; Nogué et al., 2017; Fernández-Palacios et al., 2021; Nogué et al., 2021). In addition, island ecosystems have high proportions of endemics compared with mainland areas (Whittaker and Fernández-Palacios, 2007; Kier et al., 2009) thus making them important habitats and priorities for conservation. In the biogeographical realm of Oceania, many plant species have threatened status, although the scale of the problem is still unclear, since only ~3% of species have been assessed by the IUCN (Pippard, 2009). It is likely, therefore, that Pacific islands have been susceptible to biotic homogenisation both now and in the past (e.g., Castro et al., 2007; Castro and Jaksic, 2008; Rosenblad and Sax, 2017).

Many studies of biotic similarity rely on published lists of native, non-native, or extinct or extirpated taxa to delineate a baseline for biodiversity composition, limiting the timeframe to a few centuries or potentially missing unrecorded introductions or extirpations (e.g., Baiser et al., 2012; Dornelas et al., 2014; Rosenblad and Sax, 2017; Finderup Nielsen et al., 2019), but fossil datasets have the potential to extend these timescales or capture previously unrecorded introductions or extirpations (Feurdean et al., 2010; Willis et al., 2010; Gillson et al., 2011; Blarquez et al., 2014; Birks et al., 2016a; Salgado et al., 2018; Wengrat et al., 2018; Fraser et al., 2022).

South Pacific islands, settled in two stages ~3000 and ~700 years ago (see Table 5-9 and references therein), have an abundance of palaeoecological (e.g., Hope and Spriggs, 1982; Flenley et al., 1991; Stevenson and Dodson, 1995; Flenley et al., 1999; Stevenson et al., 2001; Fall, 2005; Hope et al., 2009; Prebble et al., 2019; Gosling et al., 2020; Strandberg et al., 2023a) and archaeological information written about them (e.g., Kirch, 2000; Wilmshurst et al., 2011; Burley et al., 2015) allowing us to observe and quantify trends in biotic similarity on a longer temporal scale. By analysing 15 fossil pollen records from Melanesian and Polynesian islands, encompassing the past 5000 years and a west to east gradient of 8300 km, we quantify whether island ecosystems have become more biotically similar over time, or otherwise.

4.3 Methodology

4.3.1 Study site

This study focuses on islands in the tropical, sub-tropical, and warm temperate South Pacific Ocean and includes the geographic areas of Melanesia (n=7) and Polynesia (n=8) within the biogeographical realm of Oceania (Figure 4-1). The island of Ahuahu (Great Mercury) is situated within the Polynesian triangle, offshore of New Zealand's North Island, and experiences a warm temperate climate (see Holdaway et al., 2019; and Prebble et al., 2019). New Caledonia, Fiji, and Vanuatu are located in the tropical western Pacific geographic area of Melanesia and have a flora similar to that of Australia and Papua New Guinea (Mueller-Dombois and Fosberg, 1998). The main sources of precipitation being the ITCZ (Intertropical Convergence Zone) and SPCZ (South Pacific Convergence Zone) (Sear et al., 2020). The islands of Polynesia to the east are characterised by an Indo-Pacific flora, which includes some species from the Americas, New Zealand, and the sub-Antarctic (Mueller-Dombois and Fosberg, 1998). Throughout the Pacific, plant diversity decreases from west to east, but larger and older islands tend to be more biodiverse (Keppel et al., 2009). The island areas included in this study range from the largest, Grande Terre, New Caledonia (1,890,000 ha) to the smallest, Foa, Tonga (135 ha) and the islands' geologies are a mixture of composites, volcanics, and limestones (Table 5-9).

The settlement of the Pacific islands represents the last great migration of humans into unoccupied lands (see Table 5-9 and references therein). Archaeological evidence suggests that the first people to colonise the South Pacific islands were the Lapita, the ancestors of Polynesians (Kirch and Green, 2001). Linguistic studies indicate the Lapita's origins to be somewhere between Taiwan and the Bismarck Archipelago (Blust, 1996) and genetic studies support this (see Matisoo-Smith, 2015 for discussion).

4.3.2 Acquisition of pollen datasets

Pollen records from 15 sites (Table 5-9) were included in the analysis. These sites were chosen because together they represent both early (~3000 cal. years BP) and late (~700 cal. years BP or in the case of Rapa Nui potentially earlier settlement, see Rull (2020)) human colonisation, and the pollen records are all at least 3300 years long allowing comparisons between pre- and post-settlement measurements. In addition, they form a west-to-east gradient spanning 8300 km across the Pacific Ocean and an elevational gradient from 0–760 m.a.s.l. Sites at different elevations allow us to investigate trends from coastal regions, where humans have typically settled, to upland areas that may have escaped some of the impacts of human disturbances (Gosling et al., 2020; Norder et al., 2020).

Six datasets were accessed via the Neotoma database (Williams et al., 2018) using the *neotoma2* R package (https://github.com/NeotomaDB/neotoma2). These are: St. Louis Lac (Grande Terre) (Stevenson and Dodson, 1995), Anouwe Swamp (Aneityum) (Hope and Spriggs, 1982), Bonatoa Bog (Viti Levu), Lake Tagimaucia (Taveuni), (Hope et al., 2009), Tukou Marsh (Rapa) and Waitetoke (Ahuahu/ Great Mercury) (Prebble et al., 2019). We excluded the available pollen data from Lake Emeric, New Caledonia (Hope and Pask, 1998) accessed via the Neotoma database, due to low pollen and spore counts (~60 per sample for last 5000 years). The following pollen datasets were acquired from published papers: Ngofe Marsh (‘Uta Vava’u), Lotofoa Swamp (Foa), Finemui Swamp (Ha’afeva) (Flenley et al., 1999; Strandberg et al., 2023a); Avai’o’vuna Swamp (Pangaimotu) (Fall, 2005); Lake Lanoto’o (Upolu) (Gosling et al., 2020), and from Plum Swamp (Grande Terre) (Stevenson et al., 2001). In addition, two datasets, Yacata (Yacata Island) and Volivoli (Viti Levu), were taken from Nogué et al. (2021). One pollen record from Rano Aroi, (Rapa Nui) (Flenley et al., 1991) was digitised manually using ImageJ software (Schneider et al., 2012).

4.3.3 Age-depth models

The six fossil pollen datasets accessed via Neotoma, and those from Nogué et al. (2021), Gosling et al. (2020), Stevenson et al. (2001), and Strandberg et al. (2023a) already included calibrated ages. The Rano Aroi age-depth model was recalibrated based on the SHCal20 calibration curve for radiocarbon dates using *rbacon* (Blaauw and Christen, 2011; Hogg et al., 2020). See Strandberg et al. (2023a) for age-depth models of sites from Tonga.

4.3.4 Harmonisation of pollen datasets

Unknown or uncertain pollen/ spore identifications and taxa with the preceding notation “cf.” were removed from the datasets. In total 153 taxa were removed because of taxonomic uncertainty. Taxa with the notation “comp.” (favourably comparable) and “sim.” (similar to) were included (Benninghoff and Kapp, 1962). Notations such as “undifferentiated” or “type” were removed and taxonomic names were aggregated up one taxonomic level, e.g., *Plantago lanceolata*-type became *Plantago*. Genus-level taxa with the “type” notation were aggregated up to the family level since these types might include taxa from multiple genera, e.g., from *Percicaria*-type to Polygonaceae. Family-level data with the notation “type”, for example Euphorbiaceae-type, were removed from the analysis. Notations such as “type 1” were removed.

Poaceae of all diameter sizes were aggregated into one group. Pollen assemblages older than 5000 cal. years BP or without associated ages were removed. The R package *taxize* (version 0.9.100) (Chamberlain and Szocs, 2013) was used to validate taxonomic names except for liverworts, mosses, and subfamilies, which are not available (POWO, 2022). To obtain rank data, the NCBI taxonomy database was used (Chamberlain and Szocs, 2013; R Core Team, 2017; NCBI, 2022). The final harmonised and binned taxonomic names include 346 taxa (families=80, subfamilies=2, tribe=1, genera=224, and species= 39).

Since pollen sampling efforts are different over time and among sites, we rarefied pollen counts using the R package *vegan* (version 2.6-4) to standardise pollen richness and allow comparisons of mean rarefied pollen richness between sites (Birks and Line, 1992; Oksanen et al., 2020). However, rarefaction was not possible for the five pollen records from which only pollen percentage data were available, for example in digitised records (Table 5-11). Pollen counts were transformed to percentages prior to further statistical analyses.

4.3.5 Statistical analyses

To allow for temporal comparisons, pollen assemblages from each site were placed within 500-year intervals, and pollen data within these intervals were averaged resulting in 131 pollen assemblages. The 500-year intervals were adopted to account for relatively low sampling resolutions. We used unique site pairings for the 15 sites (105 unique pairs, excluding comparisons within a given site). We then calculated the Bray-Curtis dissimilarity index (Bray and Curtis, 1957) for each pairing (796 individual pairwise comparisons). Bray-Curtis dissimilarity was selected since it takes abundance into account whereas other methods, for example Jaccard dissimilarity index, are occurrence-based methods. Bray-Curtis dissimilarity values (0–1) were inverted so the values represent taxonomic similarity, with 1 being the most similar (100%) and 0 being the least (0%). Linear models were used to identify the slope coefficients of the trends over time, with negative trends (<0) representing homogenisation and positive trends (>0) representing the opposite, differentiation (Figure 4-1). The slopes thus indicate how often a sites pollen assemblages tends to become more biotically similar (homogenisation) or less biotically similar (differentiation) to that of the other sites through time.

A smooth spline model using the *npreg* package (Helwig, 2020) was implemented to plot overall changes in taxonomic similarity over time (Figure 5-16). To detect the role of human settlement on biotic similarity, pairwise similarity comparisons were further sorted into groups defined by whether both site/ island pairs were settled by people at that given time interval, whether just one of the pair was settled, or if neither were settled (Figure 5-17).

Finally, a linear breakpoint model was implemented to test, across the region, if changes in biotic similarity have accelerated in time. The unknown breakpoint of a linear model relating similarity among assemblages across all sites to time of comparison was estimated using the *segmented* R package (Muggeo, 2003). The data points integrated in this model are not independent from each other as the same assemblage is compared multiple times with other assemblages. This "pseudo-replication" of data points makes any significance test of this analysis meaningless but allows an interpretation of the breakpoint and model estimates.

4.4 Results

Out of a possible 105 slope coefficients (whole site to site comparisons over time), where differentiating or homogenising trends were identified (positive or negative coefficient respectively), Lake Tagimaucia (Taveuni) and St. Louis Lac (Grande Terre) showed differentiation over time in more than half of the comparisons (Figure 4-1). Avai'o'vuna Swamp (Pangaimotu), Finemui Swamp (Ha'afeva), and Yacata (Yacata Island) showed the most biotic homogenisation trends over time (Figure 4-1).

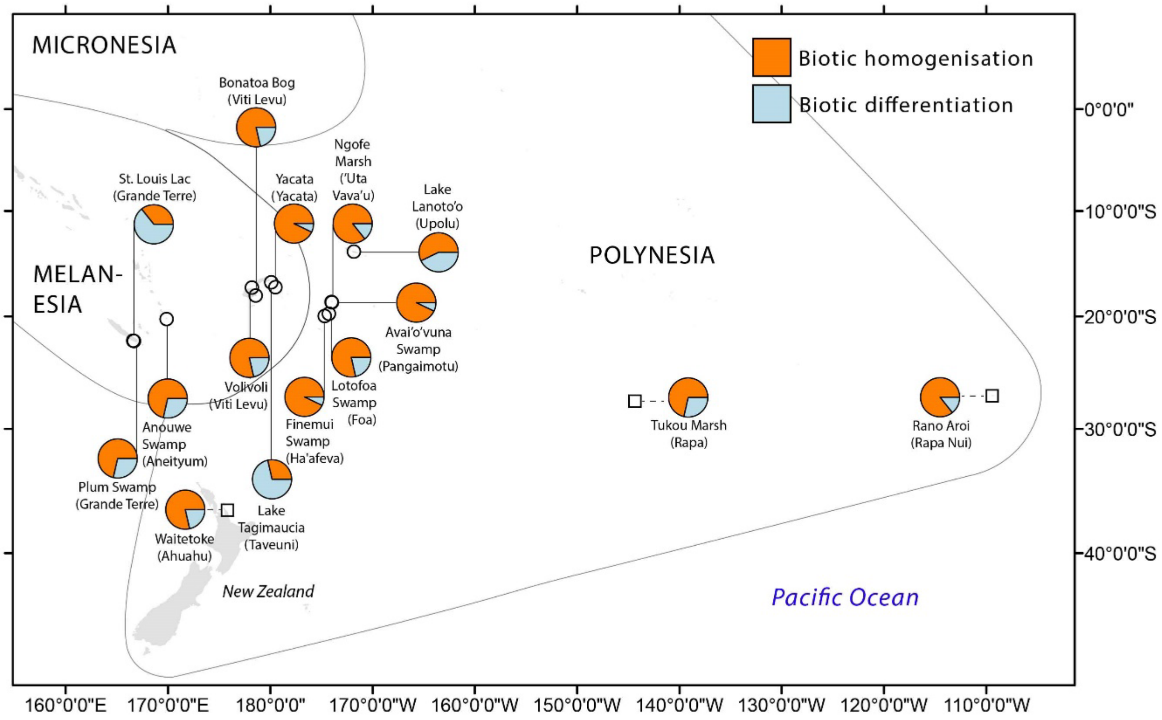

Figure 4-1 Proportions for each site showing the partitioned Bray-Curtis similarity homogenising trends (<0 slope coefficients) in orange and differentiating trends (>0 slope coefficients) in blue

over time. Circles with solid leader lines are sites estimated to have been settled ~3000 cal. years BP and squares with dashed leader lines are sites estimated to have been settled ~700 cal. years BP. Island names follow site names in parentheses. X- and Y- axis represent longitude and latitude respectively (º).

The 105 whole site to site comparisons over time show that all except two have negative median slope coefficients and have therefore become more biotically similar to other sites (Figure 4-2). Lake Tagimaucia (Taveuni) and St. Louis Lac (Grande Terre) have positive median values (Figure 4-2) indicating dissimilarity i.e., biotic differentiation compared with the other sites. Lake Lanoto'o (Upolu) and Waitetoke (Ahuahu) show relatively low biotic homogenisation. Finemui Swamp (Ha'afeva) and Yacata (Yacata Island) have the lowest median slope coefficients and have therefore become more biotically similar to other sites over time.

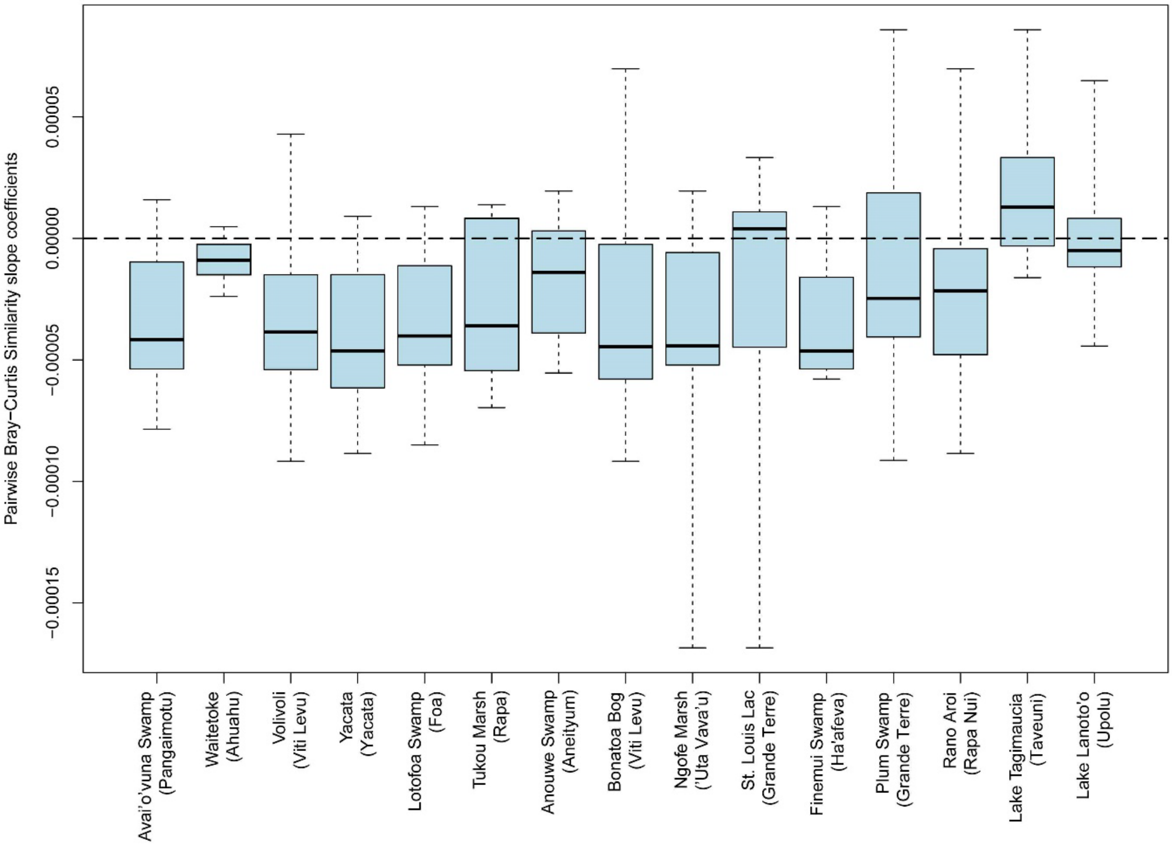

Figure 4-2 The direction and steepness of the biotic similarity trends between sites based on pairwise Bray-Curtis similarity slope coefficients. Sites are organised by elevation with the lowest (sea level) on the left to the highest on the right (760 m.a.s.l). Data points above the horizontal dashed line are differentiating trends and below this line are homogenising trends.

The breakpoint model of the similarity scores for all sites (796 pairwise site and time-interval comparisons which make up the 105 site-to-site comparisons) (Figure 4-3) shows that similarity was close to 0.8 and declining between 4650 – 3150 cal. years BP, but it accelerated after 3150 cal. years BP towards the present.

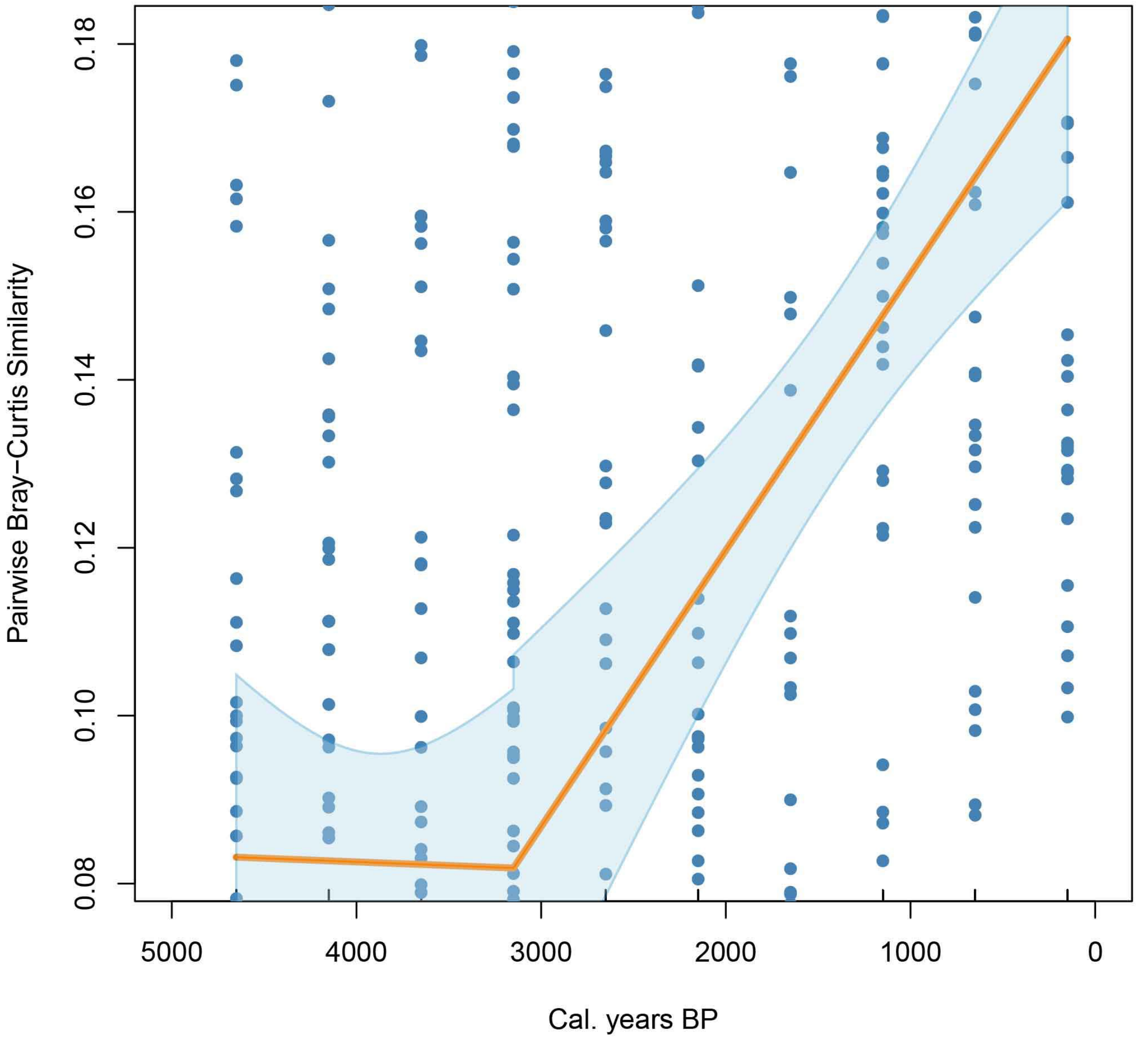

Figure 4-3 Breakpoint linear model showing pairwise Bray-Curtis similarity scores among all 15 sites on 13 islands, over the past 5000 years. The blue shaded area shows the 95% confidence interval. See Figure 5-18 for version displaying all datapoints.

4.5 Discussion

Given the large geographical area explored in this study (8300 km west to east), it is striking to find a ~3150-year long trend of biotic homogenisation across 13 islands. In addition, when incorporating the potential human dimension to our analysis, results showed that the biotic homogenisation process was enhanced when both locations were settled (Figure 5-17). As a whole, this information provides a strong indication that anthropogenic activities resulted in increased floristic similarity among the islands analysed.

4.5.1 Non-anthropogenic drivers of biotic homogenisation

Prior to 3150 cal. years BP there was no trend towards biotic homogenisation. Dynamics in pre-human settlement composition are likely related to natural drivers such as sea level change, hydroseral development of wetlands and lacustrine vegetation, and other disturbances (e.g., cyclones, droughts). Globally, drivers of change are known to have an impact on biotic homogenisation in numerous biotas and habitats, since these events can preferentially select from the species pool in similar ways across different communities. For example, drought conditions in artificial ponds have led to increased similarities among communities since extreme events act as filters to remove species intolerant to such conditions (Chase, 2007). Eutrophication of reservoirs and lakes has also been known to lead to the biotic homogenisation of diatoms, macrophytes, and invertebrate communities (Salgado et al., 2018; Wengrat et al., 2018). Scouring floods in the Scandinavian mountains have also led to the filtering of species within macroinvertebrate communities, since only those able to tolerate extreme conditions are successful in colonising disturbed environments (Lepori and Malmqvist, 2009). Finally, continued dispersal of pan-oceanic plant taxa should not be ignored as a contributing factor to biotic similarity on the islands. Indeed, on both western and eastern Pacific islands, bird dispersal of plant propagules is an important mechanism for both intra-island and internal island dispersal (see Gillespie et al., 2012 for discussion on plant dispersal mechanisms). Our results suggest that non-anthropogenic factors did not contribute to biotic homogenisation, at least in a detectable way.

4.5.2 Biotic homogenisation linked to novel anthropogenic drivers

Given that 12/15 of the sites analysed in this study are located on islands settled by humans ~3000 cal. years BP, it is perhaps unsurprising that biotic homogenisation began at around this time. The trend towards biotic homogenisation (Figure 4-3) is likely driven by novel anthropogenic drivers interacting with the ongoing natural processes previously mentioned. Within the novel drivers of change, burning as part of e.g., agricultural activities, introduction of non-native taxa, and extinctions or extirpations have been shown to have impacted island ecosystems (Nogué et al., 2017, Walentowitz, 2023). First, increased occurrence and intensity of disturbances is linked to anthropogenic modification of the islands' landscapes, for example, using slash and burn techniques (Nogué et al., 2017; Ravazzi et al., 2021; Strandberg et al., 2023b). It has also been shown that intense human impacts, such as urbanisation and intensively managed agroforestry plantations, can lead to an increase in globally distributed taxa and therefore biotic homogenisation (McKinney, 2006; Marconi and Armengot, 2020). Second, it is important to highlight that fossil pollen records from islands have also shown that non-native plant introductions increased within the last 1000 years, suggesting a potential long presence of widely distributed species (Walentowitz et al., 2023). For example, non-native species introduced to multiple islands by people, e.g., taro (*Colocasia esculenta*) may have contributed to the increased similarity of island ecosystems (Fall, 2010; Walentowitz et al., 2023). Lastly, there has been anthropogenically driven extinction or extirpation of native or endemic plant species from the Pacific islands e.g., *Pritchardia* (Prebble, 2008; Prebble and Dowe, 2008; Fall, 2010). The arrival of humans to Pacific islands is known to have coincided with many bird extinctions, (Sayol et al.; Steadman, 1995a; Steadman et al., 2002; Fall et al., 2007; Duncan et al., 2013). For example, it has been suggested that in Tonga, the decline of native birds and bats may have reduced the dispersal capabilities of many trees with large seeds such as *Calophyllum inophyllum*, *Cerbera odollam*, *Pouteria garberi*, *P. membranacea*, *Pometia pinnata*, *Syzygium quadrangulatum, S. richii*, and *Terminalia catappa* (Meehan et al., 2002; McConkey and Drake, 2006; Fall et al., 2007; McConkey and Drake, 2007). Rodent predation (introduced by both Polynesians and Europeans) on seeds is also a suggested cause for the decline of many taxa in Tonga and Rapa Nui (Easter Island) (Fall et al., 2007; Hunt, 2007). It is therefore possible that the increase in similarity between islands may have also been driven by a decrease in trees with large, animal-dispersed fruits (see Heinen et al., 2023). Finally, while human presence appears to be an important determinant of the magnitude of similarity among sites, island or site characteristics may also be significant. For example, among 30 Eastern Atlantic Ocean islands, topographically complex islands maintained native vegetation cover once colonised by humans, suggesting that topography constrains human impacts on biodiversity (Norder et al., 2020). Indeed, Lake Tagimaucia (Taveuni) and Lake Lanoto'o (Upolu) were some of the least biotically homogenised sites included in this analysis and are both located at high elevations, 680 and 760 m.a.s.l respectively (Figure 4-2). This may indicate that high elevation sites have escaped some of the most intense anthropogenic ecosystem modifications which are seen at some of the lower elevation sites, for example, Yacata (Yacata Island) and Finemui Swamp (Ha'avefa) which are located at 2 and 7 m.a.s.l. respectively.

4.5.3 Limitations and conclusions

It is important to highlight that pollen assemblages with larger sampling efforts may include more rare taxa, which may in turn make them appear to be biotically dissimilar from other sites. The mean rarefied pollen richness of records for which count data are available indicates that the sites with the richest pollen samples were Lake Tagimaucia (Taveuni), Bonatoa Bog (Viti Levu), and Waitetoke (Ahuahu) (Table 5-11). Lake Tagimaucia (Taveuni) was found to be the most biotically differentiated site compared to other sites, and it cannot be ruled out that the relatively high pollen diversity contributed to its apparent biotic differentiation.

On the other hand, the statistical method chosen may also influence observed levels of biotic similarity (e.g., Otto et al., 2020). The Bray-Curtis similarity index is strongly influenced by the most abundant taxa (McCune et al., 2002), and therefore rare taxa may have been somewhat underestimated in our analyses. Further, the use of pollen datasets excludes taxa that produce little (e.g., insect- pollinated plants) or no pollen, or pollen which is not well preserved in sediments. Another factor that is not controlled for in this study, and which may be important for explaining the observed trend, is the intensity of human impacts. Nevertheless, the almost complete unidirectional trend after 3150 cal. years BP across islands suggests the results are robust (Figure 4-3). Interestingly, sites on the same islands have different median Bray-Curtis similarity slope coefficients (e.g., Grande Terre in New Caledonia and Viti Levu in Fiji), which highlights the need for as many pollen records as possible to be included in similarity analysis such as this.

In this study we have, for the first time, tested whether South Pacific island vegetation became more similar after human arrival, and have found that it has. Some narratives point to biotic homogenisation being a largely contemporary issue exacerbated by increased commerce between islands (Castro et al., 2010), which in turn increases dispersal possibilities for plant taxa, but this analysis indicates that initial human settlement was a driver of biotic homogenisation. Future trends of biotic similarity will depend on the levels of continued human ecosystem modification, rates of non-native introductions, and rates of extinctions and extirpations. In turn, the simplification of ecosystems may reduce their resilience to future environmental stresses and increase their susceptibility to continued colonisation by non-native taxa. This study highlights the need for long, standardised palaeoecological records that can be integrated with modern ecological observations to understand modern island ecosystems more fully.

4.6 Acknowledgements

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4.7 Author contributions

NS, SN, AND MS designed the study. NS, MS, and AW analysed the data. NS and AW created the figures. All authors contributed to the writing of the manuscript.

Chapter 5 Discussion and conclusions

5.1 Overview

This chapter provides integration of the three case studies (Chapter 2, Chapter 3, and Chapter 4) and discussion on the usefulness and value of palaeoecological research conducted in this thesis for improving our knowledge of ecosystem recovery, resilience, and resistance. The research questions outlined at the start of the thesis (section 1.11) are discussed in detail, and a summary of the main findings and conclusions is also included and contain recommendations for future research.

5.2 Research questions, answered

5.2.1 What is the effect of relative sea-level fluctuations and volcanic eruption drivers on island vegetation change in Tonga?

In Chapter 2, results suggest that relative sea level fluctuations had a detectable impact on littoral, mangrove, successional, and wetland taxa within the study area. No impact from tephra falls was detected.

The in-depth botanical survey by Whistler (1992) allows for tropical pollen taxa to be classified into five habitat groups; littoral, mangrove, rainforest, successional/ disturbance, and wetland taxa. The five proportional vegetation groups from the four sites have been compared with two explanatory variables, relative sea level change and evidence of volcanic eruptions though tephra deposition, to understand if either environmental indicator drove changes in any of the vegetation groups.

Tephra deposition had no detectable impact on vegetation changes in Tonga throughout the Mid-Late Holocene (6000 – 0 cal. years BP) according to the analyses in Chapter 2. Reasons for this can be summarised as being because: 1) volcanic eruptions occurred too far away to exert impacts on vegetation, 2) the pollen sampling resolution was too low to detect potentially rapid changes and recoveries of vegetation, or 3) vegetation was resilient to tephra falls on this island and in this context. Conversely, relative sea level fluctuations had significant impacts on three of the sites, Ngofe Marsh (‘Uta Vava’u), Lotofoa Swamp (Foa), and Finemui Swamp (Ha’afeva) within four of the vegetation types, which were littoral, mangrove, successional/disturbance, and wetland taxa.

The results from Finemui Swamp, on the smallest island included in this study, Ha'afeva, shows that the island vegetation was the most sensitive to relative sea level changes, compared to the other islands investigated. This sensitivity was to relative sea level change and all vegetation groups, except rainforest taxa, had significant ($p<0.05$) relationships with relative sea level (Table 2-2). This may be because of the island or site characteristics, for example Ha'afeva was the smallest (135 ha) and lowest elevation island (14 m.a.s.l. maximum elevation) included in the study. While it is well established that small, low elevation island ecosystems are most at risk from future sea level rise (Bellard et al., 2014), it is still unclear if these island characteristics can fully explain the significant results found in the analyses.

5.2.2 What are the relative effects of the 1450s CE Kuwae eruption, ~1100 cal. years BP drying trend, and changing fire regime on vegetation?

In Chapter 3, the analyses show that the Kuwae eruption, climate transition (~1100 cal. years BP), and recent increased fire regime impacted vegetation turnover. However, the Kuwae eruption had the most lasting effect on vegetation.

In this chapter, ordination analysis was used to calculate vegetation changes from the Lake Emaotul pollen record. In particular, the use of detrended correspondence analysis (DCA) allowed for the calculation of vegetation turnover using the first DCA axis scores. Although both the Kuwae eruption and ~1100 cal. years BP climate transition led to vegetation turnover values of ~0.5 SD, the 1450s CE Kuwae volcanic eruption had a more lasting impact on vegetation turnover than the drying trend which initiated at ~1100 cal. years BP. For context, complete ecological turnover would be seen with 4 SD (Gauch and Gauch Jr, 1982; Correa-Metrio et al., 2014). Following the transition from wetter to drier climate at ~1100 cal. years BP, vegetation turnover partially recovered within ~70 years, however, following the Kuwae eruption, vegetation turnover increased again, reflecting a reduction in small trees and shrubs and an increase in grasses and vegetation did not regain its composition. Within the last ~85 years, enhanced local burning drove another increase in vegetation turnover up to 1.2 SD, and turnover values have not recovered yet. This period was characterised by a decrease in trees and an increase in herbs, grasses, and ferns.

5.2.3 Have South Pacific islands plant communities become more similar or dissimilar during the past 5000 years?

In Chapter 4, the analyses show that island flora similarity was low prior to human arrival but increased after ~3150 cal. years BP, synchronous with human arrival to 12 of the 15 locations studied.

It is well established that natural disturbances, such as, droughts, floods, treefalls, and human impacts, including the introduction of non-native species, and extinction or extirpation of native species, can increase biotic homogenisation (Connell, 1978; McKinney, 2006; Chase, 2007; Lepori and Malmqvist, 2009; Carvalheiro et al., 2013). The aim of Chapter 4 was to investigate trends in similarity and identify any periods of accelerated or decelerated change.

Fifteen pollen records from 13 South Pacific islands were analysed to investigate trends in similarity. Application of a breakpoint model to pairwise Bray-Curtis similarity scores shows that this trend towards homogenisation began at ~3150 cal. years BP, which is synchronous with human settlement of many Southwestern Pacific islands. Higher elevation sites may have escaped some of the impacts of human driven biotic homogenisation perhaps because human impacts were mostly focussed on low elevation and coastal areas (Figure 4-2).

Further work is required to better understand the importance of island characteristics for predicting levels of biotic similarity. For example, one improvement would be to increase the number of study locations included within the analyses to obtain more precise results and identify potential outliers. The effect of site or maximum island elevation, island geology, island area, isolation, climate, and human populations could also be tested in the future to better understand the roles of these factors in determining biotic similarity.

5.3 Recovery, resilience, and resistance

Palaeoecological data has previously proven useful for understanding and estimating recovery rates (e.g., Cole et al., 2014; Matthews-Bird et al., 2017; Montoya et al., 2021), resilience (e.g., Tinner and Ammann, 2005; Virah-Sawmy et al., 2009; Hamilton et al., 2018; Buma et al., 2019; Morel and Nogué, 2019), and turnover (Nogué et al., 2021). What follows is an assessment of the usefulness and value of the palaeoecological data from this thesis (Chapter 2, Chapter 3, and Chapter 4) to guide knowledge on drivers of ecosystem change, recovery, resilience, and resistance.

To date, there is generally more known about the ecosystem responses and recovery rates of vegetation in Tonga than Vanuatu. For example, in Tonga ecosystem responses and recovery rates have been investigated following a tropical cyclone (Franklin et al., 2004) and following abandonment of agricultural land (Franklin et al., 1999; Franklin, 2003). However, responses to drivers of change, such as relative sea level change and volcanic eruptions were less clear.

Since some disturbances, such as volcanic eruptions, may occur more infrequently than other disturbances for example, tropical cyclones (see Table 1-2), palaeoecological records can be valuable archives of the unknown responses to and recoveries from these events. Additionally, palaeoecological records can uncover long-term responses to change, such as responses to relative sea level changes.

In Chapter 2, two drivers of change, relative sea level, and tephra falls, were compared with proportional vegetation habitat groups, and both significant and non-significant relationships were uncovered. For example, tephra falls had no significant impact on any vegetation types. One explanation for these non-significant results is that vegetation types are resilient (sensu Holling, 1973) to changes from tephra deposition. Vegetation may have also recovered so quickly that the responses were not captured within the relatively low-resolution pollen records (i.e., engineering resilience). However, it is clear that additional research is needed since other explanations for the non-significant tephra results, such as distance from eruptions, cannot be ruled out. The higher pollen sampling resolution in Chapter 3 did however uncover information about vegetation responses to a volcanic eruption. Additionally, the tephra layer identified as being from the Kuwae eruption also provided information about the distance from the eruption.

Recovery times of specific taxa, and turnover following disturbances on Efate, Vanuatu are discussed in Chapter 3. This information, generated using palaeoecological methods, is of great value given that there is currently little known about the responses of vegetation to different environmental disturbances in Vanuatu. For example, the Lake Emaotul pollen record (Chapter 3) has shown that following a volcanic eruption and an increase in burning regime, there was a decline in small trees and shrubs and an increase in grasses. These responses may be expected to occur following future environmental disturbances. Additionally, palaeoecological data may be our only source of information on recovery rates which exceed timescales of modern observations. In Vanuatu, there is currently little empirical data available on vegetation recovery rates, turnover, and resilience, and palaeoecological records, such as the one presented in Chapter 3 along with others from the region (Hope and Spriggs, 1982; Wirrmann et al., 2011; Combettes et al., 2015), are a somewhat rare and valuable source of information.

The analyses of 15 sites across 13 islands within Chapter 4 shows an acceleration in biotic homogenisation at ~3150 cal. years BP synchronous with the human settlement of many Southwestern Pacific islands (i.e., Vanuatu, Fiji, Samoa, and Tonga).In addition, similarity scores were highest when both island pairs had been settled by humans (Figure 5-17). It is clear that early human actions have contributed to biotic homogenisation of vegetation on South Pacific islands (Chapter 4), however, further work is required to understand potential relationships between biotic homogenisation and site and island characteristics. It still remains unclear whether some ecosystems are more resilient to becoming biotically homogenised due to biogeographical factors, spatial heterogeneity, or diversity. Additionally, it is unclear if a lack of resilience leads to enhanced biotic homogenisation or if biotic homogenisation is the cause of reduced reliance or if both statements are true.

5.4 Limitations and future research

In this body of work, two palynological investigations of vegetation response to environmental change have been carried out. However, a hindrance to this process has been the lack of pollen keys and atlases from the Pacific region. Although some pollen reference slides for this region exist in the collection of John Flenley at The University of Hull, many of these slides are dried out and pollen grains are obscured. Future work would benefit from the digitisation of this resource to an online database such as The Global Pollen Project (Martin and Harvey, 2017) or the Australian Pollen and Spore Atlas website (ANU, 2007). This would improve the accessibility of the pollen reference collection and to lead to the identification of reference slides which need to be replaced.

In addition to this, little is known about the taphonomy of many pollen taxa in the South Pacific, which has hindered efforts to estimate the relationship of pollen concentrations or influx to vegetation cover or proximity. For example, it still remains unclear whether differences in pollen preservation between taxa may have contributed to patterns of biotic similarity (Chapter 4). Future research on pollen dispersal, for example the use of pollen traps, would be beneficial and assist palynologists with the quantitative reconstruction of past vegetation cover on Pacific islands, such as has been attempted in other parts of the world from relatively large sites using the REVEALS model (Regional Estimates of VEgetation Abundance from Large Sites) and relatively smaller sites using the LOVE model (LOcal Vegetation Estimate) (Sugita, 2007).

It is well known that pollen from several plant families is difficult to identify to genus and species level, for example, Brassicaceae, Caryophyllaceae, Cyperaceae and Poaceae (Fægri and Iversen, 1989). The application of sedimentary DNA (*seda*DNA) may be able to improve taxonomic resolution. For example, *seda*DNA of lake samples can identify more species than other palaeoecological methods (Alsos et al., 2015). *Seda*DNA can also allow for the identification of important plant taxa which are difficult to detect, or less well detected in pollen samples (Sjögren et al., 2017). A recent publication has also shown that *seda*DNA can be successfully applied at low latitude, i.e. Eastern Africa (high altitude), sites despite issues with temperature degradation (Boessenkool et al., 2014).

In addition to taxonomic resolution, sampling resolution has also been an important factor in the detection of responses to vegetation change. For example, volcanic eruptions were found to have no significant impacts on vegetation groups in Tonga (Chapter 2) and one explanation for this was that pollen sampling resolutions may have been too low to detect relatively rapid vegetation responses or recoveries following disturbances.

The strategy for pollen sampling from the Lake Emaotul cores (Chapter 3) aimed to overcome the resolution issue by increasing the pollen sampling resolution to every 1 cm (representing ~ 5 years) before and after the tephra layer. The increased sampling resolution allowed for the observation of short-term changes which were potentially missed in the Tonga study (Chapter 2). Therefore, one of the key recommendations of this thesis is to increase sampling resolution after disturbance events to better understand vegetation response and to estimate recovery rates.

In Chapter 2 the classification of pollen taxa into habitat groups was achieved thanks to the comprehensive botanical survey by Whistler (1992). However, this publication is now 30 years old and a new botanical survey of the Tongan islands is required to detect some of the changes which have occurred over the last 30 years. The most comprehensive botanical survey of Efate and Vanuatu comes from Mueller-Dombois and Fosberg (1998) and an online herbarium for Vanuatu is also available (Vanuatu Department of Forestry, 2021). Future studies of Tonga and Vanuatu would benefit from updated botanical surveys which reflect the current vegetation cover of the islands and recent human modification of land use. This would allow for the identification of recent non-native introductions and recent extirpations and extinctions. Additionally, the threatened or non-threatened status of many Pacific plants is still largely unknown. It is estimated that there are 30,000 plant species on Pacific islands, however, only around 3% have been surveyed (Pippard, 2009). Of the plants which have been surveyed, 57% have been assessed as threatened (Pippard, 2009). Pollen records, such as those presented here, can shed light on when these taxa began to decline and the native or non-native status of plants (e.g., Nogué et al., 2017).

However, without a comprehensive survey of plants and conservation status, fossil pollen datasets cannot reach their full potential to inform conservation strategies.

This thesis has highlighted the usefulness of legacy data (e.g. Flenley et al., 1991; Flenley et al., 1999) in a region where pollen records are scarce. Digitisation of pollen diagrams is a useful method of acquiring legacy data (e.g., Chapter 2 and Chapter 4). However, issues with digitising pollen records are: 1) only having access to percentage diagrams rather than count data, 2) missing taxa which may have been omitted from the original pollen diagrams due to low abundance, and 3) limitations associated with age-depth models. For example, in the study by Flenley et al. (1999) only one radiocarbon date was obtained for the 293 cm long sequence of Lotofoa Swamp cores, and age uncertainties are therefore high (mean ± 800 years for Lotofoa Swamp and ± 650 years for Finemui Swamp) whereas errors for Ngofe Marsh (Chapter 2), a more recent study with a greater density of radiocarbon dates, were much smaller (± 250 years).

In Chapter 4, one explanation for the increase in taxonomic similarity ~3150 cal. years BP (Figure 4-3) is a human driven change in plant dispersal syndromes. It is well known that the arrival of humans to South Pacific islands coincided with the extinction of many native animals and introduction of non-native animals (Steadman, 1993; Steadman, 1995b; Steadman et al., 2002) but it is unclear to what degree human actions modified plant dispersal pathways (but see Fall et al., 2007 for discussion). Future assessment of plant traits, for example diaspore (mostly fruits and seed) dispersal syndromes, based on fossil pollen assemblages, may reveal the answer to this question. For example, the dispersal syndromes of European plants which have become naturalised around the world has shown that epizoochorous (dispersed by attaching to animals) and thalassochorous (sea current dispersed) plants are more likely to become naturalised than anemochorous (wind) and endozoochorous (ingested by animals) dispersed plants (Moyano et al., 2022). Plant dispersal syndromes become less important when considering economic crops, since humans purposefully disperse these plants (Moyano et al., 2022). However, there is currently no database of South Pacific plant dispersal syndromes although plant trait databases containing descriptive information about fruits and seeds exists, for example BIEN (Botanical Information and Ecology Network) (Enquist et al., 2016). The LEDA-Traitbase includes information on dispersal syndromes but data is mostly limited to NW Europe (Kleyer et al., 2008). Future work could focus on identifying morphological traits of plant diaspores which would allow us to better understand how South Pacific plant dispersal syndromes have changed over time using fossil pollen records.

The timing of human arrival to Tonga was investigated through the analysis of faecal stanols (appendix E page 147). However, faecal sterol analyses from the Ngofe Marsh cores did not result in a positive identification of human or porcine faecal matter (5β-stanol ratio >0.7). Yet two samples possibly containing faecal matter were identified (5β-stanol ratio >0.3) (Figure 5-19). Future research to identify the arrival of humans and other higher mammals in the South Pacific could be performed at higher resolutions, for example, the biomarker analysis conducted on the Ngofe Marsh cores was around one sample per every ~375 years. Increased sampling resolution would increase the likelihood of identifying trends and variations in the 5β-stanol record, for example, where human or pig presence was transient (e.g., Argiriadis et al., 2018; Sear et al., 2020).

Future work could also use a combination of stanol and bile acid analyses to distinguish between higher mammals. For example, while 5β-stanols (and other stanols) can often differentiate between omnivore (e.g., humans) and ruminants (e.g., cows and sheep) (e.g., D’Anjou et al., 2012), 5β-stanols alone cannot be used to distinguish between human and porcine derived faecal matter (Bull et al., 2002). However, the combined use of stanol and bile acid analysis can differentiate between human and porcine faecal matter (Bull et al., 2002) and would help to pinpoint the timing of human arrival and introduction of pigs to South Pacific islands which in turn would help to disentangle human and abiotic disturbances or the onset of biotic homogenisation.

5.5 Conclusions

The main aim of this thesis was to understand how periods of environmental disturbances such as climate variability, fire regime change, human arrival, RSL change, and volcanic eruptions have altered South Pacific islands' ecosystems. In addition, this thesis also provides the first analysis of biotic similarity within the South Pacific using fossil pollen records. This spatial-temporal approach and the use of both fossil pollen and chironomids, in conjunction with environmental indicators such as tephra analysis has revealed the following findings.

1. Climate variability, fire regime change, human arrival, RSL change, and volcanic eruptions have been identified as drivers of vegetation change.
2. Ecosystems do not all respond in the same way to disturbances and physical island or site characteristics are likely key to understanding responses.
3. Relative sea level change is likely an important driver of vegetation change in Tonga and impacted littoral, mangrove, successional/ disturbance, and wetland vegetation at Ngofe Marsh, Lotofoa Swamp, and Finemui Swamp.
4. Volcanic eruptions have been identified as drivers of vegetation change in one case, the 1450's Kuwae eruption.
5. A shift from wetter to drier climate in Vanuatu ~1100 cal. years BP had a detectable impact on vegetation and turnover.
6. Enhanced fire regime had a detectable impact on vegetation composition and turnover and led to an increase in herbaceous taxa and a decline in forest taxa.
7. A progressive trend towards biotic homogenisation was identified to have begun at ~3150 cal. years BP synchronous with human settlement of many Southwestern Pacific islands.
8. According to the analysis in Chapter 4, human presence is likely a key driver of biotic homogenisation of plants communities on South Pacific islands.
9. Relatively high-resolution pollen sampling strategies may be required to identify vegetation responses and recovery times following disturbances.
10. The improvement of botanical surveys, improved pollen identification resources, and the use of additional proxies such as *seda*-DNA have the potential to enhance future studies of vegetation change in South Pacific islands.
11. Faecal biomarker analysis may be helpful for identifying the timing of human arrival to Pacific islands especially when used in combination with bile acid analysis.

Appendix A Previous palaeoecological studies from the Pacific region

Table 5-1 Previous palaeoecological studies using fossil pollen on Pacific islands.

Country	Group/ Territory name	Island	Site name	Type	Sub region	Latitude	Longitude	Island type (Nunn et al., 2016)	Published in
Federated States of Micronesia	Caroline Islands	Kosrae	Israc		Melanesia	5.163	162.5574	Volcanic high island	Ward (1988)
Federated States of Micronesia	Caroline Islands	Kosrae	Yewal		Melanesia	5.17	162.585	Volcanic high island	Ward (1988)
Federated States of Micronesia	Caroline Islands	Kosrae	Innem Basin		Melanesia	5.197	163	Volcanic high island	Ward (1988)
New Zealand	Cook Islands	Rarotonga	Karekare	Swamp	Polynesia	-21.216	-159.74	Composite high island	Fujiki et al. (2014)
New Zealand	Cook Islands	Atiu	Roto	Lake	Polynesia	-20.0098	-158.123	Composite high island	Parkes (1994)

New Zealand	Cook Islands	Atiu	Roto	Lake	Polynesia	-20.0085	-158.122	Composite high island	Prebble unpublished work
New Zealand	Cook Islands	Mangaia	Veitatei	Swamp	Polynesia	-21.9447	-157.933	Composite high island	Ellison (1994); Kirch and Ellison (1994)
New Zealand	Cook Islands	Mangaia	Tamarua	Swamp	Polynesia	-21.95	-157.913	Composite high island	Ellison (1994); Kirch and Ellison (1994)
Chile	Easter Island	Easter Island	Rano Kau	Lake	Polynesia	-27.1866	-109.436	Volcanic high island	Flenley et al. (1991)
Chile	Easter Island	Easter Island	Rano Kau	Lake	Polynesia	-27.1866	-109.436	Volcanic high island	Butler and J (2001); Butler and Flenley (2010)
Chile	Easter Island	Easter Island	Rano Kau	Lake	Polynesia	-27.1866	-109.436	Volcanic high island	Horrocks et al. (2012)
Chile	Easter Island	Easter Island	Rano Kau	Lake	Polynesia	-27.1866	-109.436	Volcanic high island	Horrocks et al. (2013)
Chile	Easter Island	Easter Island	Rano Kau	Lake	Polynesia	-27.1866	-109.436	Volcanic high island	Butler et al. (2004)

Chile	Easter Island	Easter Island	Rano Aroi	Swamp	Polynesia	-27.0937	-109.374	Volcanic high island	Margalef et al. (2014)
Chile	Easter Island	Easter Island	Rano Aroi	Swamp	Polynesia	-27.0937	-109.374	Volcanic high island	Horrocks et al. (2015)
Chile	Easter Island	Easter Island	Rano Aroi	Swamp	Polynesia	-27.0937	-109.374	Volcanic high island	Rull et al. (2015)
Chile	Easter Island	Easter Island	Rano Aroi	Swamp	Polynesia	-27.0937	-109.374	Volcanic high island	Peteet et al. (2003)
Chile	Easter Island	Easter Island	Rarauku Lake	Lake	Polynesia	-27.1218	-109.289	Volcanic high island	Dumont et al. (1998)
Chile	Easter Island	Easter Island	Rarauku Lake	Lake	Polynesia	-27.1218	-109.289	Volcanic high island	Mann et al. (2008)
Chile	Easter Island	Easter Island	Rarauku Lake	Lake	Polynesia	-27.1218	-109.289	Volcanic high island	Cañellas-Bolta et al. (2012); Cañellas-Bolta et al. (2014); Cañellas-Bolta et al. (2016)
Chile	Easter Island	Easter Island	Rano Kau/ Rano Aroi/	Swamp and lake	Polynesia	Many	Many	Volcanic high island	Flenley and King (1984)

			Rano Ranaku						
Republic of Fiji		Viti Levu	Lake Tagamaucia	Lake	Melanesia	-16.8018	-179.915	Composite high island	Southern (1986); Hope (1996); Hope et al. (2009)
Republic of Fiji		Totoya	Mangrove sites (six)	Infilled estuaries	Melanesia	-18.9336	-179.852	Volcanic high island	Cole (1996); Clark and Cole (1997); Hope et al. (2009)
Republic of Fiji		Yacata	Yacata Pond	Infilled karst	Melanesia	-17.2585	-179.511	Composite high island	Hope et al. (2009)
Republic of Fiji		Kaibu	Soleve	Infilled karst	Melanesia	-17.2585	-179.511	Composite high island	Hope et al. (2009)
Republic of Fiji		Mago	Mudflats	Infilled karst	Melanesia	-17.4445	-179.149	Composite high island	Latham et al. (1983); Hope et al. (2009)
Republic of Fiji		Viti Levu	Cavaure	Mangrove karst	Melanesia	-17.3418	-178.979	Composite high island	Latham et al. (1983); Hope et al. (2009)

Republic of Fiji		Lakeba	Nabuni	Valley fill	Melanesia	-18.2121	-178.776	Composite high island	Hope et al. (2009)
Republic of Fiji		Lakeba	Waitubu	Valley fill	Melanesia	-18.2121	-178.776	Composite high island	Hope et al. (2009)
Republic of Fiji		Viti Levu	Volivoli Lagoon	Sand plain lagoon	Melanesia	-18.1239	177.3753	Composite high island	Hope et al. (2009)
Republic of Fiji		Viti Levu	Doge Doge Swamp	Sedge swamp	Melanesia	-18.1677	177.5521	Composite high island	Hope et al. (2009)
Republic of Fiji		Viti Levu	Navatu	Infilled estuary	Melanesia	-17.4314	177.8046	Composite high island	Hope et al. (2009)
Republic of Fiji		Viti Levu	Vunimoli	Infilled estuary	Melanesia	-18.2491	178.002	Composite high island	Hope et al. (2009)
Republic of Fiji		Viti Levu	Wainisavulevu	Buried peat	Melanesia	-17.7306	178.0182	Composite high island	Southern (1986); Hope et al. (2009)
Republic of Fiji		Viti Levu	Nadrau Swamp	Sedge swamp	Melanesia	-17.7306	178.0182	Composite high island	Southern (1986); Hope et al. (2009)
Republic of Fiji		Viti Levu	Meli Meli	Infilled estuary	Melanesia	-18.1819	178.194	Composite high island	Southern (1986); Hope et al. (2009)

Republic of Fiji		Viti Levu	Bonatoa Bog	Infilled estuary	Melanesia	-18.0667	178.5344	Composite high island	Southern (1986); Hope et al. (1999); Hope et al. (2009)
Republic of Fiji		Viti Levu	Raralevu	Infilled estuary	Melanesia	-18.0667	178.5344	Composite high island	Southern (1986); Hope et al. (2009)
Republic of Fiji		Vanua Levu	Sari Swamp	Infilled estuary	Melanesia	-16.6173	179.5383	Volcanic high island	Hope et al. (2009)
French Polynesia		Raivavae	Raririua	Marsh	Polynesia	-23.8682	-147.679	Volcanic high island	Prebble et al. (2019)
French Polynesia		Rapa	Tukou	Marsh	Polynesia	-27.604	-144.352	Volcanic high island	Prebble et al. (2012); Prebble et al. (2019)
USA	Mariana Islands	Guam	Tipalao Marsh	Marsh	Micronesia	13.45	144.6333	Composite high island	Athens and Ward (1995)
USA	Mariana Islands	Guam	Lost Water Marsh	Marsh	Micronesia	13.45	144.6333	Composite high island	Ward (1994) unpublished work featured in Hope

									et al. (1999)
USA	Mariana Islands	Tinian Island	Lake Hagoi	Lake	Micronesia	14.96667	145.6333	Limestone high island	Athens and Ward (1999)
French Polynesia	Marquesas	Nuku Hiva	Tovi'I Marsh	Swamp	Polynesia	-8.87404	-140.146	Volcanic high island	Allen et al. (2011)
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Fournier Swamp	Swamp	Melanesia	-21.5866	165.3448	Continental island	Wirrmann et al. (2011)
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Lac Saint Louis	Swamp	Melanesia	-22.2327	166.5548	Continental island	Stevenson and Dodson (1995); Stevenson (2004)
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Plum	Swamp	Melanesia	-22.2667	166.6167	Continental island	Stevenson et al. (2001)
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Grand Lac	Lake	Melanesia	-22.2645	166.911	Continental island	Wirrmann et al. (2006)
French Overseas	New Caledonia	New Caledonia (La	Lake Emeric	Lake	Melanesia	-22.2844	166.9814	Continental island	Hope and Pask (1998)

Territory		Grande Terre)							
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Xere Wapo	Lake	Melanesia	-22.2864	166.9879	Continental island	Stevenson and Hope (2005)
French Overseas Territory	New Caledonia	New Caledonia (La Grande Terre)	Lake Suprin	Lake	Melanesia	-22.2873	166.9918	Continental island	Hope and Pask (1998)
Australia	Norfolk Island	Norfolk Island	Kingston Common		-	-29.02	167.59	-	Macphail et al. (2001)
Samoa		Upolu	Lanoto'o	Lake	Polynesia	-13.9093	-171.828	Volcanic high island	Parkes (1994)
Samoa		Upolu	Lanoto’o		Polynesia	-13.9093	-171.828	Volcanic high island	Gosling et al. (2020)
French Polynesia	Society Islands	Mo'orea	4 locations	Archaeological	Polynesia	-17.4851	-149.84	Volcanic high island	Kahn et al. (2015b)
French Polynesia	Society Islands	Mo'orea	Lake Temae	Lake	Polynesia	-17.4849	-149.769	Volcanic high island	Stevenson et al. (2017)
French Polynesia	Society Islands	Mo'orea	Lake Temae	Lake	Polynesia	-17.4849	-149.769	Volcanic high island	Parkes (1994)

French Polynesia	Society Islands	Tahiti	Vaifanaumire	Swamp	Polynesia	-17.6333	-149.533	Volcanic high island	Prebble et al. (2016)
French Polynesia	Society Islands	Tahiti	Vaihiria	Lake	Polynesia	-17.6803	-149.417	Volcanic high island	Parkes et al. (1992)
Solomon Islands		Guadalcanal	Lauhutu Swamp	Swamp	Melanesia	-9.5	160.0833	Composite high island	Haberle (1996)
Solomon Islands		Guadalcanal	Mela Swamp	Swamp	Melanesia	-9.5	160.0833	Composite high island	Haberle (1996)
Tonga		Tongatapu	Folaha Swamp	Swamp	Polynesia	-21.1833	-175.183	Reef island	Ellison (1989)
Tonga		‘Eua	Ano’a’pepe		Polynesia	-21.4008	-174.918	Limestone high island	Unpublished work mentioned in Fall (2010)
Tonga		Ha’afeva	Finemui Swamp	Swamp	Polynesia	-19.9489	-174.712	Limestone low island	Flenley et al. (1999)
Tonga		Foa	Lotofoa Swamp	Swamp	Polynesia	-19.7467	-174.308	Limestone low island	Flenley et al (1999)
Tonga		Vava’u	Ngofe Marsh	Marsh	Polynesia	-18.6647	-174.044	Limestone high island	Unpublished work mentioned in Fall (2010)

Tonga		Vava’u	Avai’o’vuna Swamp	Swamp	Polynesia	-18.698	-173.988	Limestone high island	Fall (2005)
Vanuatu		Efate	Emaotfer	Swamp	Melanesia	-17.7859	168.4037	Composite high island	Wirrmann et al. (2011)
Vanuatu		Efate	Emaotfer	Swamp	Melanesia	-17.7859	168.4037	Composite high island	Combettes et al. (2015)
Vanuatu		Aneityum	Anawau	Swamp	Melanesia	-20.2234	169.7692	Volcanic high island	Hope and Spriggs (1982)
Federated States of Micronesia	Yap		Fool Swamp	Swamp	Micronesia	9.48841	138.0788	Composite high island	Dodson and Intoh (1999)
Federated States of Micronesia	Yap		Thool Swamp	Swamp	Micronesia	9.53748	138.165	Composite high island	Dodson and Intoh (1999)

Appendix B Supplementary information for chapter 2

Figure 5-1 The location of the Ngofe Marsh core. Imagery date 29th April 2017 (Google Earth Pro, 2023).

Ngofe Marsh core stratigraphy

The maximum age for the sequence of the Ngofe Marsh core sequence is *c.*7700 cal. years BP at 664 cm depth. The sedimentary sequences consist of silty clay between 690−630 cm (−7340 cal. years BP), clay between 630−617 cm (7340− 7210 cal. years BP) clay, and gyttja between 617−206 cm (7210−2040 cal. years BP). Above the gyttja is a layer of reed peat between 206−20 cm (2040−160 cal. years BP).

Pollen preparation methodology

A solution of 10% HCl was used to dissolve the *Lycopodium* tablets and any carbonates. To disaggregate organic material, the samples were boiled in 10% KOH for 10 min. The samples were passed through two nested sieves, 180 µm and 10 µm. The fraction ≥10 µm was retained for pollen analysis and the >180 µm fraction was retained for macrocharcoal analysis. The samples were boiled with 40% HF for

30 minutes to remove silicates. Acetolysis was achieved through the removal of water using glacial acetic acid (CH_3COOH), and then a solution of 9:1 acetic acid to H_2SO_4. The samples were boiled in the acetolysis solution for 3 minutes and the reaction was stopped with glacial acetic acid. Some samples with high organic content were treated with a second round of acetolysis to further remove organics. The slides were stained with safranin and mounted with glycerine jelly (Bennett and Willis, 2001).

Tephra geochemistry

Subsamples from tephra layers T1-T5 were washed clean with deionised water and the coarsest fraction of grains (~63–125 μm) were picked out by hand. These grains were then mounted in epoxy resin and cut and polished. The samples were then sputter-coated in carbon using a JXA8530F Hyperprobe at the University of Auckland. Points were analysed using an accelerating voltage of 15 kV and a 2-Na electron beam current. Then a 10-μm defocused beam was utilised to reduce Na loss. A 5-μm diameter beam was used for smaller grains. The analysis was concluded with a 10-s peak and 10-s background dwell times for all elements. Finally, to test the migration of Na, some analyses were collected in duplicate 1-s accumulated peak measurements with 1-s dwell time during the second measurement. Accumulated Na measurements indicate that post-measurement correction of the migration of Na was not necessary. The calibration of the analyses and quality check were done against secondary glass standards: ATHO-G (MPI-DING), BCR-2G, (USGS) and VG-568 (NMNH 72854).

Table 5-2 Site and island characteristics. Maximum island elevation, island area, and island type come from Nunn et al. (2016).

Site name	**Island**	**Island size (ha)**	**Latitude (º)**	**Longitude (º)**	**Site elevation (m a.s.l.)**	**Wetland area (~m2)**	**Maximum island elevation (m a.s.l)**	**Distance to coast (m)**	**Vegetation description**	**Island type**	**Reference**

Avai’o’vuna Swamp	Pangaimotu/ ‘Uta Vava’u	12720	-18.6971	-173.9887	1.5	50	88	430	Cyperaceae wetland	Limestone high island	Fall (2005)
Finemui Swamp	Ha’afeva	135	-19.9489	-174.712	7	4,000	14	500	Wetland dominated by *Persicaria* cf. *glabra*	Limestone low island	Flenley et al. (1999)
Lotofoa Swamp	Foa	1572	-19.7467	-174.308	3	125,000	24	880	Wetland dominated by *Ludwigia octovalvis*, herbaceous, and shrubby vegetation	Limestone low island	Flenley et al. (1999)
Ngofe Marsh	Uta’ Vava’u	12720	-18.6647	-174.044	4	105,000	88	800	Cyperaceae wetland	Limestone high island	This study

Table 5-3 Radiocarbon dates from Ngofe Marsh. Dates were provided by SUERC NERC Radiocarbon Laboratory. *Outlier (not included in age-depth model).

Lab ID (SUERC)	**Lab ID (Southampton)**	**^{14}C age**	**Error (years)**	**Depth (cm)**
NA	surface	-67	5	0
SUERC-92960	Ngo100	1204	37	97
SUERC-92961	Ngo201	1843	37	188
SUERC-95672	Ngo334*	3980	37	377
SUERC-95671	Ngo387	3239	36	389
SUERC-92970	Ngo448	4776	36	441
SUERC-92971	Ngo660	6898	37	664

Table 5-4 Description of the explanatory variables included in the analysis for each site. Relative sea-level (RSL) and tephra layers. All calibrated years are extracted from the age-depth models.

Study sites	**Explanatory variables (Drivers of change)**
Ngofe Marsh (‘Uta Vava’u Island, Vava’u Group)	RSL change and four tephra layers. The tephra layers are named: T2 (~3990 cal. years BP, 7 cm thick), T3 (~3680 cal. years BP, 13 cm thick), T4 (~1370 cal. years BP, 2 cm thick), and T5 (~371 cal. years BP, 13 cm thick) (Fig. 2).

Avai’ovuna Swamp (Pangaimotu Island, Vava’u Group)	RSL change and tephra layers from Ngofe Marsh.
Lotofoa Swamp (Foa Island, Ha’apai Group)	RSL change and evidence of a volcanic eruption ~ 3840 cal. years BP (~50 cm thick).
Finemui Swamp (Ha’afeva Island, Ha’apai Group)	RSL change and evidence of volcanic eruptions ~3460 and ~5210 cal. years BP (~9 and ~37 cm thick, respectively)

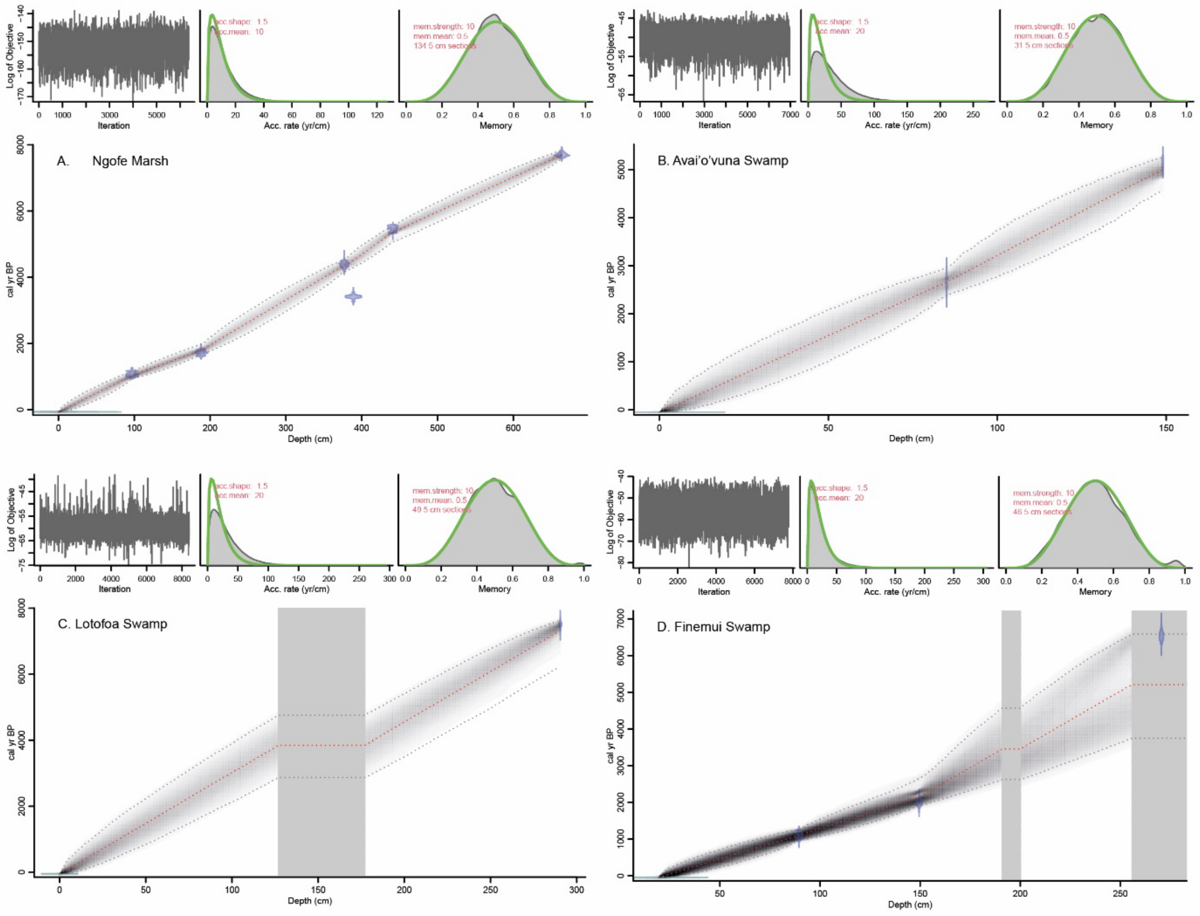

Figure 5-2 Age-depth model for a) Ngofe Marsh, b) Avai’o’vuna Swamp, c) Lotofoa Swamp and d) Finemui Swamp.

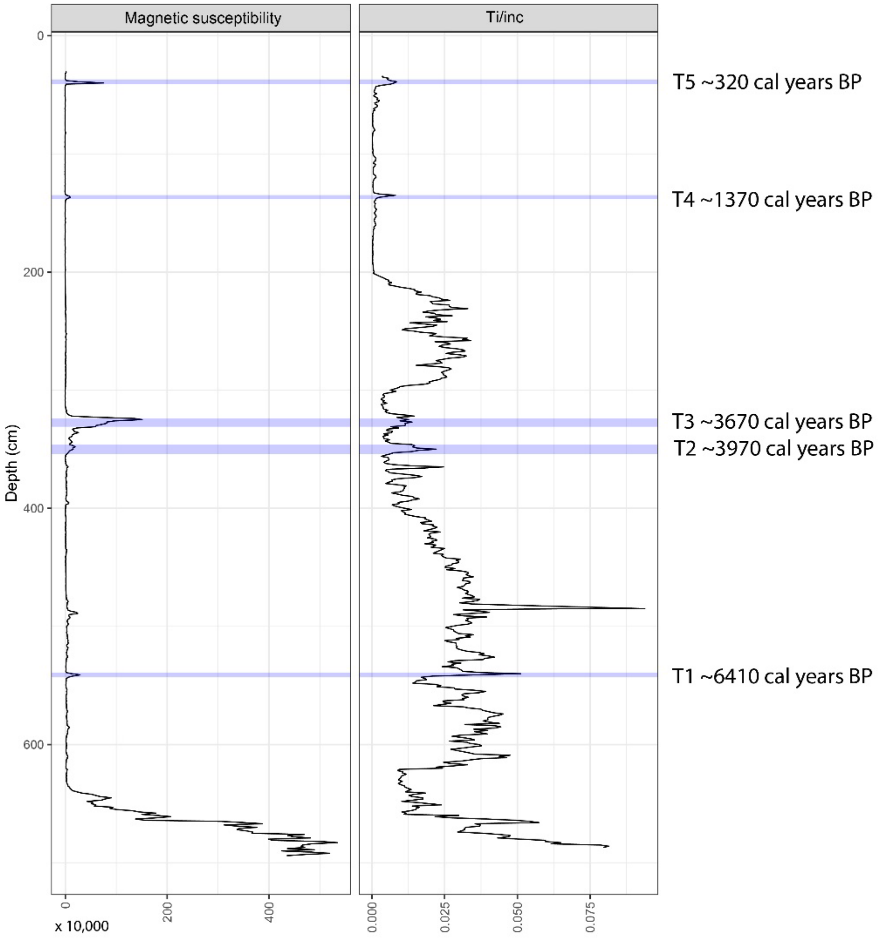

Figure 5-3 Magnetic susceptibility (Vol. Susc.Meas. in SI) and Ti/incoherent scatter for Ngofe Marsh. Blue shading indicates confirmed tephra layers labelled T1-T5. The ages are inferred from the age-depth model.

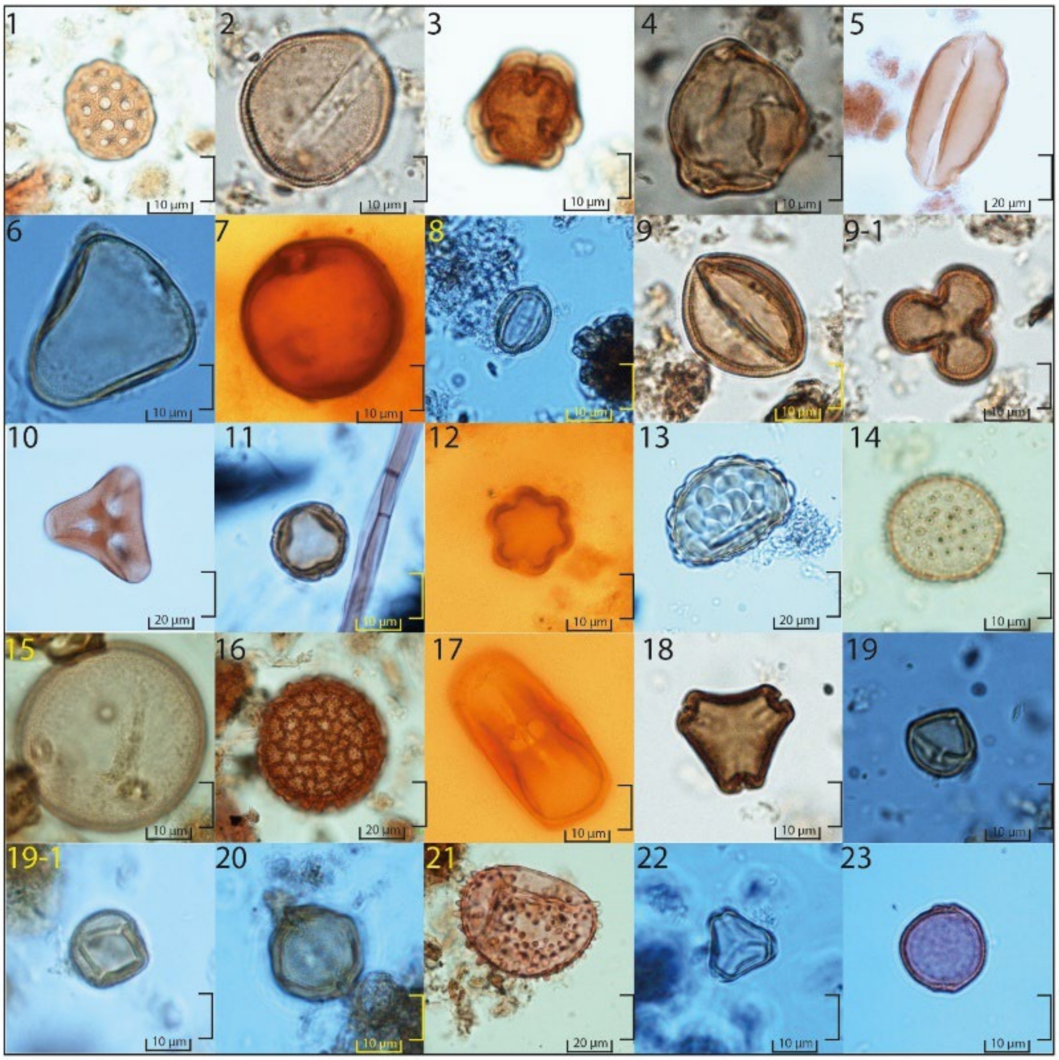

Figure 5-4 Key pollen and spores from Ngofe Marsh, Tongan names are in brackets. 1. Amaranthaceae, 2. Arecaceae type-2, 3. *Bischofia*, 4. *Casuarina* (toa), 5. *Cocos nucifera* (niu), 6. Cyperaceae, 7. *Dysoxylum* (moʻota), 8. *Eleaocarpus* (maʻamaʻalava), 9. *Homalanthus* (fonua mamala), 10. Loranthaceae, 11. *Macaranga* (loupata), 12. Melastomataceae, 13. *Microsorum*, 14. *Pandanus* (fafa), 15. Poaceae, 16. Polygonaceae, 17. *Pouteria*, 18. Rhamnaceae, 19. Rhizophoraceae, 20. *Rhus* (tavahi), 21. *Stenochlaena* (pasivaka), 22. *Syzygium* (fekika), 23. *Trema* (mangele).

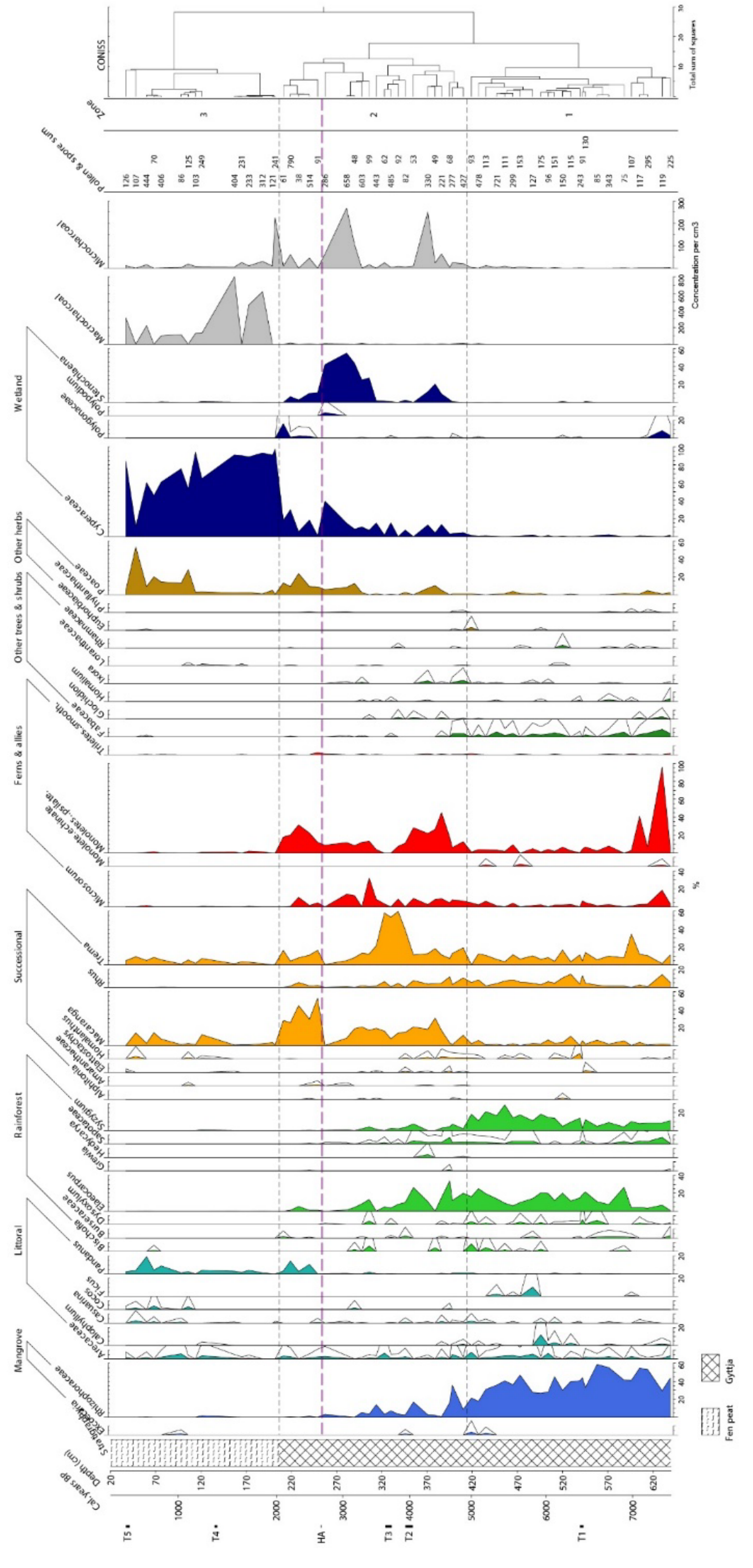
Cal. years BP
Depth (cm)
Stratigraphy
Mangrove
Excoecaria
Rhizophoraceae
Littoral
Arecaceae
Calophyllum
Casuarina
Cocos
Ficus
Pandanus
Rainforest
Bischofia
Burseraceae
Dysoxylum
Elaeocarpus
Grewia
Heckarya
Sapotaceae
Syzygium
Successional
Alphitonia
Amaranthaceae
Elattostachys
Homalanthus
Macaranga
Rhus
Trema
Ferns & allies
Microsorum
Monolete-echinate
Monoletes - psilate
Other trees & shrubs
Trilete-smooth
Fabaceae
Glochidion
Homalium
Ixora
Loranthaceae
Rhamnaceae
Euphorbiaceae
Phyllanthaceae
Other herbs
Poaceae
Wetland
Cyperaceae
Polygonaceae
Polypodium
Stenochlaena
Macrocharcoal
Microcharcoal
Concentration per cm3
Pollen & spore sum
Zone
1
2
3
CONISS
Total sum of squares
%
Fen peat
Gyttja
T5
T4
HA
T3
T2
T1
1000
2000
3000
4000
5000
6000
7000
20
70
120
170
220
270
320
370
420
470
520
570
620

Figure 5-5 Pollen diagram with CONISS dendrogram. Pollen percentage diagram from Ngofe Marsh displaying taxa >2%. Pollen and fern spores are included in the total sum. Varia have been omitted from the CONISS calculations (Grimm, 1987). Zonation is based on the CONISS dendrogram and represented as fine dashed lines. Tephra layers are indicated as T1-T5 and are shaded in blue. Human arrival (HA) is represented as a purple dashed line. The pollen diagram was created using Tilia software (Grimm, 1990).

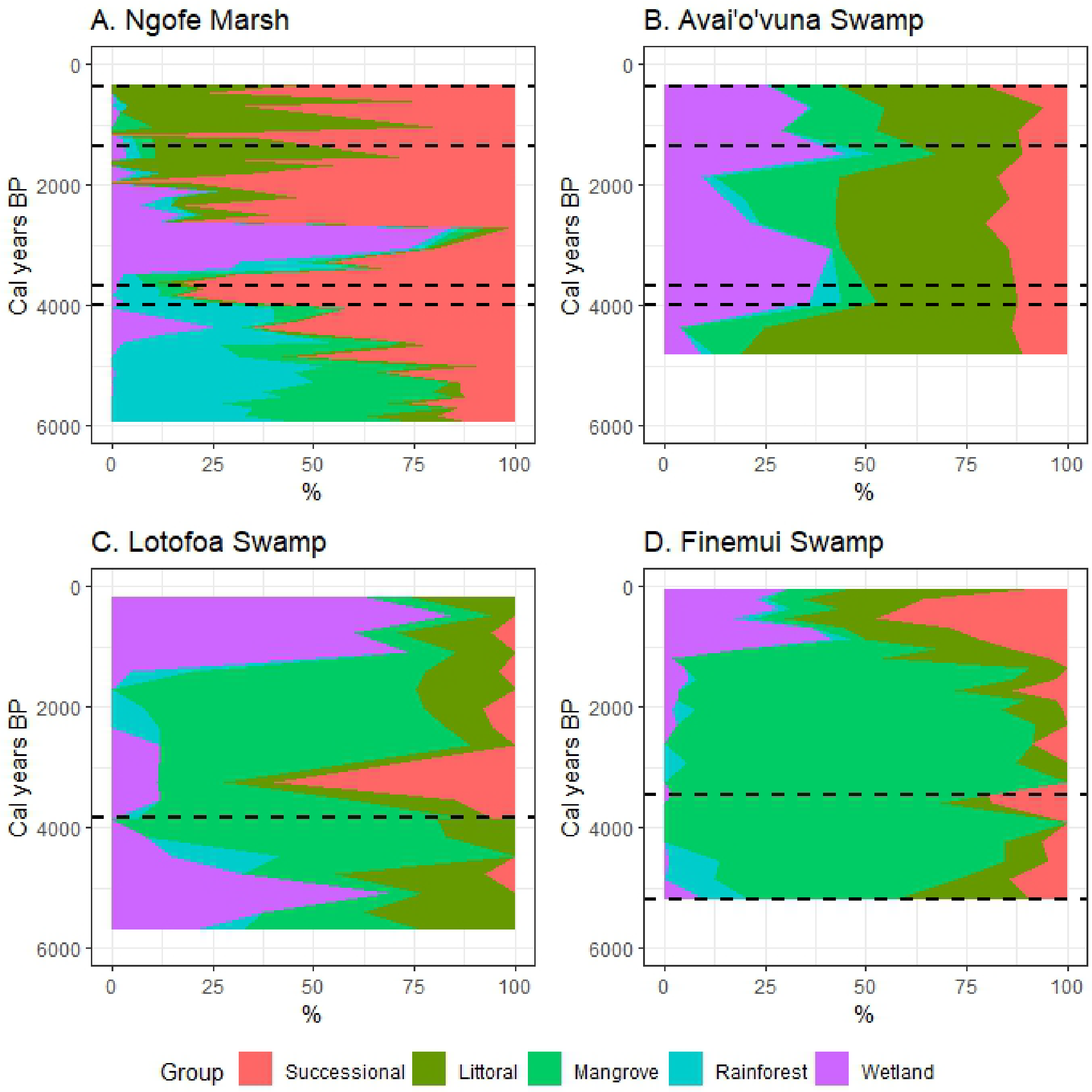

Figure 5-6 Stacked pollen sums for a) Ngofe Marsh, b) Avai'o'vuna Swamp, c) Lotofoa Swamp and d) Finemui Swamp grouped into successional/ disturbance, littoral, mangrove, rainforest, and wetland

vegetation. Horizonal dashed lines indicate the location of tephra layers. Note that Cyperaceae has been removed from the Ngofe Marsh wetland group since it dominated the pollen record.

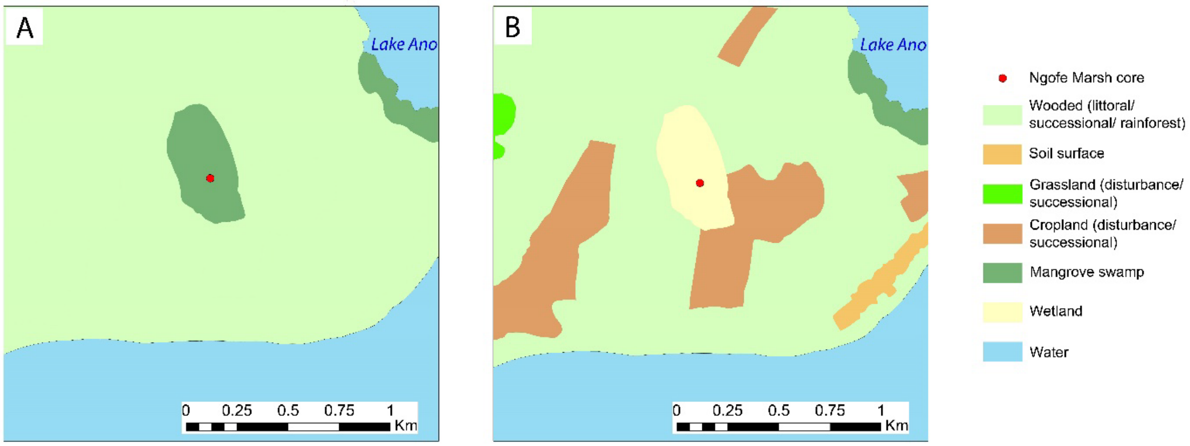

Figure 5-7 A. Hypothetical distribution of vegetation habitat types around Ngofe Marsh ~6000–5000 cal. years BP. B. recent distribution of land-use types from LINZ (2019).Supplementary information for chapter 3

Carbon-to-nitrogen ratio method

To obtain total organic carbon values 5% hydrochloric acid was added to samples in beakers to remove calcium carbonates. The solution was left overnight and then topped up with de-ionised water and left until the sample settled. Once the water was clear, the sample was decanted. This process was repeated three times. The remaining solution was dried overnight at 40°C. The dried samples were then homogenised in an agate pestle and mortar.

To obtain N values, the sediments were freeze dried. Both C and N samples are weighed into tin capsules and were analysed using the Isoprime precisION with an Elementar elemental analyser. BROC3 and Spirulina standards were used for C and N measurements.

Pollen and spore analysis

We added one tablet containing ~9666 or ~14285 *Lycopodium* exotic spores (batch numbers 3862 and 100320201 respectively, from Lund University) to each sample for calculating concentrations (Stockmarr, 1971). A solution of 10% HCl was used to dissolve the *Lycopodium* tablets and any carbonates. To disaggregate organic material, the samples were boiled in 10% KOH for 10 minutes. The samples were passed through two nested sieves, 125 µm and 10 µm. The fraction >10 µm was retained for further pollen analysis. The samples were boiled with 40% HF for 30 minutes to remove silicates. Acetolysis was achieved through the removal of water using glacial acetic acid (CH_3COOH), and then addition of a solution of 9:1 acetic acid to H_2SO_4. The samples were boiled in the acetolysis solution for 3 minutes and the reaction was stopped with glacial acetic acid. The slides were mounted with glycerine jelly (Moore et al., 1991).

Appendix C Supplementary information for chapter 3

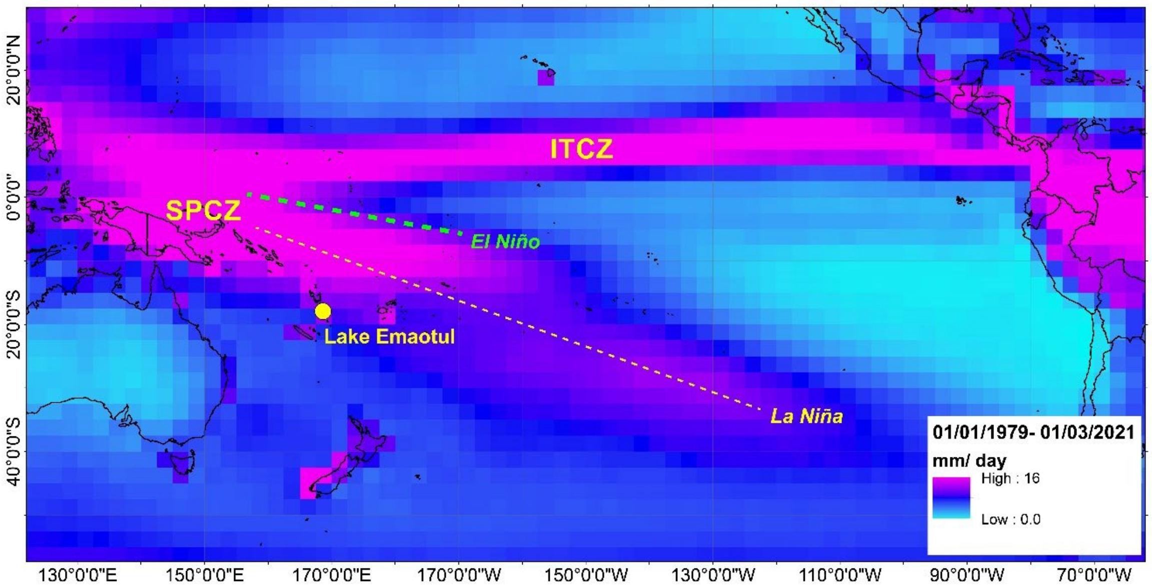

Figure 5-8 GPCP satellite-gauge 1979 to 2021 mean precipitation mm/day (provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov/) (Adler et al., 2003). The yellow dashed line indicates the extend and direction of the S PCZ in La Niña conditions and the coarse green dashed line shows the extent during El Niño conditions.

Table 5-5 Radiocarbon and Pb210 dates, cc refers to the calibration curve used in *rbacon* (Blaauw and Christen, 2011).

Laboratory ID	**Age (Calibrated years before 1950)**	**error**	**Depth (cm)**
surface	-65	1	0
3474-1	-65	1	0.25
3508-1	-64.67	1	0.75
3537-1	-64.49	1	1.25

3537-2	-64.18	1	1.75
3508-2	-63.93	1	2.25
3537-3	-63.57	1	2.75
3537-4	-63.07	1	3.25
3537-5	-62.2	1	3.75
3474-2	-61.25	1	4.25
3537-6	-60.52	1	4.75
3537-7	-59.71	1.1	5.25
3537-8	-58.56	1.3	5.75
3508-3	-57	1.6	6.25
3537-9	-56.26	1.7	6.75
3537-10	-55.56	1.9	7.25
3537-11	-54.4	2.1	7.75
3474-3	-53.5	2.3	8.25
3537-12	-52.75	2.4	8.75
3537-13	-51.83	2.6	9.25
3537-14	-50.47	2.9	9.75
3508-4	-48.32	3.3	10.5
3537-15	-46.68	3.7	11.5
3474-4	-45.06	4	12.5
3537-16	-43.19	4.4	13.5
3508-5	-40.8	4.8	14.5

3537-17	-37.39	5.5	15.5
3474-5	-33.86	6.2	16.5
3537-18	-29.32	7.1	17.5
3508-6	-25.2	8	18.5
3537-19	-19.22	9.2	19.5
3474-6-L	-10.33	10.9	20.5
3537-20	0.44	13.1	21.5
3508-7	11.81	15.4	22.5
3537-21	34.71	19.9	23.5
D-AMS 026249 (L1 28-29)	124	24	48.8
D-AMS 026250 (L1 58-59)	-58	25	78.8
SUERC-67469 (L1 90-91)	349	37	110.8
UBA-46366 (L1A 72-73)	711	22	172.79
D-AMS 026251 (L2 58-59)	923	26	197.82
SUERC-67470 (L3 15-16)	1262	35	258.71
D-AMS 026252 (L3 76-77)	1608	25	319.71

SUERC-67471 (L3A 58-59)	1853	37	338.34

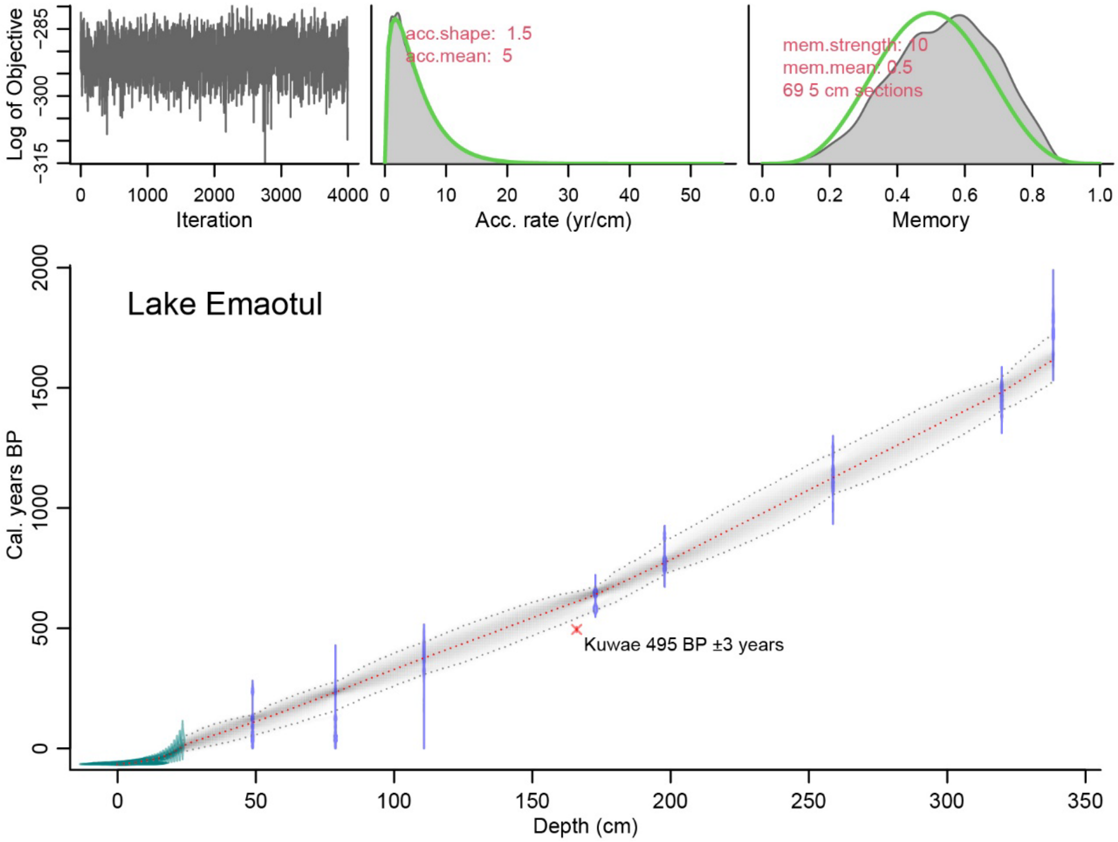

Figure 5-9 *rbacon* age-depth model for Lake Emaotul, Efate, Vanuatu calibrated using the Southern Hemisphere calibration curve (Hogg et al., 2020). (RStudio Team, 2015, Blaauw and Christen, 2011, R Core Team, 2017) after Sear et al (2020) and (Maloney et al., 2022).

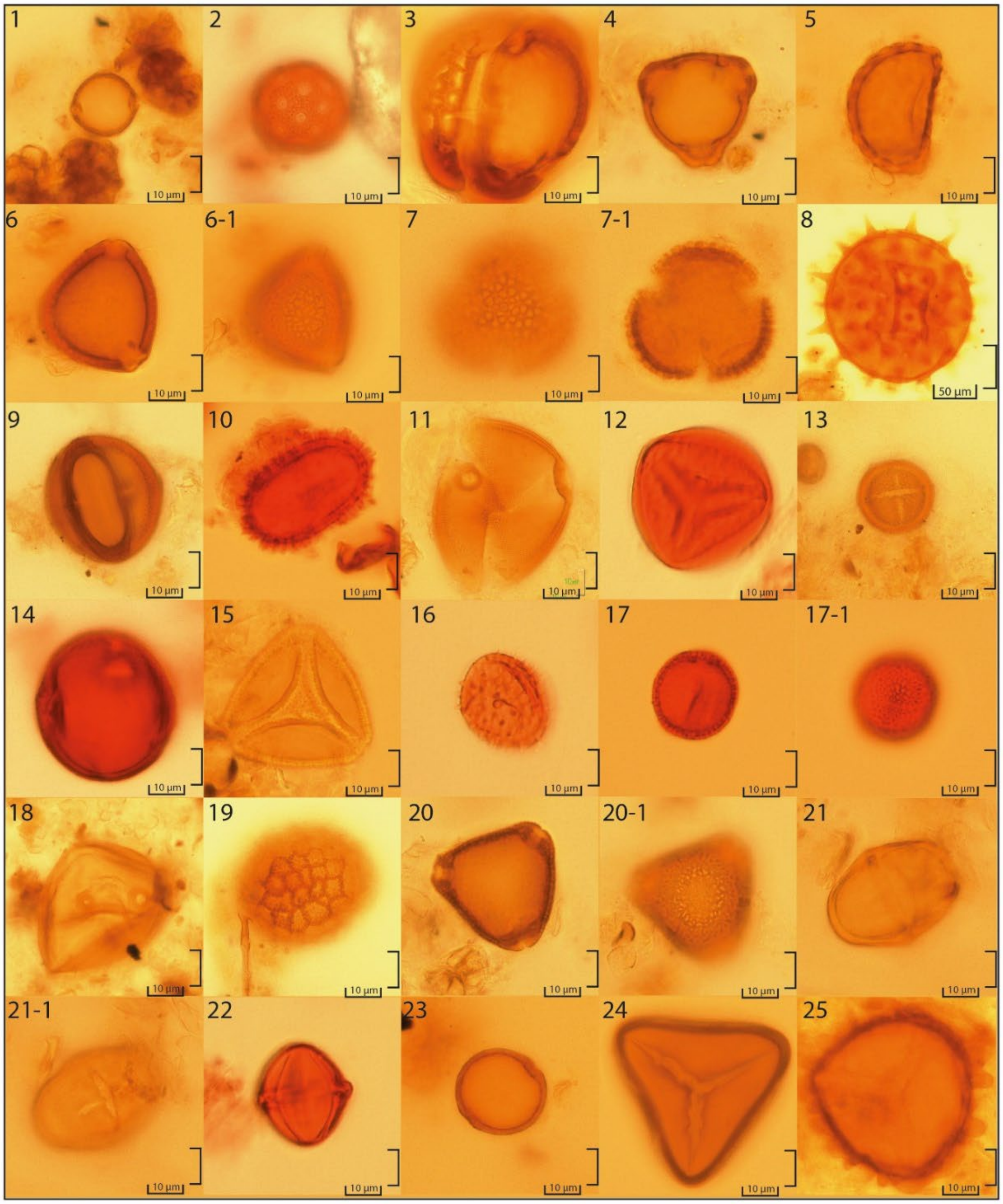

Figure 5-10 Key pollen and spore types. 1. *Acalypha*. 2. Amaranthaceae/ Caryophyllaceae. 3. *Barringtonia*. 4. *Casuarina*. 5. Davalliaceae. 6. *Erythrina*. 7. Euphorbiaceae/ Rubiaceae. 8. *Hibiscus tiliaceus*. 9. *Homalanthus*. 10. *Hypolepis*. 11. *Leucaena*. 12. *Lycopodiella cernua.* 13. *Macaranga.* 14. Meliaceae. 15. *Nymphoides.* 16. *Pandanus.* 17. *Phyllanthus.* 18. Poaceae. 19. Polygonaceae. 20. Sapindaceae. 21. Sapotaceae. 22. Solanaceae. 23. *Trema.* 24. Trilete gemmate spore. 25. Trilete, psilate spore.

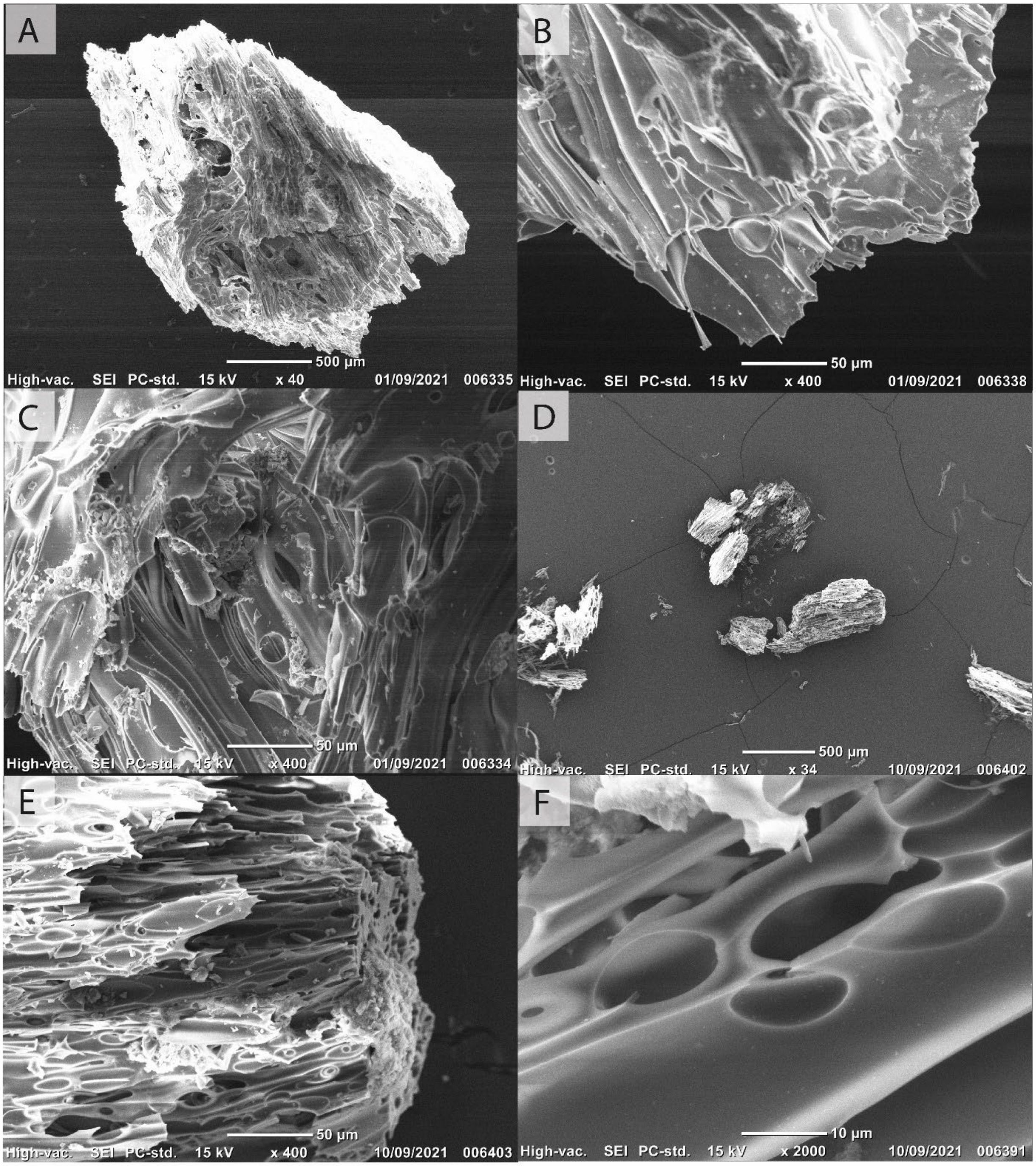

Figure 5-11 Scanning electron microscope images of pumice from 160–166 cm.

Table 5-6 Summary of the mean temporal resolution of palaeoecological methods used in this study proxies.

Proxy	**Environmental driver**	**Mean time resolution**
Chironomids	Aquatic ecosystem	~160 years (~33 cm)
C/N	Source of organic matter	~10 years (~ 2cm)
Itrax	Erosion	Sub annual (0.2 mm)
Tephra	Volcanic activity??	Discrete horizon, plus dispersed shards in some levels
Pollen	Vegetation	~70 years (~14 cm) and ~5 years (1 cm) directly above and below the Kuwae ash
Micro-and macro-charcoal	Fire	~70 years (~14 cm) and ~5 years (1 cm) directly above and below the Kuwae ash

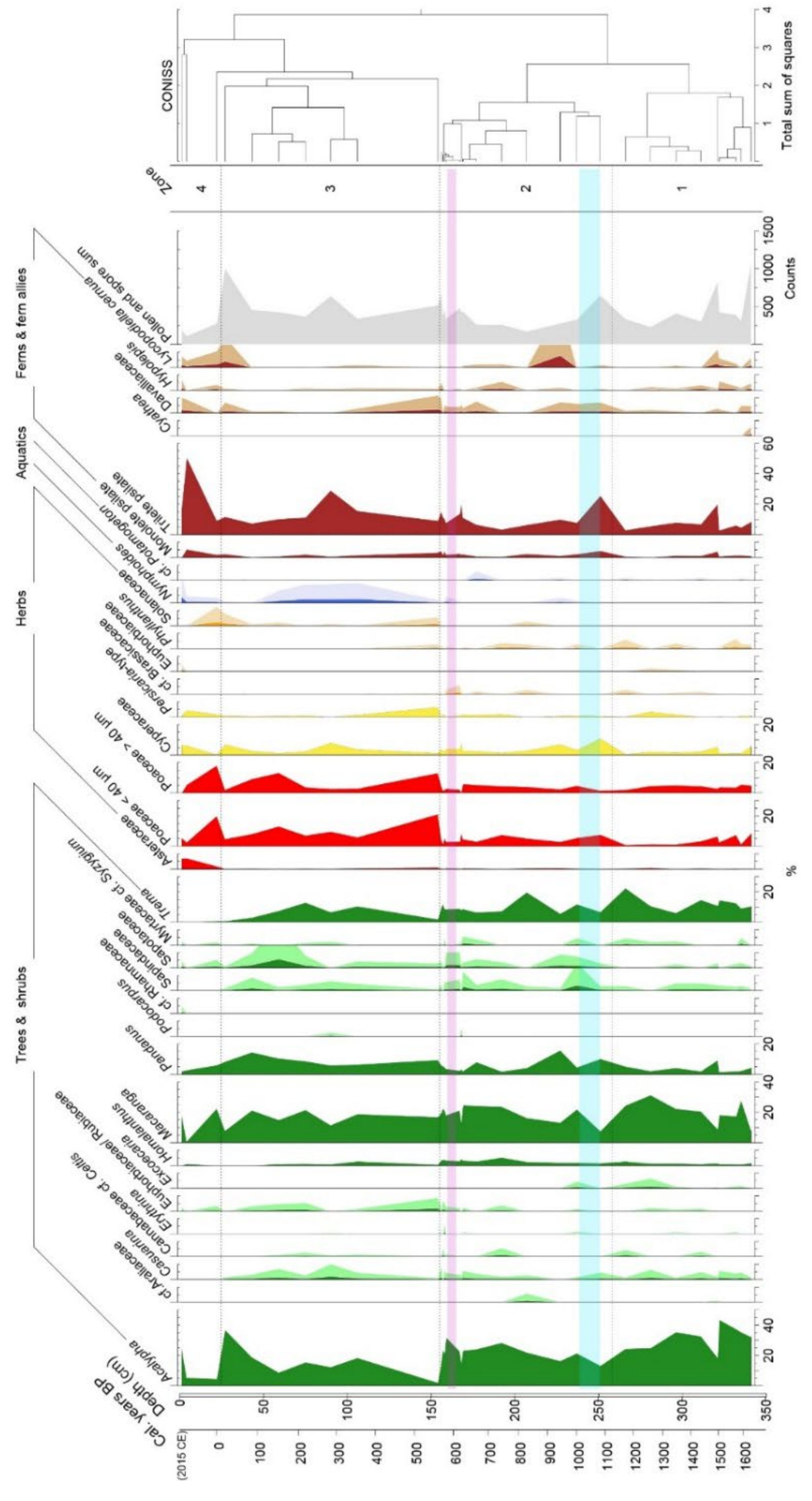
Trees & shrubs
Herbs
Aquatics
Ferns & fern allies
Acalypha
cf.Araliaceae
Casuarina
Cannabaceae cf. Celtis
Erythrina
Euphorbiaceae/ Rubiaceae
Excoecaria
Homalanthus
Macaranga
Pandanus
Podocarpus
cf. Rhamnaceae
Sapindaceae
Sapotaceae
Myrtaceae cf. Syzygium
Trema
Asteraceae
Poaceae < 40 µm
Poaceae > 40 µm
Cyperaceae
Persicaria-type
cf. Brassicaceae
Euphorbiaceae
Phyllanthus
Solanaceae
Nymphoides
cf. Potamogeton
Monolete psilate
Trilete psilate
Cyathea
Davalliaceae
Hypolepis
Lycopodiella cernua
Pollen and spore sum
Zone
4
3
2
1
CONISS
Total sum of squares
1
2
3
4
Counts
500
1000
1500
%
20
40
60
Depth (cm)
0
50
100
150
200
250
300
350
Cal. years BP
(2015 CE)
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600

Figure 5-12 CONISS calculation of the pollen percentage diagram for Lake Emaotul showing pollen and spores which have been taxonomically identified and have >1% abundance. CONISS calculations were based on all taxa except those which are unidentified (Grimm, 1987). Taxa are grouped into trees and shrubs (green), dryland herbs (red), wetland herbs (yellow), other herbs (orange), aquatic plants (blue), and ferns and fern allies (brown). Taxa which occur in low abundances have been shown with x 5 exaggeration (pale shaded colours). The lilac shaded area represents the area where Kuwae volcanic ash was identified and the cyan shaded area represents the transition from wetter to drier climate.

Table 5-7 Canonical Correspondence Analysis correlation scores.

Environmental driver	**Proxy**	**CCA axis-1**	**CCA axis-2**
Magnetic susceptibility	Tephra and erosion	0.08167	0.7514
Ti/inc	Erosion	0.93972	-0.1108
Microcharcoal	Regional fires	0.46558	-0.5196
Macrocharcoal	Local fires	-0.47496	-0.5499
Precipitation	Precipitation	0.60693	-0.1712

Table 5-8 Palaeoecological change indicated from chironomids and pollen in aquatic and terrestrial settings attributed to volcanic ash fallout in Oceania and South America.

Continent	**Country**	**Site**	**Depositional setting**	**Location**	**Site elevation (m. a.s.l)**	**Tephra date**	**Ash (or ignimbrite*) thickness (cm)**	**Proxy type**	**Response and interpretation**	**Recovery time (years)**	**Comment**	**Reference**
Oceania	New Zealand	Review of 18 sites from North Island (Te Ika-a-Māui)	Lacustrine and wetland	Multiple at varying distances from volcanic epicentre Lake Taupo (38°47'26.78" S 175°54'14.68" E)	Multiple	1850 cal years BP (Taupo)	Multiple (42*-0.5)	Fossil pollen and charcoal	Proximal podocarp/ hardwood forests were destroyed by ignimbrite. Pteridium esculentum, Poaceae, Asteraceae and Gonocarpus increased.	Proximal forest ~200 C14 years	Local climate was likely an important factor for recovery rates	Wilmshurst and McGlone (1996)

Oceania	New Zealand	Matakana	Wetland	37°29'22.59" S 175°59'59.98" E	1	665 cal. years BP (Kaharoa)	3	Fossil pollen	Leucopogon fasciculatus (shrub) and Tupeia antarctica (shrub) became extirpated from the area		Anthropogenic activity may have contributed to vegetation changes	Giles et al. (1999)
Oceania	Tonga	Lotofoa Swamp	Wetland	19°44'48.12" S 174°18'28.80" W	3	~3800 cal. years BP	50	Fossil pollen	Vegetation change from ferns to coastal forests and then to more open conditions	>3800	No return to pre-eruption conditions has been observed perhaps due to human arrival ~2800	Flenley et al. (1999)

											years ago	
South America	Ecuador	Laguna Baños	Lacustrine surrounded by páramo vegetation	0°19'19.68"S 78°9'10.50" W	3821	1500 cal. years BP (Cosanga region)	>5	Fossil pollen	Slight increase in herbs (mostly Poaceae)	<100		Matthews-Bird et al. (2017); Montoya et al. (2021)
South America	Ecuador	Laguna Baños	Lacustrine surrounded by páramo vegetation	0°19'19.68"S 78°9'10.50" W	3821	1500 cal. years BP (Cosanga region)	>5	Chironomids and C/N ratio	Chironomid regime shift. C/N ratio increased.	>1500		Matthews-Bird et al. (2017); Montoya et al. (2021)
South America	Ecuador	Laguna Baños	Lacustrine surrounded by páramo veget	0°19'10.16"S 78° 9'34.79"W	3835	Uncertain, potentially 1785-1786 CE	≥10	Diatoms and chironomids	Chironomids showed a decrease in abundance	Short-lived		Michelutti et al. (2015)

			ation.			Nevado Cayambe or Pichincha (1553 or 1660 CE)			although species composition stayed the same.			
South America	Ecuador	Vinillos	Wetland surrounded by glacial forests	0°36′2.8″S, 77°50′48.8″ W	2090	Multiple (4) between 45–42 k. cal years BP.	18, 25, 40 and 23.	Fossil pollen, non-pollen palynomorphs and charcoal.	Slight increase in Alnus. Following the 40 cm tephra deposition fungal NPPs disappeared and there was an increase in Ilex, Melastomataceae and Weinmannia.	Not estimated since recurrent disturbances occurred		Loughlin et al. (2018)

									Eruptions were a source of ignition.			
South America	Ecuador	Laguna Pindo	Lacustrine surrounded by pre-montane vegetation	1°27'7.92"S 78°4'50.82" W	1248	900 cal. years BP (Tungurahua)	>5	Fossil pollen	Opening up of forest canopy	~150		Matthews-Bird et al. (2017); Montoya et al. (2021)
South America	Ecuador	Laguna Pindo	Lacustrine surrounded by pre-montane vegetation	1°27'7.92"S 78°4'50.82" W	1248	900 cal. years BP (Tungurahua)	>5	Chironomids and C/N ratio	No change in chironomids, decline in C/N ratio			Matthews-Bird et al. (2017); Montoya et al. (2021)
South America	Chile	Lake Galletué	Lacustrine	38°40'47.6"S 71°17'30.7" W	1150	~1957 CE (Llaima)	~5	Fossil pollen	Increase in Poaceae (grasses)			Urrutia et al. (2007)

									perhaps due to percolation of pollen grains			
South America	Chile	Lake Galletué	Lacustrine	38°40'47.6"S 71°17'30.7"W	1150	~ 1957 CE (Llaima)	~5	Chironomids	Chironomids: Ablabesmyia was replaced by Parakiefferiella interpreted as a sedimentological change	Brief change		Urrutia et al. (2007)
South America	Argentina	Lake Mascardi	Lacustrine surrounded by subantarctic forest	41°20'0.00"S 71°33'60.00"W	800	Two tephra layers	≥10 (both)	Chironomids	Decreased diversity and equitability	Short-lived		Massaferro and Corley (1998)
South Am	Chile	Laguna Mir	Lacustrine	46° 8'40.00"S 73°26'	120	Multiple (22) possi	Multiple (0.1–8)	Fossil pollen	Long-term increase of	Long-term following		Haberle et al.

erica		and a		40.00" W		bly including Mount Hudson)			Nothofagus 4800–1200 cal. years BP.	repeated disturbances		(2000)
South America	Chile	Gran Campo-2	Wetland	52°48' 37.0"S 72°55' 46.0" W	70	4254 ± 120 cal. years BP (Mount Burney)	~8	Fossil pollen	Decline in Nothofagus and initiation of primary succession.	800		Fesq-Martin et al. (2004)

Appendix D Supplementary information for chapter 4

Table 5-9 Palaeoecological records included in this study (part 1).

Site name	**Site ID (this study)**	**Neotoma Site ID**	**Latitude**	**Longitude**	**Site elevation (m.a.s.l)**	**Country**	**Island name**	**Approximate arrival of humans (Cal. years BP)**
St. Louis Lac	1	28240	-22.23278	166.55	5	New Caledonia	Grande Terre	~3000 (Sand, 1997)
Plum Swamp	2	NA	-22.261461	166.626675	10	New Caledonia	Grande Terre	~3000 (Sand, 1997)
Anouwe Swamp	3	28318	-20.23932	169.82227	4	Vanuatu	Aneityum	3000 (Petchey et al., 2014)
Waitetoke	4	23921	-36.61015	175.78865	1	New Zealand	Ahuahu/ Great Mercury	700 (Wilmshurst et al., 2011)
Volivoli	5	NA	-17.310000	178.170000	2	Fiji	Viti Levu	2900 (Anderson and Clark, 1999)
Bonatoa Bog	6	9979	-18.0667	178.5333	4	Fiji	Viti Levu	2900 (Anderson and Clark, 1999)

Lake Tagimaucia	7	27226	-16.8217	-179.939	680	Fiji	Taveuni	2900 (Anderson and Clark, 1999)
Yacata	8	NA	-17.258464	-179.510585	2	Fiji	Yacata	2900 (Anderson and Clark, 1999)
Finemui Swamp	9	NA	-19.9489	-174.712	7	Tonga	Ha'afeva	2765 (Burley et al., 2015)
Lotofoa Swamp	10	NA	-19.7467	-174.308	3	Tonga	Foa	2765 (Burley et al., 2015)
Ngofe Marsh	11	NA	-18.6647	-174.044	4	Tonga	‘Uta Vava'u	2780 (Burley et al., 2015)
Avai’o’vuna Swamp	12	NA	-18.697111	-173.988747	0	Tonga	Uta Vava'u/ Pangaimotu	2780 (Burley et al., 2015)
Lake Lanoto'o	13	NA	-13.9093	-171.828	760	Samoa	Upolu	2800 (Leach and Green, 1989)
Tukou Marsh	14	23925	-27.604	-144.352	3	French Polynesia	Rapa	700 (Kennett et al., 2006)
Rano Aroi	15	NA	-27.1865	-109.435	430	Chile	Rapa Nui/ Easter Island	700 (Hunt and Lipo, 2006) but see Rull

								(2020) for discussion on earlier settlement estimates

Table 5-10 Palaeoecological records included in this study (part 2).

Site name	**Island area (ha) Nunn et al. (2016)*or Google Earth Pro (2023)**	**Island type Nunn et al. (2016) * or Hayward (1976)**	**Maximum island elevation (m) Nunn et al. (2016) * or Google Earth Pro (2023)**	**Distance from nearest mainland (km) Weigelt et al. (2013) *or Google Earth Pro (2023)**	**Minimum age Cal year BP**	**Maximum age Cal years BP**	**Type**	**Reference / Pollen analyst**
St. Louis Lac	1891479.34	Continental island	450	1353.55	592	6688	Wetland	Stevenson and Dodson (1995)
Plum Swamp	1891479.34	Continental island	647	1353.55	124	23,020	Wetland	Stevenson et al. (2001)
Anouwe Swamp	17928.56	Volcanic high island	852	1816.91	1419	16,087	Wetland	Hope and Spriggs (1982)
Waitetoke	1872*	Volcanic*	819*	6*	-58	5370	Wetland	Holdaway et al. (2019); Prebble et al. (2019)
Volivoli	1182706	Composite high island	1323	2706.89	0	4873	Lagoon	Hope et al. (2009)
Bonatoa Bog	1182706	Composite high island	1323	2706.89	-34	4075	Wetland	Hope et al. (2009)
Lake Tagimaucia	52728.56	Volcanic high island	1241	2829.38	83	17,062	Lake	Hope et al. (2009)

Yacata	943.95	Composite high island	256	~ 2922.1	0	4939	Lake	Hope et al. (2009)
Finemui Swamp	135.45	Limestone low island	14	3340.86	-69	5874	Wetland	Flenley et al. (1999)
Lotofoa Swamp	1571.78	Limestone low island	24	3385.72	-49	7008	Wetland	Flenley et al. (1999)
Ngofe Marsh	12719.52	Limestone high island	88	3468.1	-67	7693	Wetland	Strandberg et al. (2023a in press)
Avai’o’vuna Swamp	12719.52	Limestone low island	8	3468.1	-47	4987	Wetland	Fall (2005)
Lake Lanoto'o	121546.4	Volcanic high island	1100	3887.14	545	10,004	Lake	Gosling et al. (2020)
Tukou Marsh	5413.68	Volcanic high island	650	6009.78	-32	8250	Wetland	Prebble et al. (2019)
Rano Aroi	21350.09	Volcanic high island	507	3523.41	-27	41,506	Wetland	Flenley et al. (1991)

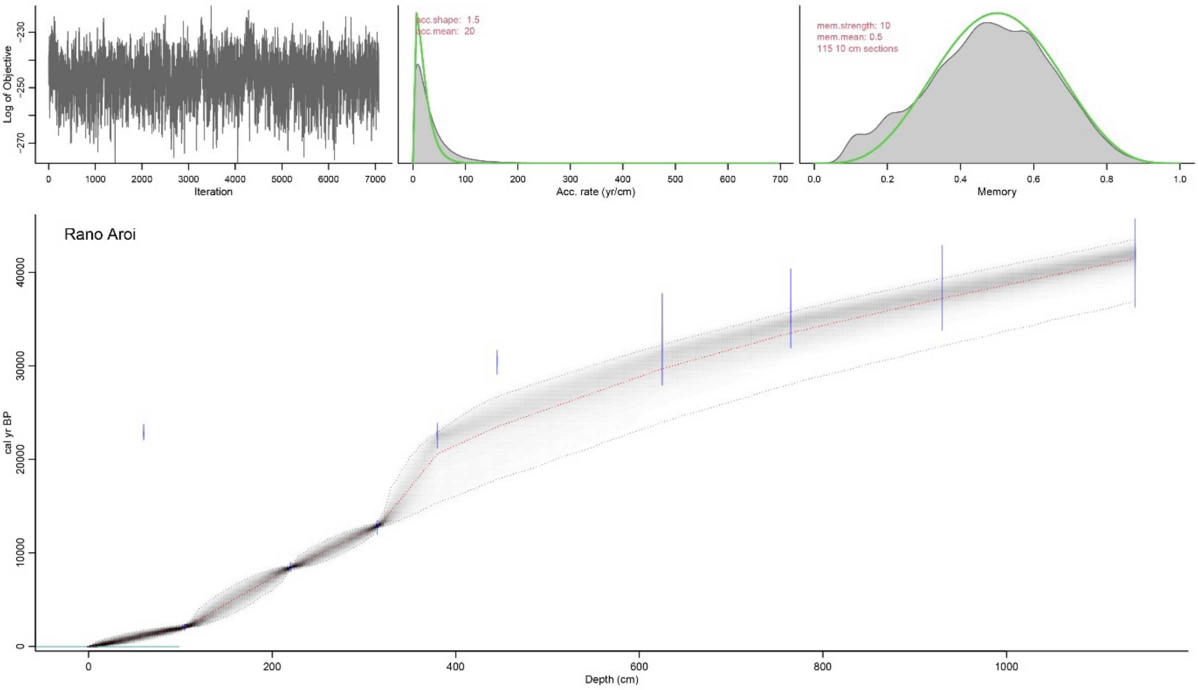

Figure 5-13 Rano Aroi age-depth model updated from Flenley et al. (1999). Radiocarbon dates were recalibrated using the SHCal20 calibration curve using *rbacon* (Blaauw and Christen, 2011, Hogg et al., 2020).

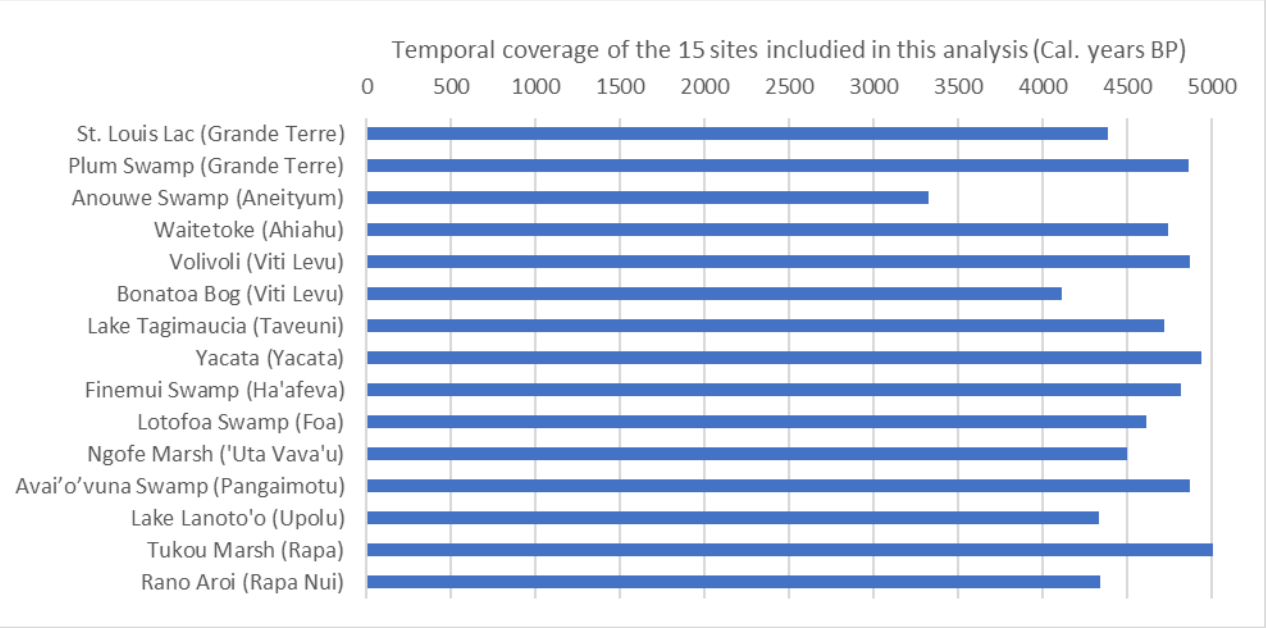

Figure 5-14 The length of pollen records with pollen assemblages older than 5000 cal. years BP removed.

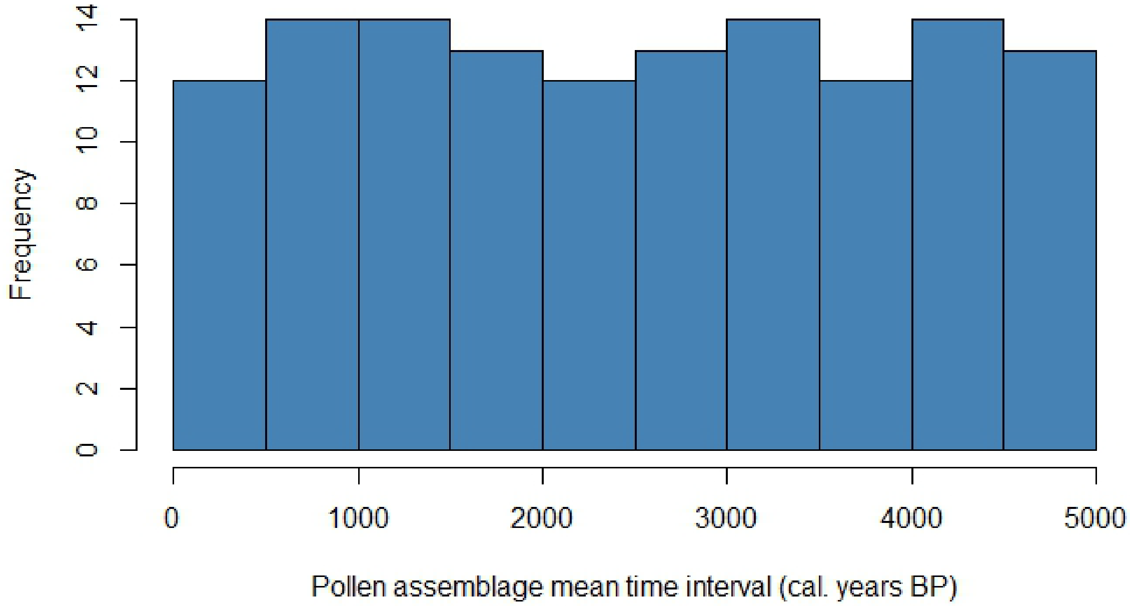

Figure 5-15 Distribution of 500-year time intervals for all sites.

Table 5-11 Descriptions of the pollen data after harmonisation and prior to binning

Site name	**Pollen data format (prior to rescaling to %)**	**Mean pollen & spore sum**	**Minimum pollen & spore sum**	**Total number of taxa**	**Mean rarefied richness**	**Reference/ Pollen analyst**
Plum Swamp	Count	378	35	71	2.3	Stevenson et al. (2001)
St. Louis Lac	Count	397	3	50	9.2	Stevenson (2004)
Anouwe Swamp	Count	75	9	49	6.4	Hope and Spriggs (1982)
Waitetoke	Count	350	230	94	23	Holdaway et al. (2019); Prebble et al. (2019)
Volivoli	Percentage	NA	Unknown	53	NA	Hope et al. (2009)

Bonatoa Bog	Count	303	206	83	25.6	Hope et al. (2009)
Lake Tagimaucia	Count	510	270	115	34.7	Hope et al. (2009)
Yacata	Percentage	NA	Unknown	35	NA	Hope et al. (2009)
Finemui Swamp	Percentage	NA	Normally 200 but occasionally fewer	38	NA	Flenley et al. (1999)
Lotofoa Swamp	Percentage	NA	Normally 200 but occasionally fewer	34	NA	Flenley et al. (1999)
Ngofe Marsh	Count	223	42	47	8.6	Strandberg et al. (2023a in press)
Avai’o’vuna Swamp	Count	362	60	67	14.3	Fall (2005)
Lake Lanoto'o	Count	207	149	34	16.4	Gosling et al. (2020)
Tukou Marsh	Count	210	82	43	10.3	Prebble et al. (2019)
Rano Aroi	Percentage	NA	200 terrestrial pollen in most cases	17	NA	Flenley et al. (1991)

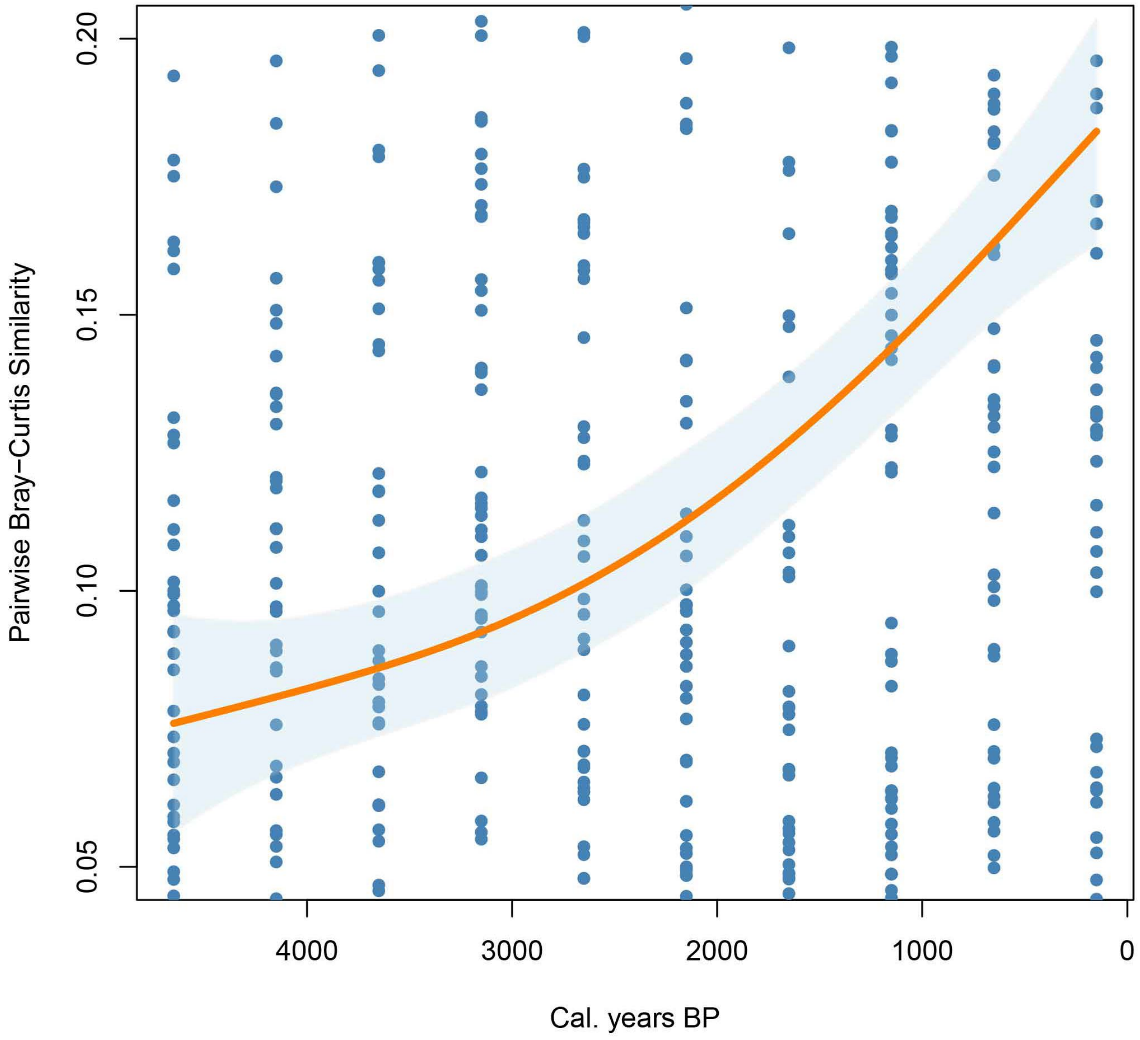

Figure 5-16 Smooth spline showing pairwise Bray-Curtis similarity scores among all 15 sites on 13 islands, over the past 5000 cal. years. 1= indicate greatest similarity and 0= lowest similarity.

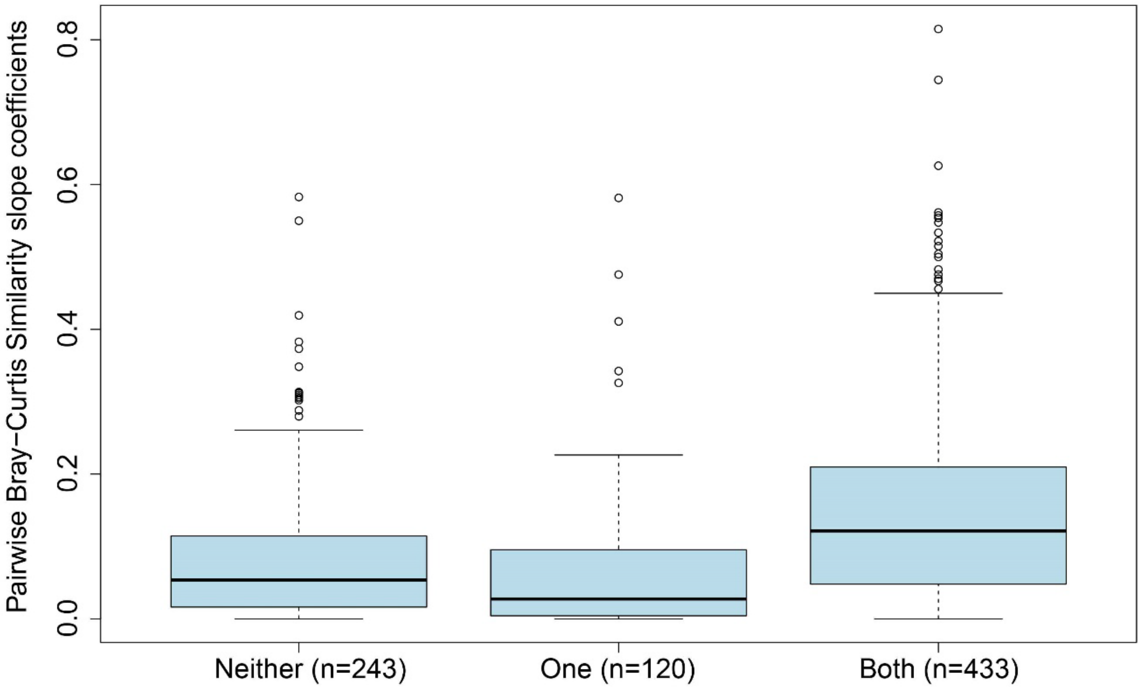

Figure 5-17 Pairwise Bray-Curtis comparisons grouped by if neither, one, or both of the islands was settled during a time interval. N= number of pairwise comparisons.

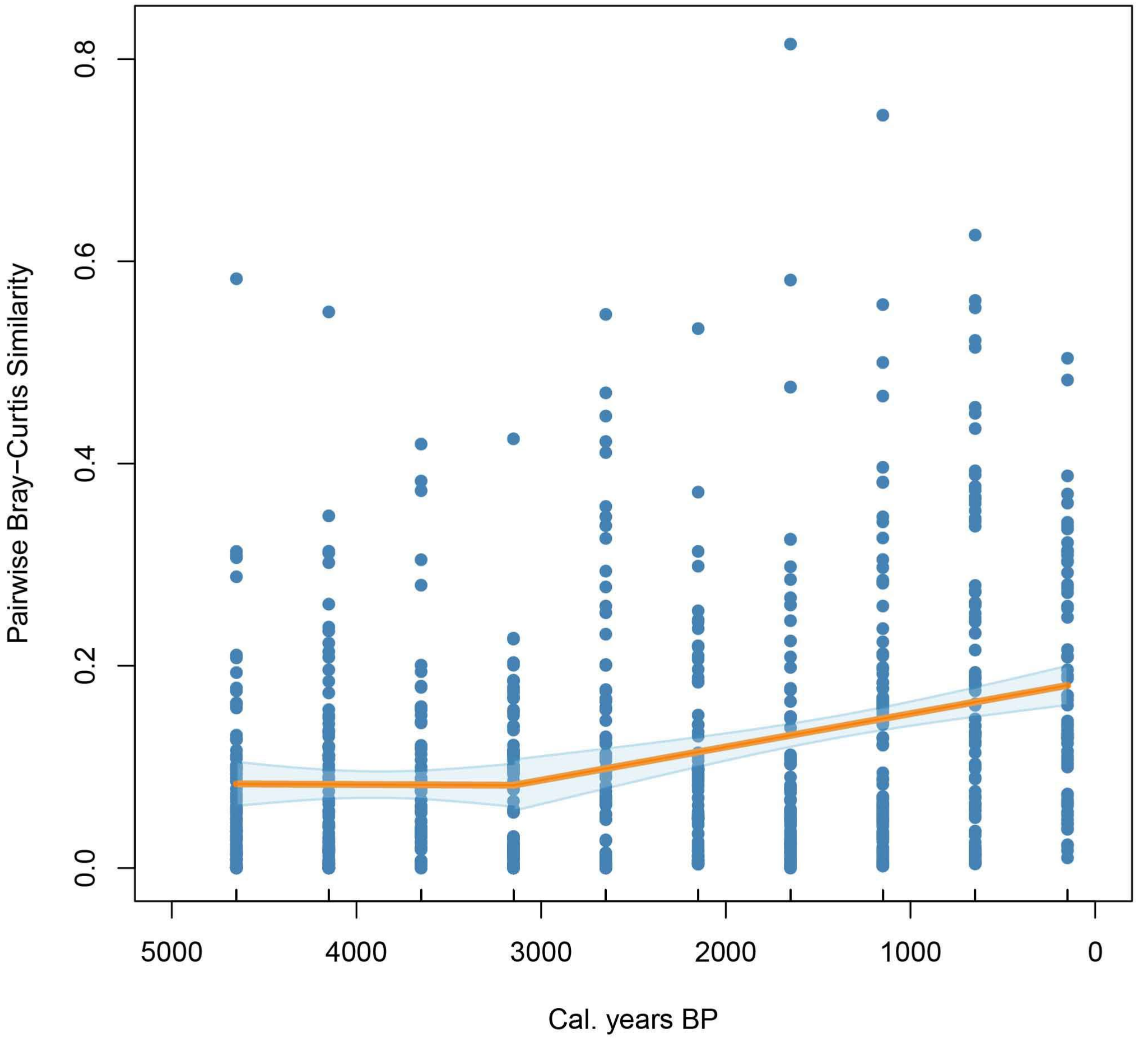

Figure 5-18 Breakpoint linear model showing pairwise Bray-Curtis similarity scores among all 15 sites on 13 islands, over the past 5000 years. The blue shaded area shows the 95% confidence interval.

Appendix E Faecal biomarker extraction and data analysis

E.1.1 Methodology

Faecal sterols were analysed to investigate when humans and pigs arrived within the catchment area of Ngofe Marsh. Seventeen subsamples (1 sample ~375 years) were freeze-dried and then ground in an agate pestle and mortar which had been cleaned with ethanol. The subsamples were then weighed and wrapped in foil, which had been sterilised in a furnace at 450 °C. The samples were transferred into microwave extraction tubes. Microwave-assisted extracted was completed using 15 ml DCM:CH3OH (2:1 v/v), the samples were heated to 70 °C for 10 min and held at 70 °C for a further 10 min and then left to cool for 20 min. Samples were then centrifuged at 1700 rpm for 3 min and the supernatant was decanted into a 28 ml test tube. This was repeated twice more after adding 6 ml of DCM:CH3OH (2:1 v/v). The solvents were blown dry under nitrogen to obtain the TLE (total lipid extract).

The TLE was then saponified, 2 ml of KOH was added to CH3OH 5M and heated to 120 °C for 1 h. The samples were then acidified to pH 3-4 with HCl 6M in an ice bath. Once at room temperature, 5 ml of DCM extracted DD-H2O. The saponified TLE was extracted with 5 ml CHCl3 three times and then filtered through an anhydrous sodium sulphate column and then blown dry under nitrogen.

The saponified TLE was dissolved in 1 ml of DCM:2-propanol (2:1 v/v) and sonicated. An aminopropyl column was pre-treated with 6 ml of DCM:2- propanol (2:1 v/v) and then the samples were loaded onto the columns. To elute the neutral fraction the column was applied with 6 ml DCM:2-propanol (2:1 v/v) and drained into a 7 ml vial. To elute the acid fraction the column was washed applied with 6 ml 3% acetic acid in methanol (v/v) into another 7 ml vial. Both acid and neutral fractions were dried under nitrogen.

The neutral fraction was dissolved in 1 ml of DCM. Then a silica gel column was preconditioned with DCM. The sample was loaded onto the column, a series of solvents was used to elute compounds into 7 ml vials. Hexane: DCM (2:1) (relative volume 3) was used to obtain aliphatics and aromatics. DCM (relative volume 3) was used to obtain ketones and wax esters and DCM:CH3OH (1:1) (relative volume 2) to obtain alcohols.

To derivatise the alcohol faction, 30 µl of BSTFA with 1% TMCS was added to the sample and heated to 70 °C for < 3 h. The samples were then dried down under nitrogen and then dissolved in hexane for analysis with GC and GC-MS. The data processing was done using XCalibur software, version 3.0. Compound signatures were compared with those in Prost et al. (2017) and total peak areas for each compound were detected.

Soils can harbour background levels of 5β-stanols (Bethell et al., 1994). Therefore, whilst it is possible to base faecal matter detection on 5β-stanols abundances (Gendre et al., 1994), it is perhaps more prudent to use ratios. A ratio was used to normalise the peak area values, this was the sum of the 5β-stanols (coprostanol and epicoprostanol) over the sum of the 5β-stanols plus 5a-stanol (5a-cholestanol). This ratio has previously been used by Simpson et al. (1998); Bull et al. (1999a); Bull et al. (1999b); and Bull et al. (1999c). A ratio of 0.7 or greater suggests the presence of faecal matter in modern samples (Grimalt et al., 1990). However, Simpson et al. (1998) argue that values this high may not occur in older samples due to partial degradation of the molecules over time, such as in archaeological soils. Prost et al. (2017) suggests that faecal inputs with a ratio between 0.3–0.7 can neither confirm nor exclude the presence of faecal matter, whereas ratio value of <0.3 suggest no presence of faecal matter.

E.1.2 Results and discussion

Detecting the presence of humans, and the animals they introduced, within ecosystems is important to pinpoint the onset of impacts and disentangle human impacts from other environmental changes (e.g., Raposeiro et al., 2021). Faecal stanol analysis was conducted on the Ngofe Marsh (Tonga) sedimentary sequence (Chapter 2) to detect the presence of human and porcine (pig) faecal matter, and therefore human arrival, since humans introduced pigs to Tonga (Steadman, 1993).

The ratio was generally low (0.06 –0.25) until ~ 3240 cal. years BP (Figure 5-19). The sample at ~3250 cal. years BP exhibits the highest ratio of the sequence at 0.42. Thereafter, values vary between 0.048–0.29 until the most recent sample, dated to ~645 cal. years BP, also surpassed the 0.3 ratio threshold at 0.32.

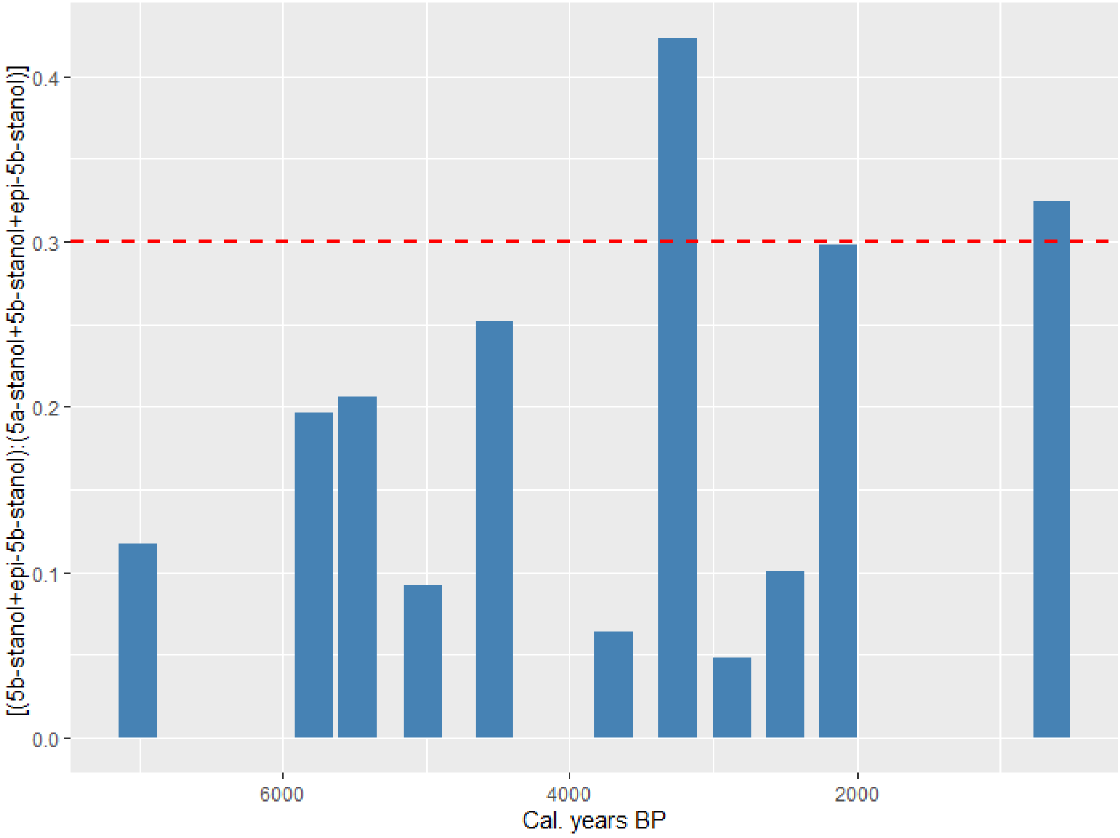

Figure 5-19 The ratio shown is: 5β-stanols (coprostanol and epicoprostanol) over the sum of the 5β-stanols plus 5a-stanol (5a-cholestanol) over time. The red dashed vertical line shows the threshold for possible faecal matter (Prost et al., 2017).

Two samples surpassed the 0.3 ratio threshold for possible faecal matter (Figure 5-19), the first was dated to ~3240 cal. years BP (95% confidence interval 3591–2880 cal years BP) and the second was dated to ~645 cal. years BP (95% confidence interval 835–445 cal. years BP). It is possible that both ratio values indicate the presence of human or porcine faecal matter. However, the timing of the earlier (0.42) value (~3240 cal. years BP) is earlier than estimated human arrival in the Vava'u island group which, according to archaeological data, it is between 2805–2680 cal. years BP (Burley et al., 2015). The ~3240 cal. years BP sample is also earlier than the vegetation changes, found at Ngofe Marsh, which appear to be consistent with human arrival ~2670 cal. years BP, this was indicated by an increase in native secondary forest taxa *Macaranga* and *Pandanus* (see Chapter 2). No increase in micro- and macro-charcoal is associated with human arrival and there are no instances of cultivated crops which would help to detect the timing of human arrival (Chapter 2), such as *Colocasia esculenta* (taro) or *Ipomea batatas* (sweet potato), known to appear in the palaeoecological record when people settled islands in the Pacific (e.g., Prebble, 2008).

The second instance that the ratio values surpassed the 0.3 threshold at ~645 cal. years BP occurred when humans were present and established in Tonga, yet since neither value surpasses 0.7, it cannot be said with confidence that the faecal matter of humans and pigs has been detected. Faecal stanols were also detected before ~3240 cal. years BP, but did not surpass the 0.3 threshold for possible faecal matter. One explanation of this early finding of faecal stanols might be since faecal stanols can be produced by microbial conversion of cholesterol to 5β-stanols, at least in anoxic sediments (Argiriadis et al., 2018).

There are a number of possibilities for why the 0.7 threshold for probable faecal matter was not met. One explanation is that faecal stanols have been degraded over time. For example, aerobic bacteria are known to degrade 5β-stanols in soils (Elhmmali et al., 1997). Degradation can also occur in anaerobic conditions (Canuel and Martens, 1996). Another explanation is that there were few humans or pigs in the catchment of Ngofe Marsh. Finally, the relatively low sampling resolution might explain why ≥0.7 values were not identified. Increased sampling resolution might better show periods of increased and decreased human occupation within the catchment.

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